Ontogeny and Homology in the Male Palpus of Orb-weaving Spiders and Their Relatives, with Comments on Phylogeny (Araneoclada: Araneoidea, Deinopoidea)

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Ontogeny and Homology in the Male Palpus of Orb-weaving Spiders and Their Relatives, with Comments on Phylogeny (Araneoclada: Araneoidea, Deinopoidea)

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ABSTRACT

Coddington, Jonathan A. Ontogeny and Homology in the Male Palpus of Orb-weaving Spiders and Their Relatives, with Comments on Phylogeny (Araneoclada: Araneoidea, Deinopoidea). *Smithsonian Contributions to Zoology*, number 496, 52 pages, 108 figures, 1 table, 1990.—The higher level cladistic structure of cribellate spiders (Araneomorphae) and ontogenetic evidence relevant to the homology of sclerites in the male spider palp are reviewed, with the aim of clarifying orb-weaver phylogeny. The habitual use of a small set of terms for rather different palpal structures seems to have obscured homologies and therefore the monophyly of groups. Outgroup comparison of palp structure in various cribellate superfamilies (e.g., Dictynoidea and Amaurobioidea) can be used to polarize characters in orb-weaving spiders (Orbiculariae), and palp structure in Deinopoidea to polarize palp characters in Araneoidea. Results are that the radix of Linyphiidae and Araneidae may be synapomorphic, but the "radix" in such families as Oecobiidae, Uloboridae, and Theridiidae is in each case an autapomorphy of those taxa. The "terminal apophysis" in lycosoid taxa is entirely different from that in Araneoidea, and even within Araneoidea "terminal apophyses" in Theridiidae, Araneidae, and Tetragnathidae apparently are not homologous. On the other hand, possession of a median apophysis is probably primitive for Araneoidea. Problems surrounding the use of the terms "median apophysis" and "conductor" for various uloborid sclerites are discussed. A tentative cladogram of 32 orbicularian taxa, based on 87 binary and multistate characters, is presented.

Contents

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Introduction

On the whole, the century-long effort to homologize the palpal sclerites of male spiders across families and superfamilies seems to have been a rather dismal failure. Spider taxonomists have often hoped that the comparative morphology of the external male genitalia would be useful in higher level phylogenetic analysis (Wagner, 1888; J. Nelson, 1909; Comstock, 1910; Gassmann, 1925; Gerhardt and Kaestner, 1938; Archer, 1948; Lehtinen, 1967; Shear, 1967; Levi, 1980a; Heimer and Nentwig, 1982), but our efforts to make it so have not been particularly convincing or successful. Despite the lack of clear homologies, many workers continue to use the same terms for a variety of sclerites, and to hypothesize transformations among them. The implausibility of some of these hypotheses can go unappreciated because they are often proposed in isolation for single taxa. Thus their concordance with other character systems is difficult to evaluate. Taxonomic revisions and other studies of the last twenty years have provided us with a wealth of comparative morphological work on palp structure and function, and a review of this evidence is badly needed. For the first time since Shear (1967), this paper reviews the comparative morphology of male palpal characters, especially in orb-weaving spiders, and in their potential outgroups.

When comparing palp studies, it is often difficult to know whether authors intended homology or not. There are two basic naming traditions in studies of palps. One is strictly evolution-ary and phylogenetic, and applies the same name to sclerites only if they are thought to be homologues. The second tradition is more pragmatic, and uses a small set of classical terms to describe all sclerites. Proponents of the latter view generally are cautious or agnostic about homology, and avoid new terms. Sometimes they imply homology, and sometimes not. Sometimes they also cite functional evidence to justify use of the same term, although one almost never has direct evidence of palp function on which to draw. However, because discerning homology is the entire point of this paper, I have chosen to treat the use of identical terms for two structures as at least a weak homology hypothesis. However, I also try to note the view of the author if that was not their intent.

Outgroup comparison is an essential method in phylogenetic analysis (Farris, 1982; Patterson, 1982; Maddison et al., 1984), but it is of little use if characters are not correctly homologized. Among spiders generally, the homologies of palpal sclerites are so confused that traditional terms have little meaning as homologies (e.g., median apophysis, conductor, terminal apophysis, subterminal apophysis, radix, stipes).

Characters that show homoplasy are especially difficult to interpret. For example, Levi (1983b) used the presence of a median apophysis as a derived character to define a group including Argiopinae, Mastophorinae, Araneinae, and Gasteracanthinae. However, outgroup comparison within Araneoidea and beyond to Deinopoidea suggests that the presence of a median apophysis, per se, is an araneoid primitive feature. Taxa lacking it may be derived, rather than the opposite (the primitive status of the median apophysis is equivocal in some reconstructions, see "Conclusions"). Of course, the median apophyses of particular araneid groups may have some

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subsidiary feature that indicates the monophyly of those groups. Another example is Opell's (1979) use of the term "radix" to describe an element in the embolic division of uloborids, although he also regarded the homology with araneoid sclerites as questionable. In light of evidence that uloborids and araneoids are closely related (Coddington, 1986a, b), sclerite homology becomes an important issue. In fact, the uloborid and araneoid radices seem to be different structures, and thus Opell's caution was entirely justified. These examples show that the possible or plausible in one reconstruction can become doubtful in the larger phylogenetic context.

Solid progress in understanding araneoid phylogeny will depend on solid understanding of araneoid outgroups. In the case of the cribellate and ecribellate orb weavers, the context of the problem initially is as large as the infraorder Araneomorphae. Phylogenetic patterns in that group, although still little understood, must be reviewed before phylogenetic problems within orb weavers can be addressed.

This paper is organized into four parts. The first part attempts to circumscribe the problem of identifying the outgroup to orb-weaving spiders by reviewing what is known, or likely to be true, of the phylogeny of Araneomorphae. This first problem is not insuperable, because parsimony suggests that wholly ecribellate groups be considered less likely as potential outgroups to the orb weavers. The second part reviews what is known of the ontogeny of male palpal organs. The literature is not extensive, but the general patterns yield thought-provoking guidelines for the interpretation of palpal sclerites. The third part then reviews and compares palp structure within orb weavers and among the potential outgroups. The final part summarizes the results in the context of nongenitalic characters, and discusses cladograms for orb weavers.

The majority of the data for this study comes from illustrations of male palpi published by taxonomists doing revisionary work (e.g., Levi, from 1954 to 1986; Lehtinen, 1967; Grasshoff, 1968; Forster and co-workers, from 1959 to 1987; Millidge, 1977, 1980; Dondale and Redner, 1978, 1982; Opell, 1979, 1983, 1984; Coddington, 1986c), as well as comparative morphological studies (Merrett, 1963; van Helsdingen, 1965, 1969; Lehtinen, 1978, 1980; Shear, 1981; Heimer, 1982). The enduring utility of good taxonomic illustrations is a realization of the latter half of this century, at least in araneology. Illustrations are to a very great extent the data of comparative morphology, and frequently outlast the value of the reasoning based on them. It seems that analytic or schematic illustrations (e.g., Figures 5–8) are among the most useful for understanding broader patterns, because the authors present clearly how sclerites relate to each other in the palps that they study. The few taxonomists who routinely include such drawings as part of their alpha-level work have made the understanding of palp morphology in the groups they study enormously easier.

At the other extreme, one can identify an "iconographic" tradition. In this, the superficial appearance of a palp under the microscope is simply transferred to paper, almost as an abstract design. Although compound microscopy can reveal otherwise invisible characters, a simple cover slip mount often permits only extreme lateral or mesal views of the palp. The featureless cymbium takes up most of the drawing, and the sclerites peek out on one side of the drawing or the other. Although species identifications are possible with such glyphs, understanding the three dimensional structure of the palp is difficult. For some reason, these kinds of illustrations are especially frequent in linyphiid taxonomy. Alternative mounting techniques exist (Coddington, 1983), but they are not commonly used.

This paper also tests the hypothesis of orb-weaver monophyly (recently reviewed by Coddington, 1986a) by using Deinopoidea (Deinopidae plus Uloboridae) as the putative outgroup to Araneoidea, and evaluating the evolution of the araneoid male palp from that point of view. As such it reviews a different set of evidence than Coddington (1986a), but one brought to bear on the same question. Although the present effort is certainly not a final statement on orb-weaver phylogeny, it is somewhat more exact and more complete than past efforts (Coddington, 1986a, b, c). This paper surveys a great deal of morphological diversity, and attempts to synthesize and integrate the results with several other complex character systems. It nevertheless remains a working hypothesis, in need of criticism and test by other data sets.

Materials and Methods

A paper such as this without drawings would ask the reader to look up hundreds of illustrations in the original literature, no small task. At the other extreme, one cannot mechanically reproduce all the relevant illustrations and ignore the loss in quality, to say nothing of the disparity in drawing styles and labelling schemes (or lack of them). The middle course seemed to be quick line copies of illustrations, to give the reader some idea of the consistency and diversity of male palpal morphology. Although I hope these drawings make the arguments intelligible, they are a poor substitute for the originals. Seriously interested workers should certainly consult the cited works (identified in each figure legend).

The selections aim to represent fairly palp sclerite diversity among araneomorph cribellate taxa and orb weavers. To facilitate comparison, all the drawings have been made roughly the same size, with scale bars omitted, although obviously the palps vary in size. Drawings of right palps have been inverted to make all appear as left palps.

The taxa included in Figure 108 exemplify orbicularian lineages and their potential outgroups. Araneoid family groups whose monophyly is questionable are represented by two genera each in order to display clearly putative family synapomorphies (thus *Araneus* and *Cyclosa* for Araneidae; *Meta* and *Leucauge* for metines; *Tetragnatha* and *Glenognatha* for tetragnathines; *Nephila* and *Nephilengys* for nephilines). As many uloborid genera as possible are included because reconstruction of the correct uloborid ground plan is critical to the phylogeny of orb weavers. Family or superfamily categories exemplify the remaining taxa.

ABBREVIATIONS.—Sclerite terms and their abbreviations as used in this work are listed below. In the figures and this list abbreviations in parentheses are the labelling schemes of the original authors that do not agree with the designations in this work.

An	Annulus
BH	Basal hematodocha
C	Conductor
CL	Column
CTA	Cyatholipid tegular apophysis
CY	Cymbium
DH	Distal hematodocha
DiTA	Dictynid tegular apophysis
E	Embolus
EM	Embolic membrane
ETA	Eresid tegular apophysis
f	Fulcrum
F	Fundus
(fc)	Functional conductor
iL1	Inside first leg
iL4	Inside fourth leg
LC	Lamella characteristica
M, MA(ma)	Median apophysis
MEA	Metine embolic apophysis
MH	Median hematodocha
NSSC	Nonsticky spiral construction
OEA	Oecobiid embolic apophysis
oL1	Outside first leg
oL3,4	Outside third and fourth legs
oL4	Outside fourth leg
OTA	Oecobiid tegular apophysis
OTL I	Oecobiid tegular lobe I
OTL II	Oecobiid tegular lobe II
PA	Parembolic apophysis
PC	Paracymbium
Pe	Petiole
PLS	Posterior lateral spinneret
PM	Paramedian apophysis
R(r)	Radix
S	Stipes
SPT	Suprategulum
SS	Sticky spiral
SSC	Sticky spiral construction
ST	Subtegulum
T	Tegulum
TA(ta)	Terminal apophysis
TTA	Theridiid tegular apophysis
UEA	Uloborid embolic apophysis
?	Doubtful homology

TERMINOLOGY.—In general, I have followed Comstock's original usage for sclerite names (Comstock, 1910), except when the presumption of homology seems clearly wrong. In the latter cases, as a compromise between homology and stability of names, I have included a taxon reference in the name of the sclerite, e.g., oecobiid tegular apophysis (OTA), or metine embolic apophysis (MEA). This coordinates the names of sclerites with the groups they define, and still retains the descriptive part of the name. Labels on drawings become slightly more complex. As evidence accumulates that groups are related, the taxon reference can be adjusted to reflect new classifications. In this paper, I use this system when the analysis has shown that the same name has been used for unequivocally different structures. On the other hand, I see no reason to change the traditional names of sclerites in those groups in which the names were first used.

METHODS TO RECOGNIZE HOMOLOGUES.—Taxonomists traditionally have used Remane's (1956) criteria of detailed similarity, ontogeny or intermediate forms, and position as means to recognize homologues. Often these guides are sufficient. A newer and equally powerful way to test homology hypotheses is by concordance with other character distributions (Patterson, 1982). When one tests existing sclerite homology hypotheses against other character systems in spiders, the result is substantial homoplasy among sclerites. The morphological vocabulary does not correspond to the existing diversity of palpal sclerites. Existing notions of homology as implied by identical terms are rarely concordant with other characters. One can infer that palpal sclerites are much more changeable in evolutionary time than formerly believed, and thus that our terminology for them is awry.

Concordance constrains homology hypotheses in the following way. If all characters in a data set except one agree on a particular tree topology, and further suggest that the deviant feature arose twice, then the initial coding of the deviant character is probably wrong, regardless of the phenotypic evidence. Following this line of reasoning, one can use the fit of a transformation theory about one character to a tree implied by it and other characters to test the homology of that character (Mickevich, 1982). Two states that must have originated independently because of the context of other characters should be recoded as not homologous. Although this method eliminates some homoplasy by emending hypotheses of homology to eliminate apparent convergences, the length of the cladogram rarely changes. Because the emendations recode egregious homoplasies as new characters, the length that the new "character" adds to the tree usually balances the

homoplasy that is eliminated. The consistency index of the tree also improves. One gains conceptual clarity by having transformational hypotheses about characters accord with the globally most parsimonious taxon cladogram.

Like any coding scheme, this proposal can be misused and misapplied. As a rule of thumb for cases where terminology and homology are extremely discordant, judicious application will result in a more balanced terminology that rectifies obvious mistakes in recognition of homology. One might adopt specific criteria for recoding, such as "recode character X if overall tree length increases 5% or more under the assumption of Dollo parsimony for that character." Such criteria are arbitrary, however, and as yet cladistic theory lacks a rational basis for choice. Instead, I have simply changed sclerite names (and thus changed homology hypotheses) when it seemed to me that the evidence was overwhelmingly against the hypothesis of homology. When the homoplasy occurs within a single family, I have not generally recoded the character (e.g., uloborid embolic apophysis; Table 1, character 18), in recognition that sclerite homologies within families are best left to the specialists in that group. On the other hand, much of the homoplasy in the data is apparently due to secondary loss of features (e.g., median apophysis; Table 1, character 9), and of course this kind of homoplasy does not affect hypotheses of homology.

I have also tried to specify transformation series for multistate characters as unambiguously as possible. Insistence on unambiguous transformation series can result in longer cladograms than can be obtained with unordered, or Fitch, optimization (Mickevich, 1982). However, the Fitch-optimized transformation series may be incompatible with deterministic transformational hypotheses. Explicit transformation schemes are certainly preferable to unordered networks if the transformation series adds no length to the tree. I have therefore specified transformation series wherever possible, according to the following method. The method is overly complex, because it seeks to perform an analysis that is not currently possible with any single phylogenetic computer software package.

I used the PAUP version 2.4 computer package installed on an IBM 4381 computer (Swofford, 1986) to find shortest taxon trees with the MULPARS option, GLOBAL branch swapping, and Farris optimization. Although a priori I felt that several characters would be best represented by branching and/or asymetric character state trees (Coddington, 1987), I treated all multistate characters as either unordered or linearly ordered, because PAUP 2.4 does not permit user-input transformation series, and it does not easily indicate when support for a node is ambiguous. I then used MacClade version 2.1 (Maddison and Maddison, 1987) to deduce specific transformation series that agreed with the taxon trees from PAUP for each multistate character. The data required only two branched character-state trees (a and b), in addition to the ordered (o) and reversible (r) transformation series (Table 1). Although MacClade helped

considerably to deduce homologies among palpal sclerites, its tree-finding algorithms are inadequate to verify that the new coding still supports the same taxon tree. For that, I used the CREAD and DWAG.S options in PHYSYS (Farris and Mickevich, 1984) to check overall tree length and found no additional equally parsimonious trees. PHYSYS, however, does not report all equally parsimonious mappings of characters that may exist for a particular tree topology. Also, even with the CREAD option structured to give unordered character state trees, PHYSYS counts tree length differently from MacClade and PAUP. The same topology, data, and character state trees yield longer overall lengths in the former than in the latter computer packages. The lengths reported here are those calculated by PAUP.

The trees reported for this study are therefore as parsimonious as those obtained by unordered, or Fitch, optimization. However, the transformation series for multistate characters are also specified as unambiguously as possible, subject to the constraint that the coding scheme does not add length to the tree.

Basically this method accepts the minimum tree length found by Fitch optimization as a constraint, but within that constraint the method specifies transformation series as explicitly as possible. As such, it takes a less extreme position about analysis of character evolution than, for example, true Transformation Series Analysis (Mickevich, 1982). This method was used to investigate the homology of the radix, terminal apophysis, conductor, and median apophysis in a variety of orb-weaving taxa.

Mapping character transformations on cladograms is another intractable methodological problem. The placements of 18 of the 154 changes mapped in Figure 108 are ambiguous, in that they could have been placed at other particular nodes on the tree without affecting total tree length. Many of these ambiguities are actually due to missing data, not biological or logical ambiguity. If two taxa share an apomorphy, but the state in the immediate outgroup is unknown, the exact generality of the apomorphy will be ambiguous. For example cheliceral denticles (Table 1, character 35) are known to occur sporadically in the taxa listed in Figure 108, but for a majority of those taxa, the presence or absence of cheliceral denticles is unknown, and thus gain of cheliceral denticles is ambiguous in three places on the tree. I resolved the mapping ambiguity in such cases by presuming that the character arose exactly where it first certainly occurs. In cases where the ambiguity is biological (e.g., did the cribellate ancestor of the now entirely ecribellate Araneoidea produce puffed cribellate silk, Table 1, character 83), I have again mapped the character as arising exactly where it is known to occur, (at the node subtending Deinopidae and Uloboridae). However, the reader should be aware that some changes could conceivably have occurred elsewhere than where they are depicted in Figure 108. Unfortunately so many permutations of these ambiguities exist

that an exhaustive list of all possible mappings is impractical, and probably not worth the time. Important ambiguities that affect homologies in palpal sclerites are pointed out in the text.

Cribellate Phylogeny and the Orbicularian Outgroup Problem

What does the taxon "orb weavers" include? At present, the available evidence suggests that the uloborids and deinopids are the sister taxon to the Araneoidea, and no evidence links either group convincingly with any other cribellate or ecribellate group (Coddington, 1986a). If Deinopoidea (Uloboridae and Deinopidae; Deinopoidea has priority over Uloboroidea by Deinopides C.L. Koch, 1851) and Araneoidea are sister taxa, each may serve as the other's outgroup when a question concerns intragroup relations. Their inclusive taxon may be called Orbiculariae (Walckenaer, 1802) without any nomenclatural ramifications, because the name is above the rank of superfamily.

The orb-weaver monophyly hypothesis thus far has either been accepted as the strongest available hypothesis for the relationships of orb weavers (Opell, 1987), or has been questioned regarding the homology for, or independence of, each of the ten or so apparent synapomorphies for Orbiculariae (Shear, 1986:387–395; Eberhard, 1987; Robinson, 1987; Vollrath, 1987). However, arguing whether or not two obviously very similar features are really homologous or convergent (especially on the grounds of inferred adaptive value) probably will be fruitless, because it is so difficult to decide homology by focusing exclusively on the feature in question. Put another way, if the features were not extremely similar, the hypothesis of homology would not even be credible. Taxa with the rank of superfamily nearly always differ in small details, even when the features are obviously homologues. This is roughly the situation in orb weavers.

Instead the monophyly hypothesis can be rejected more decisively by finding numerous, strong apomorphies that link either Deinopoidea or Araneoidea with other, non-orb-weaving groups. Despite substantial searches, neither I nor any other author have found any such suite of characters. Consequently, it is most reasonable to follow Hennig's principle (Hennig, 1966:121) and conclude that the available evidence supports the monophyly of the two extant orb-weaving lineages.

The sister taxon to Orbiculariae is unknown at present. However, it seems reasonable to begin the search in taxa that contain some cribellate members, simply because Orbiculariae contains the cribellate Deinopoidea. This argument is based on minimizing homoplasy in the transformation series for the cribellum. Although most arachnologists agree it has been lost more than once, we must still prefer hypotheses that minimize the number of losses, all other evidence being equal. Several proposed suprafamilial groups in spiders contain both cribellate and ecribellate taxa (Lehtinen, 1967, 1986; Forster 1970; Forster and Wilton, 1973; Levi, 1982a; Forster et al., 1987).

None of them have a cribellate lineage located deep within an ecribellate clade, whether inferred from an explicit cladogram (of which there are, admittedly, very few), or merely from nomenclatural ranking. This unlikely instance is illustrated in a general way in Figure 1a, which is the more likely scenario (that is, loss of the cribellum being irreversible), but I know of no examples among spiders. Figure 1b illustrates the transfer of Filistatidae to either liphistiomorphs or mygalomorphs by Lehtinen (1986). The hypothesis entails the independent evolution of the cribellum. The evidence against this notion seems overwhelming, because of the complexity of the cribellum (Figures 2, 3). Although the case represented by Figure 1b is conceivable, we have no evidence to prefer this more complex scenario in the case of orb weavers; and so I set it aside until the unlikely event that evidence supporting it should appear.

The possibility remains that the sister group to orb weavers is entirely ecribellate, and that its stem taxon lost the cribellum independently. This would require a new instance of the loss of the cribellum and would add more homoplasy to the overall araneomorph cladogram. Even though the cribellum has been lost several times, there is no reason to hypothesize unnecessary additional losses, especially in the stem lineages of large taxa. One guesses, therefore, that the sister group to orb weavers probably involves other relatively generalized cribellate taxa.

The question then becomes which cribellate taxa are most likely to harbor the sister taxon or, alternatively, what suprafamilial phylogenetic hypotheses involving cribellates, formulated on the basis of explicit synapomorphy schemes, are at hand? Several authors have proposed such schemes: Wunderlich (1987), Lehtinen (1978, 1980, 1986), Forster et al. (1987), Forster (1970), Forster and Wilton (1973), and Homann (1971). Because the hypotheses of Wunderlich (1987) focus primarily on relationships within Araneoidea, it makes more sense to discuss them after a review of araneocladan phylogeny. Araneoclada are araneomorph spiders exclusive of the "hypochiloids," e.g., Hypochilidae, Gradungulidae, and Austrochilidae (Forster et al., 1987).

Lehtinen (1967, 1978, 1980, 1986) has repeatedly emphasized his view that three basic groups of spiders exist: his Araneomorpha (very different from Araneomorphae); his Amaurobiomorpha; and his Theraphosomorpha. Because Lehtinen's Araneomorpha is virtually the same as the classical Araneoidea, the existing synapomorphy argument for Araneoidea probably applies (Coddington, 1986a, fig. 12.26).

In a like manner, Lehtinen's Amaurobiomorpha is basically the old Araneomorphae, less the monophyletic Araneoidea, and those groups he transferred to the polyphyletic Theraphosomorpha. Lehtinen has provided no credible synapomorphies for Amaurobiomorpha. Indeed, insofar as the Amaurobiomorpha is only a haphazardly diminished Araneomorphae, current evidence suggests that it is a paraphyletic miscellany (Figures 3, 108).

Lehtinen (1978) apparently defined Theraphosomorpha on palp structure; all the included groups supposedly lack a subtegulum. However, detailed phylogenetic work has shown both that liphistiomorphs have complex bulbs, and that secondary fusion or paedomorphosis (cf. comments on *Segestria* in "Ontogeny") is a more parsimonious explanation for mygalomorph bulbs that lack distinct subtegula (Raven, 1985:14; Haupt, 1979, 1983; Kraus, 1978). Insofar as Theraphosomorpha was equivalent to the old Orthognatha, it was paraphyletic (Platnick and Gertsch, 1976). However, Lehtinen's most recent reformulation has made it truly polyphyletic, since it unites some subsidiary araneocladan groups (e.g., scytodoid families and Filistatidae; Lehtinen, 1986) with the monophyletic Lisphistiomorphae (Platnick and Sedgwick, 1984; Platnick and Goboloff, 1985) and monophyletic Mygalomorphae (Raven, 1985:8–10).

Lehtinen (1986) defined the scytodoid families (and included the cribellate Filistatidae) on the basis of two characters that may be synapomorphies: the cheliceral lamina and the fused tegulum and subtegulum. Given the large number of synapomorphies for Araneomorphae, Neocribellatae, and Araneoclada detailed in Figure 2 (characters 16–21, 9–15, 1, and 2, respectively), the suggestion that the scytodoid families happened to have evolved all these features independently of the remaining araneomorphs has little in its favor. However, within the scytodoids, Lehtinen's hypothesis does represent the scenario portrayed in Figure 1*b*, because he argues that Filistatidae is the sister taxon of Pholcidae, and those two families are the sister group of his Scytodoidea. Against the putative araneomorph or neocribellate or araneocladan synapomorphies in Figures 2 and 3, he mentions two features defining Filistatidae + Pholcidae, one pertaining to the female vulva and one to the spinnerets. Lehtinen neglected to describe either of these features, and thus one is left to wonder what about them he thought was synapomorphic. Forster and Platnick (1984, 1985) have already shown that the general type of vulva Lehtinen mentions is widespread among haplogyne spiders, and my own work (1989), Glatz (1972), and Kovoor (1977b) on spinneret structure fails to disclose any plausible synapomorphies in pholcid and filistatid spigots. The filistatid cribellum does exhibit minor autapomorphic details, but that evidence hardly refutes its homology with other cribella (Forster and Gray, 1979; Kovoor, 1977b). Although Filistatidae may well be the sister group of the ecribellate scytodoid families, until Lehtinen is able to present more detailed evidence for his claim, the classification of Forster et al. (1987) is clearly the better supported hypothesis. In sum, none of Lehtinen's suprafamilial groupings contribute to the discovery of the sister taxon of orb weavers.

The work of Platnick (1977), Platnick and Gertsch (1976), Raven (1985), and Forster et al. (1987) has clarified the stem taxa of Araneomorphae (Figure 2, characters 12 and 13 are added from my own work on spinnerets and cuticle). They did not address groupings within Araneoclada, however, and thus

their work does not bear on the issue of the orbicularian sister taxon. Forster and Platnick (1984, 1985) also recently relimited Palpimanoidea and Dysderoidea, but none of these groups include cribellates. Moreover, these authors made no suggestion that their close relatives were cribellate, and so by the above arguments they are unlikely to be, or to include, the sister taxon of Orbiculariae. Wunderlich (1987) did suggest a relationship between Palpimanoidea and Orbiculariae, which is discussed under "Alternative Cladograms for Orbiculariae."

Forster (1970), and Forster and Wilton (1973) provided tentative diagnoses for two araneocladan groups that did include cribellates. The Dictynoidea included Dictynidae, Hahniidae, Desidae, Cybaeidae, Argyronetidae, Amaurobioididae, Anyphaenidae, and Megadictynidae (with Nicodamidae included in the latter). Platnick (1974) later synonymized Amaurobioididae with the older name Anyphaenidae. The Amaurobioidea included the Amaurobiidae, Agelenidae, Stiphidiidae, Amphinectidae, Neolanidae, Ctenidae, and Psechridae, and probably Pisauridae as well. Unfortunately, they did not assign Uloboridae or Deinopidae to either group, and also omitted the Oecobiidae, Filistatidae, and Eresidae. The fundamental division between the two superfamilies was based on the condition of the posterior tracheal system. Dictynoidea exhibit a highly branched system, and Amaurobioidea exhibit a simpler plan of two or four trunks. Based on outgroup comparison to Filistatidae, Austrochilidae, and Gradungulidae (Forster et al., 1987) the simple condition is primitive and the branched condition thus becomes a putative synapomorphy for Dictynoidea.

Something like the branched dictynoid condition is apparent in some uloborids from Opell's careful survey (Opell, 1979). However, a detailed analysis of the dictynoid condition is still lacking, and so it is difficult to decide if the similarity is evidence of synapomorphy. Opell (pers. comm.) has since discovered that the more primitive genera such as *Tangaroa* and *Waitkera* have paired and unbranched tracheae, and that only the more derived genera, such as, *Uloborus*, *Philoponella*, and *Zosis*, have branched tracheae in the abdomen. Deinopids have simpler, unbranched tracheae, as do the majority of araneoids. Thus, "branched" tracheae are apparently independent apomorphies in Dictynoidea and in those uloborids that have them (Figure 3, character 7; Figure 108, character 32).

Based solely on the results of the tracheal evidence, Amaurobioidea would have been founded based on symplesiomorphies. However, the distribution of two features provides evidence for that taxon. First, Forster (1970:17) noted that most of his amaurobioid families had divided cribella, whereas the dictynoid families had entire cribella (Figure 3, character 10). Charles Griswold (in litt.) has pointed out that *Badumna* (Desidae), which Forster included in Dictynoidea, has a divided cribellum. Forster (1970:17) had addressed this point, and expressed some doubt that the *Badumna* group of genera (under the name *Ixeuticus*) belonged among the dictynoids. Also, various genera with divided cribella were

placed in Dictynidae by Lehtinen (1967). However, Lehtinen's "Dictynidae" may be polyphyletic. Given these exceptions one should carefully consider whether or not mixed groups of spiders with entire and divided cribella represent monophyletic groups.

Deinopoids also have entire cribella. By outgroup comparison to hypochilids and austrochiloids, the undivided condition is primitive, and so a divided cribellum provisionally supports Amaurobioidea. It also suggests the inclusion of Eresidae, Oecobiidae, Filistatidae, Zoropsidae, and the scytodoid families, the latter through the synapomorphies with Filistatidae suggested by Lehtinen.

Second, Lehtinen's (1980) work on trichobothrial distribution patterns may provide weak corroboration for Amaurobioidea. He claimed to have surveyed many spider families and genera to show that metatarsal trichobothria are either single and more or less subdistal, with tarsal trichobothria absent, or the metatarsal trichobothria are multiple in a single row combined with one or two rows on the tarsus. Actually, this is known to be not quite true, as Raven (1985) showed that Lehtinen's observations of mygalomorphs were in error.

However, among araneomorphs, two differences may occur: presence or absence of a tarsal trichobothrial row, and number and placement of metatarsal trichobothria. The hypochilid and austrochiloid families indicate that one or a few metatarsal trichobothria, with no tarsal trichobothria, is the plesiomorphic state. That primitive condition persists in the cribellate Dictynoidea, Oecobiidae, Eresidae, Uloboridae, and Deinopidae. Most families of Amaurobioidea have the derived condition of tarsal and, especially, metatarsal trichobothria in rows (Figure 3, characters 8 and 9). More work needs to be done to investigate the validity of this surprisingly simple character, especially because Lehtinen's quick survey may not have realistically reported the variability of the character in Araneoclada.

Homann (1971) distinguished three basic kinds of tapeta, of which the grate-shaped condition clearly seems derived. Grate-shaped tapeta occur only in the classical "lycosoid" families: Stiphidiidae, Acanthoctenidae, Psechridae, Zoropsidae, Tengellidae, Cycloctenidae, Lycosidae, Oxyopidae, Pisauridae, Ctenidae, Senoculidae, and possibly Toxopidae as well. The first five families currently contain cribellate genera. The strong overlap between lycosoids (defined by the synapomorphy of grate-shaped tapeta in at least the posterior median eyes) and Forster's Amaurobioidea argues that lycosoids are a monophyletic subsidiary group of amaurobioids. The remaining amaurobioids (probably paraphyletic) generally exhibit canoe tapeta, probably the primitive condition for most araneocladan groups.

Orbiculariae either lack tapeta altogether (deinopoids, sporadic araneoid genera), or retain canoe tapeta (most araneoids). If the canoe tapetum evolved only once, none of the lycosoid families are likely to be the sister taxon of Orbiculariae. The contrary hypothesis would require that the

orbicularian stem lineage converged on the canoe tapetum independently.

(Apropos of the tapetal evidence to place Psechridae, Robinson and Lubin (1979) argued that the web of *Fecenia* was a "proto-orb," and raised the issue of homology with true orbs. If the authors intended to identify Psechridae as the sister taxon to orb weavers, they would have to ignore the implications of grate-shaped tapeta. Furthermore, *Fecenia*'s sister genus *Psechrus* makes a rather typical cribellate sheet web, from which *Fecenia*'s slightly specialized architecture probably evolved. Therefore the orb-like qualities of *Fecenia*'s web are probably superficial resemblances.)

In sum, available evidence suggests that Forster's Dictynoidea and Amaurobioidea approximate "first drafts" of monophyletic subgroups of Araneoclada, and that the lycosoid hunting spiders are a subsidiary group within Amaurobioidea. Even though lycosoids are thus unlikely to harbor the orbicularian outgroup, the above arguments are still weak enough so that the cribellate lycosoids, as well as more generalized amaurobioids and dictynoids, should be compared when considering orbicularian sclerite homologies in detail.

Some araneocladan cribellate taxa cannot be easily placed in either the Dictynoidea or Amaurobioidea. These are Filistatidae, Oecobiidae, Eresidae, and, of course, the Orbiculariae. All except the latter have divided cribella, which suggests affinities to the Amaurobioidea, but none except the Filistatidae have the amaurobioid trichobothrial pattern. Because of the cheliceral lamina and the fusion of the subtegulum and tegulum, Filistatidae may be the sister taxon of the rest of the Scytodoidea. Some eresids also have a cheliceral lamina. Filistatids do share the amaurobioid trichobothrial pattern. On the basis of this evidence, and that the filistatid palp is derived, scytodoids seem a much less likely candidate than the remaining four groups. Thus, palp structure in Oecobiidae, Eresidae, Dictynoidea, and Amaurobioidea should be surveyed as potential outgroups (Figure 3) to infer character polarities within the Orbiculariae itself.

Ontogeny of the Male Spider Palp

The ontogenetic evidence can be summarized quickly, because only a few studies of palp ontogeny exist. However, the meager ontogenetic evidence makes generalizations at familial and superfamilial levels speculative and deceptively concordant. At best, therefore, this discussion of the ontogenetic evidence is an essay on what one might infer if the available ontogenetic evidence truly summarized palp ontogeny. Comparative analysis of palpal sclerites among spider families usually uses other criteria, such as morphology (subtegulum), function (conductor), or position (terminal apophysis), and has not explicitly used ontogeny. Indeed, the phylogenetic implications of the ontogeny of the male palp have not really been considered from a modern perspective. Consideration of the ontogenetic data may well clarify some

confusion, or at least offer an informative perspective on speculations about homology.

The first substantial study of palp ontogeny is that of Wagner (1886) on *Salticus* (Salticidae). Subsequent studies are by Szombathy (1915) on *Agelena similis* (Agelenidae); Barrows (1925) on *Steatoda borealis* (Theridiidae), *Phidippus audax* (Salticidae), and *Lycosa nidicola* (Lycosidae); Gassmann (1925) on *Lepthyphantes nebulosus* (Linyphiidae); Harm (1931, 1934) on *Segestria bavarica* (Segestriidae) and *Evarcha marcgravi* (Salticidae); Bhatnagar and Rempel (1962) on *Latrodectus curacaviensis* (Theridiidae; probably either *mactans* or *variolus*); and Sadana (1971) on *Lycosa chaperi* (Lycosidae). Because Wagner's study was published in Russian, only those comments other authors have made about his results are available to me. However, Szombathy (1915) noted essential agreement between his study and that of Wagner. As usual in ontogenetic studies, the authors distinguished varying numbers of developmental "stages," but the validity of these subdivisions is not really relevant. The identity, timing, and sequence of developmental events seems most important. Their results can be summarized as follows.

1. In all cases the palpal bulb arises from hypodermal cells (the "claw fundament"), which accumulate at the distal end of the tarsus before the molt. In immatures and females the claw fundament secretes the palpal claw. An invagination at the tip of the tarsus outlines the cylindrical anlage of the palpal bulb, thus initiating the future alveolus. Rudimentary palpal claws are often contemporaneous with the developing palpal bulb (*Segestria, Lycosa, Latrodectus*); consequently the early hypothesis that the bulb is the literal, transformed homologue of the palpal claw (Barrows, 1925:511; Harm, 1931:668) is rather decisively refuted (G. Nelson, 1978; Patterson, 1982).

2. The claw fundament in a subadult male, as in immatures and females (Barrows, 1925:507), is responsible for the secretion of the ventral claw flexor tendon and the dorsal claw extensor tendon. Dorsal and ventral lobes of the claw fundament that secrete nascent tendons were only identified explicitly by Bhatnagar and Rempel (1962), although other authors (Harm, 1934; Barrows, 1925; Szombathy, 1915; Sadana, 1971) refer to cell masses performing the same role. Barrows (1925, figs. 46, 50–52) presented photographs showing both lobes. In view of their future fates (paragraphs 6 and 7), the individuality of these lobes at this early stage of development is quite important. The otherwise excellent drawings of Harm (1931, figs. 21–28; 1934, figs. 7–9) do not show the lobes in *Segestria* and *Evarcha*, although they may indeed have been present.

3. In spiders with complex palpi (*Latrodectus, Steatoda, Lepthyphantes*) the tendon secretion begins but is incomplete. In *Segestria* and *Evarcha* the tendons are completely formed and insert on the rudimentary palpal claw in subadult males. In a later stadium the tendon insertion on the claw dissolves and shifts to the base of the palpal bulb. Adult palpi of *"Mygale"* also have tendons inserting on the base of the bulb (Szombathy,

1915; probably Theraphosidae). The developmental sequence seen in *Segestria* also occurs in *Lycosa,* but the insertion on the base of the palpal bulb also dissolves, so that the final situation comes to resemble the three genera mentioned above. In *Agelena,* Szombathy (1915, figs. 1, 3b) also figured tendons inserting on the bulb in an intermediate developmental stage, but these evidently disappear by the final molt.

4. In all cases, in the ventral, distal portion of the developing bulb an invagination of cells (*Steatoda, Latrodectus, Lycosa*), or growing cell mass (*Agelena, Lepthyphantes, Evarcha, Segestria*) develops. The cell mass is the anlage of the future sperm duct. Reports conflict as to whether the sperm duct develops by an inpocketing of cells (invagination) or whether the internal growing cell mass simply forms itself into a tube. The difference might be an artifact of different sectioning procedures. Regardless of the exact process, the sperm duct anlage grows from the distal tip of the palp and later spirals around the inside periphery of the developing bulb.

5. In *Latrodectus, Lepthyphantes, Lycosa, Evarcha, Agelena,* and *Steatoda* the ventral lobe with the nascent sperm duct separates into a basal and apical portion, at about the same time the sperm duct begins to form. The basal portion becomes the subtegulum and tegulum, the apical the embolic division. In *Segestria* no marked separation occurs. In all of the above taxa, the basal separation of subtegulum and tegulum is one of the last developmental events. In *Evarcha* the separation is incomplete, although in the palps of many salticid genera a subtegulum and tegulum are distinguishable.

6. Late in development, the dorsal lobe in *Latrodectus* bifurcates (cf. paragraph 2). One process becomes the median apophysis, and the other becomes the conductor. The early development of these sclerites was not investigated in the other taxa, so that the generality of this very important event is not established. Szombathy (1915), however, did mention that the anlage of the "conductor" was discernible at a very early stage, even before sperm duct formation.

7. Sclerites of the embolic division (terminal apophysis, subterminal apophysis, embolus, radix) are also among the last developmental events in those taxa where any of them occur (*Lepthyphantes, Lycosa, Latrodectus*). They arise by differentiation of the apical division.

8. In general in the case of complex palpi the last stage of development is characterized by a period of remarkable differential growth in which the sclerites assume their species-typical shapes.

The foregoing is indeed rather little evidence (only seven studies, some quite cursory), but taken together they suggest a general picture of palp development (Figure 4). This picture has important implications for our understanding of spider palp morphology in general, for our ability to discriminate among various tegular sclerites, and for the distinction between sclerites of the embolic division and those of more basal divisions.

First, the separation of the subtegulum from the tegulum

seems to be a late event in development, occurring long after the separation of the basal and embolic divisions of the bulb, and after the differentiation of the tegular apophyses (median apophysis and/or conductor, if they are present). Based on analyzes of the bulb in *Liphistius* (Mesothelae) and/or *Atypus* (Orthognatha), Kraus (1978, 1984), Haupt (1979, 1983) and Song and Haupt (1984) have agreed that a tripartite palp structure may be primitive for all spiders (i.e., subtegulum, tegulum, embolic division). They thus disagreed with most previous workers who felt that a tripartite palp typified only the Araneomorpha, although later workers have largely accepted Kraus' conclusions. The scanty ontogenetic evidence argues that palps are, more exactly, first bipartite (basal and embolic division), then tripartite; the separation of the subtegulum and tegulum is a much later event, more or less contemporaneous with the elaboration of sclerites in the embolic division. Thus, spider taxa, such as mygalomorphs and haplogynes that lack separate subtegular and tegular divisions, and an elaborate embolic division, may well lack them secondarily by truncation of the developmental process (paedomorphosis). Another implication is that examination of "haplogyne" or mygalomorph palp ontogeny ought to show no signs of separation, rather than separation and subsequent fusion. The hypothesis that mygalomorph palps fail to differentiate the distal and median divisions is slightly different from that of Song and Haupt (1984), who argued instead that mygalomorph sclerites were the result of fusion, thus terminal addition to the developmental program, rather than failure to divide. The difference is not great, but it may be testable by ontogenetic information from liphistiids and primitive mygalomorphs.

The second implication (from *Latrodectus*) is that the median apophysis and conductor are intimately related because they both arise from the dorsal lobe of the claw fundament. The dorsal lobe differentiates very early from the rest of the palp. The claw fundament ventral lobe, which otherwise would secrete the ventral tendon, in penultimate instar males also produces all other parts of the palp (e.g., subtegulum, tegulum, embolic division plus its associated sclerites in complex palpi, and the sperm duct). The median apophysis and conductor, if they are even distinguishable in the adult palp, are apparently closely associated in development. In *Latrodectus* the dorsal lobe grows distally to become the conductor, and proximally to become the median apophysis. Because of the last stage of differential growth, either might easily come to be closest in position to the embolus in the mature palp. Hence, any attempt to specify which tegular process in a given spider taxon is the developmental homologue of either the "median apophysis" or "conductor" in another taxon is probably no better than a guess without examination of its ontogeny. Lehtinen (1967:412) did codify a positional and morphological definition of the median apophysis as the sclerite that originates from a distinctly unsclerotized lateral area of the tegulum. Although this has been the working definition of a "median apophysis" for many workers, it need not always refer to the distal portion of the

claw fundament ventral lobe (Figure 4). Thus, the two criteria cannot be unambiguously related to each other. Nevertheless, a basic developmental distinction may exist between the rest of the palp and a lobe that differentiates into the median apophysis and conductor.

Third, the distinction between the embolic division and the basal division (subtegulum and tegulum together) may occur early on and therefore may be quite basic. Sclerites associated with the embolic division develop, on the other hand, quite late. Therefore, this evidence suggests that apophyses should not easily "migrate" from the embolic division to the tegulum, or visa versa.

The first implication (tegulum-subtegulum separation) is corroborated by all the studies of palp ontogeny cited, the second and third primarily are based on Bhatnagar and Rempel (1962). Szombathy (1915) and Barrows (1925) provide weakly corroborative but still inconclusive details. Bhatnagar and Rempel (1962) were the only investigators to identify the parts of the claw fundament responsible for tendon secretion in the earliest stages, and to follow the fate of the dorsal lobe throughout palp ontogeny. Szombathy (1915) mentioned the appearance of the conductor at an early stage, but did not specify its origin. He did not mention the median apophysis, but Gering (1953) found that in other agelenid spiders the median apophysis does insert close to the conductor. Barrows (1925, figs. 46, 50–52) photographed recognizable dorsal and ventral lobes, but did not follow development through to the stage where the conductor and median apophysis become obvious. Gassmann (1925) worked on a linyphiid in which both a median apophysis and conductor are reduced. Harm (1931, 1934) also worked on taxa that also lack these structures (*Evarcha, Segestria*).

These results predict that use of the terms "median apophysis" and "conductor" will be frequently confusing (and perhaps confused as well). Also, the distinction between subtegulum and tegulum may be expected to be variable among taxa. On the other hand, the sclerites of the embolic division develop long after the separation of the embolic and basal division. On these grounds it seems unlikely that any homologues of embolic sclerites will ever insert directly on the tegulum (although conceivably the last stage of differential growth could cause such a conformation). Therefore tegular sclerites in addition to the median apophysis and conductor ought to be novelties of the taxon in question, not homologues of "missing" embolic sclerites. In taxa with complex embolic divisions (e.g., linyphiine linyphiids) ontogenetic criteria probably will not distinguish more than the embolus, possibly the radix, and a set of "other apophyses".

If the study of Bhatnagar and Rempel (1962) characterizes only *Latrodectus*, or even just theridiids among the araneoids, the generality of these implications will obviously be seriously restricted. Much more comparative ontogenetic data must be acquired before we can place much reliance on Bhatnagar and Rempel's results. The need for caution is underscored by the

knowledge that theridiids are highly derived araneoid spiders in several other respects (Coddington, 1986a). However, the results of Bhatnagar and Rempel do provide a basis to begin outgroup analysis of palp sclerite homology in the Araneoidea.

Palp Homologies among Cribellates

Among neocribellate taxa in general, the following pattern is probably primitive for Araneoclada: cymbium without a paracymbium (but N.B. liphistiids and hypochilids!), basal hematodocha, petiolar sclerite, subtegulum, median hematodocha, tegulum with two apophyses ("median apophysis," "conductor") more or less juxtaposed to the embolus, and a simple embolus without apophyses. The basal hematodocha is rarely absent, and the extent of the median hematodocha is occasionally difficult to judge from published figures. Complete distal hematodochae between the embolus or embolic division and the tegulum are apparently rare. Although the condition of the palpal tibia is not really part of this discussion, many araneocladan cribellate taxa seem to have male tibial apophyses, and these structures may be synapomorphic for a large araneocladan group.

Besides the confusion around the more obscure sclerites such as the radix, stipes, or terminal apophysis, authors also vary as to which tegular apophysis they label median apophysis and which conductor. If a tegular apophyses inserts on the tegulum close to the base of the embolus, and especially if it supports the resting embolus, it is usually termed the conductor. The remaining tegular apophysis is then the median apophysis, especially if it inserts in an unsclerotized area of the tegulum (Lehtinen, 1967:412). The embolus often is a comma-shaped sclerite (e.g., Figures 9–20), sharply tapering, that curves around the tegulum in a clockwise direction (left palp, ventral view, Figures 9–44, but N.B. *Amaurobioides*, Figure 29).

GENERAL CONFORMATION

This general description occurs fairly frequently. It can be recognized in paleocribellates (Hypochilidae: *Hypochilus*, Figure 9) and primitive neocribellates (Austrochilidae, *Thaida*, Figure 10, homology of tegular apophyses uncertain). It is even more obvious in higher cribellates, e.g., Tengellidae: *Tengella* (Wolff, 1977, figs. 3, 7); Dictynidae (*Paradictyna*, single tegular apophysis labelled as DiTA, Figure 21; see also figures throughout Chamberlin and Gertsch, 1958); Desidae (*Matachia, Paramatachia, Notomatachia, Desis, Goyenia, Tuakana, Badumna*, Figures 22–28); Anyphaenidae (*Amaurobioides*, Figure 29), Nicodamidae (*Nicodamus*, Figure 30); Megadictynidae (*Megadictyna*, tegular sclerites reduced, Figure 31), Stiphidiidae (*Cambridgea, Procambridgea*, Figures 11, 12); Agelenidae (*Tararua, Neoramia, Mahura, Orepukia*, Figures 13–16); Neolanidae (*Neolana*, tegular apophysis reduced, Figure 17); Psechridae (*Fecenia*, Figure 18); Eresidae (*Ma-*

gunia, one tegular apophysis reduced, Figure 19); and Amphinectidae (*Amphinecta*, Figure 20). The same general description seems to fit holarctic faunas as well, e.g., Anyphaenidae, Clubionidae, Philodromidae, Thomisidae (Dondale and Redner, 1978, 1982), Oxyopidae (Brady, 1964), other Dictynidae (Chamberlin and Gertsch, 1958), and nearctic Amaurobiidae (Leech, 1972).

ERESIDAE

Palp structure in Eresidae is poorly known. Like those groups mentioned above, most eresids apparently have only one tegular apophysis (ETA, Figure 19). The conformation is apparently unique to eresids, and consequently eresid palp structure offers no evidence as to their placement within Araneoclada.

OECOBIIDAE

Oecobiidae are better studied (Shear, 1970; Baum, 1972) than Eresidae. Shear, followed by Baum, set aside considerations of homology and freely used Comstock's (1910) classical terms to describe oecobiid palpal sclerites. According to their terminology, the oecobiid tegulum and embolic division possess a radix, stipes, terminal apophysis, and "functional conductor" in addition to the usual araneocladan median apophysis. The cladogram in Figure 3 makes homology dubious, because the assertion would add enormous length to the cladogram. The reservations of both Shear and Baum about the homology of these sclerites therefore seem justified. Figure 3 instead suggests that the peculiar conformation of the oecobiid bulb is either autapomorphic or synapomorphic for Oecobiidae and Hersiliidae. The various apophyses or sclerites named by these authors (Figure 5) are probably family autapomorphies. The "radix" may not need a name because it is simply the portion of the tegulum from which the reservoir exits. Also, the radix does not fulfill the morphological criteria for homology with araneid or linyphiid radices (a distinct sclerite between the tegulum and the embolus, both of which are set off from the tegulum by a stalk or hematodocha). Because it does not articulate, the radix apophysis is just a tegular lobe, and may be called the oecobiid tegular lobe (Figure 5, OTL I). The stipes is either the base of the embolic sclerite (Figure 5), and thus requires no name, or, in the case of some *Oecobius* species, is a distinct tegular sclerite. In any case, the reservoir does not pass through this sclerite, and thus it is doubly unlikely to be a stipes homologue. Where distinct, it might be named to signify the monophyly of that oecobiid group. Likewise, the oecobiid "terminal apophysis" is a distinct tegular sclerite. Although the "terminal apophysis" might be a homologue of the araneocladan conductor or median apophysis, no evidence suggests which of these it might be, and thus it may be called the oecobiid tegular apophysis (OTA). Unlike any araneocladan conductor, the "functional conductor"

(fc) is an appendage of the embolic sclerite, and might be better termed the oecobiid embolic apophysis (OEA, Figure 5). Finally, their median apophysis (Figure 5, (ma)) seems to be merely a second tegular lobe, not a free sclerite, and it is quite basal on the tegulum. Thus it might be called the oecobiid tegular lobe II (OTL II, Figure 5).

Names are unimportant, but names should at least coincide with monophyletic groups. The terminology adopted above emphasizes the monophyly of Oecobiidae, can be applied to *Uroctea*, and does not overstate the case for homology with the plesiomorphic araneocladan sclerites.

DICTYNIDAE AS OUTGROUP TO ORBICULARIAE

Because various authors have suggested that uloborids may be derived from dictynid stock, dictynid palps deserve more detailed attention. Dictynidae (Figure 21) have rather derived palps in comparison with the rest of the Dictynoidea. They possess only one tegular apophysis, probably a homologue of the median apophysis or the conductor. The point is moot, and it seems sensible to call it the dictynid tegular apophysis (DiTA). The conformation and particular appearance of this apophysis is a synapomorphy of at least most dictynids in the narrow sense (not that of Lehtinen, 1967:350–362), as Chamberlin and Gertsch (1958:8) long ago realized. Secondly, in the dictynid palp the embolus usually is apical on the tegulum and has a large base, also unusual.

Although the typical uloborid palp may present a superficially similar appearance, it is built quite differently. In typical uloborids the large tegular apophysis (probably homologous to the conductor, see "Uloboridae") is apical, and the embolus is subapical, thus partly covered by the tegular apophysis (Figures 32–42). Also, several uloborid genera have two tegular apophyses, which argues against a single tegular apophysis as plesiomorphic for Deinopoidea (see "Deinopidae"). Even if that were not so, the tegular apophysis is the large apical structure in the uloborid palp, not the embolic base as in dictynids. Thus, although some deinopoids and most dictynids have only a single tegular apophysis rather than two, they have different and opposite relationships to the embolus in each case.

Largely because of the different conformation, the shape of the tegular apophysis is also quite different. The deinopoid tegular apophysis is larger and covers the more slender base of the embolus, whereas the dictynid tegular apophysis is small, and its slender base is often covered by the robust embolic base instead (Figure 21). Although dictynids and some uloborids share the bare fact of a single tegular apophysis, that condition is too common elsewhere (possibly *Procambridgea*, Figure 12; *Neolana*, Figure 17; *Magunia*, Figure 19; *Megadictyna*, Figure 31) to support an argument for synapomorphy. Furthermore, dictynids have tibial apophyses. Uloborids and deinopids (in common with araneoids and primitive araneomorphs) lack them altogether, apparently the plesiomorphic condition for Araneoclada. (Sporadic linyphiid genera do have tibial apophy-

ses.) Thus palp structure does not support a dictynoid-orbicularian link.

To sum up, this review of the likely outgroups to Orbiculariae has highlighted several points. First, the araneocladan bauplan includes three apically grouped tegular sclerites: embolus, conductor, and median apophysis. Either of the latter two can be lost or fused, which amounts phenotypically to the same thing. The embolus often originates ectally, and coils in a clockwise direction. The embolic division is almost always simple, without lobes, apophyses, or distal hematodochae as they occur in Araneoidea. The remaining portions of the palp (e.g., tegulum, subtegulum, hematodochae) are unmodified from the basic araneomorph condition.

On the other hand, some cribellate araneocladan groups, such as Filistatidae, Eresidae, and Oecobiidae, depart drastically from the araneocladan bauplan. Until they are better studied, each probably deserves an exclusive sclerite terminology; the wholesale use of terms first applied to araneoids, as in the case of oecobiids, only obscures their distinctive morphology. None of these groups have palps that resemble orbicularian palps to any marked extent. Thus the orbicularian sister group is more likely among the more generalized Amaurobioidea or Dictynoidea (or either or both together). Within these superfamilies, the evidence of male palpi does not particularly support the choice of Dictynidae, despite the fusion or loss of one of the tegular sclerites. Orbiculariae itself is supported by 14 synapomorphies (characters 44–46, 49, 64, 65, 67–69, 73, 77, 78, 81, 82; Figure 108).

Palp Homologies among Deinopoidea

The next two sections discuss palp homologies in Deinopoidea and Araneoidea. Character codings are listed in Table 1, and the resultant cladogram is presented in Figure 108. Although the discussion of sclerite homologies draws on the cladogram to settle ambiguities in character state trees, comments on the cladogram results at the level of taxa are presented throughout the following discussion.

DEINOPIDAE

Deinopidae are more derived in many ways than uloborids and have a peculiar palp (Figures 43, 44), with one central, distal, tegular apophysis. Although it is at present impossible to say with certainty which of the araneocladan tegular apophyses the deinopid structure represents, the apical insertion next to the embolus argues that it is more likely to be a conductor than the usually more lateral median apophysis. On the other hand, the insertion of the deinopid structure on the tegulum via a flexible connection would point towards homology with the median apophysis. At any rate, in Table 1 Deinopidae is coded as lacking a median apophysis and possessing a conductor (characters 9, 15). The embolus is usually elongate, and coils from slightly more than once to as many as 6 times around the

reduced conductor. The embolic coils are much bulkier than the tegular apophysis. The embolus lacks lobes or apophyses. The deinopid tegulum is also reduced to a band of sclerotized tissue that covers the reservoir of the sperm duct. The strongly spiralled embolus and single central tegular apophysis in Deinopidae is autapomorphic by outgroup comparison to Uloboridae and Araneoidea. All deinopids are entelegyne (Table 1, character 24).

ULOBORIDAE

The primitive uloborid palp was probably more like that of *Waitkera* (Figure 32; Opell, pers. comm.), rather than *Tangaroa* (Figure 33), as first supposed (Opell, 1979). The *Tangaroa* palp is derived because it lacks all tegular apophyses other than the embolus. Other aspects of its morphology are also unique (Opell, 1983). *Waitkera*, by contrast, still retains two tegular apophyses. The apical uloborid apophysis is probably homologous to the single apical apophysis of *Deinopis* and *Menneus*. On other grounds (Opell, 1979; Coddington, 1986a, b) the families appear to be sister taxa.

Although Opell (1979) called the apical uloborid sclerite the median apophysis, and the lateral sclerite the conductor, the respective positions of the sclerites (by outgroup comparison to other Orbiculariae and Araneoclada) suggest that the labelling should be reversed. First, by positional criteria, the more apical sclerite that is closer to the insertion of the embolus is usually called the conductor. Second, when groups do lose one of the tegular apophyses, it is usually the lateral one rather than the apical. More derived uloborids such as *Uloborus* have only the apical apophysis. *Waitkera*'s second tegular apophysis (Figure 32) is therefore probably the median apophysis. Using this revised terminology, then, Opell's conclusions may be rephrased as all uloborids except *Tangaroa* have the conductor, but only *Waitkera* (Figure 32), *Polenecia* Figure 35), *Siratoba* (Figure 42), *Ariston* (Opell, 1979, plate 3a), *Hyptiotes* (Figure 37; Opell, 1979, pls. 3d, 4d), *Miagrammopes* (Figure 38; Opell, 1979, pl. 5a), and *Sybota* (Opell, 1979, pl. 6a), retain the median apophysis.

However, the absence of the median apophysis in some of the remaining uloborid genera is not beyond doubt. Opell (1979) and Lubin et al. (1982) suggested that *Conifaber*, *Purumitra*, *Octonoba*, and *Zosis* had a unique sclerite, the "tegular spur" (Figure 41; Table 1, character 13; Opell, 1979, pls. 6c, 7c). The tegular spur is on the lateral side of the tegulum, and especially in *Zosis* and *Conifaber*, is shaped roughly like the median apophysis of *Waitkera* or *Polenecia*. In view of araneoid and more distant outgroups, it seems simpler to interpret the tegular spur as a modified median apophysis, rather than supposing the loss of the median apophysis and the gain of the tegular spur. In the same three genera, Opell (1979) coded a lobe of the conductor as homologous with the median apophysis, but that hypothesis (fusion of the median apophysis and conductor, with appearance of a novel tegular sclerite)

seems more complex than necessary to explain the data available.

Uloborus, *Philoponella*, and *Ponella* lack the second tegular (median) apophysis (Figure 108, character 9). Opell (1979: 456–458) suggested that the two had fused, which seems reasonable because the apical conductor is quite complex. In view of the ontogenetic evidence reviewed above, the alternative that the two sclerites fail to separate might be considered. Either process would result in much the same appearance. Opell (1979, pls. 4a,c, 6e) also showed that in some cases if the conductor is torn off the palp, the median apophysis comes away with it, leaving the embolus and basal division behind.

In sum, the homology of the median apophysis in Uloboridae is a frustratingly difficult problem that may never be satisfactorily solved. (Note that the consistency of character 9 in Figure 108 is only 0.12.) In any case, it seems simpler to suppose that the tegular spur is homologous to the median apophysis rather than supposing loss of the median apophysis and gain of a new sclerite.

The uloborid "radix" also poses interpretive problems, not unlike those analyzed in connection with oecobiids. Opell (1979) identified a mesal lobe at the base of the embolus as a "radix," although he doubted homology between that sclerite and the araneoid radix. The doubt seems justified, because the uloborid structure is always a lateral outgrowth of the embolic sclerite, is never basal to it, never has a hematodocha joining it to either the tegulum or the embolus, and never has the ejaculatory duct passing through it. Criteria of concordance with other characters also argue that the uloborid and araneid structures are different, and the two are coded as different structures in Table 1 and Figure 108 (characters 18 and 22). For similar reasons as in the case of oecobiids, therefore, it makes more sense to call the uloborid sclerite the uloborid embolic apophysis (UEA, Figures 32, 35; see also Opell, 1979, pl. 6e).

However, even if one accepts that the uloborid embolic apophysis (UEA) is not homologous to the araneoid radix, problems still remain within uloborids themselves. Figure 108 suggests that the uloborid embolic apophysis arose three times independently: once in the lineage including *Tangaroa*, *Waitkera*, *Polenecia*, *Siratoba*, and *Ariston* (hereafter referred to as the "*Waitkera* clade"); once in the doublet *Hyptiotes*-*Miagrammopes*; and once in the doublet *Philoponella*-*Octonoba*. Even if one supposes that the absence of the UEA in *Tangaroa* is derived, Figure 108 still would most parsimoniously suggest three separate origins for the sclerite. In fact, the hypothesis that the UEA is homologous wherever it occurs would necessitate four steps of additional homoplasy in Figure 108. Clearly, detailed consideration of uloborid embolic morphology is required by specialists to determine if these results are reliable.

Opell (1979) also coded the presence of the median hematodocha (Table 1: character 5) in the uloborid genera *Octonoba*, *Purumitra*, *Zosis*, *Philoponella*, and *Uloborus* as a

derived state, and its absence in the eight genera for which males were known as primitive. A median hematodocha, however, occurs in deinopids, the sister taxon to uloborids (*Deinopis spinosus, D. longipes, Menneus camelus, M. angulatus*, pers. obs.) and in a majority of Araneoidea (pers. obs.). The structure is also present in many other spider groups (Shear, 1967, and below). Either the median hematodocha has originated more than once in the orb weavers (in which case the different states are not cladistic homologues) or else loss has occurred twice in the uloborids. Opell (1983, 1984) and Lubin et al. (1982) have recently shown that median hematodochae are also present in *Hyptiotes, Miagrammopes, Lubinella* and *Conifaber*. Figure 108 (character 5) suggests that loss of the median hematodocha has occurred twice in uloborids, once in the *Waitkera* clade and again in *Sybota*. However, in this case, insisting that the absence of the median hematodocha is primitive for uloborids would cause only one step of additional homoplasy in Figure 108. From a parsimony point of view, the alternatives are much more nearly balanced than for the uloborid embolic apophysis.

Heimer (1982) implied that the uloborid cymbial setae had a similar function to the araneoid paracymbium: to arrest the rotation of the palpal bulb during expansion by engaging the median apophysis. Opell (1979, figs. 19, 28) figured strong setae on the mesal cymbial margin that he considered as part of a stridulation mechanism (Figures 32, 33). In fact, only in the taxa with a stridulation mechanism (*Waitkera, Tangaroa, Polenecia*; Table 1, character 62) are the setae really robust, although most uloborids have them (Table 1, character 3). In any case Heimer's (1982) suggestion does not seem to hold for uloborids in general. The cymbial margin in Deinopidae is simple, so that homology of the uloborid setae with the araneoid paracymbium is again refuted. The paracymbium (Table 1, character 4, consistency index 0.80) is apparently unique to araneoids, among the taxa considered here.

The features of the deinopoid palp that are plesiomorphic for Araneoidea are apparently the following (many of these features are probably plesiomorphic for Orbiculariae, as well). The conformation of the deinopoid palp is consistent: a cup-shaped subtegulum, a large tegulum with apical conductor, and, if present, the median apophysis closely juxtaposed. The subapical embolus originates dorsally and laterally, and then curves clockwise around the base of the conductor. The deinopoid cymbial margin is simple, lacking a discrete lobe resembling a paracymbium. Although a cymbial lobe occurs sporadically within other araneocladan taxa (Hypochilidae, Dysderoidea, Palpimanoidea), its distribution does not refute the paracymbium as a synapomorphy for Araneoidea.

The homology of the deinopoid and araneoid basal hematodocha and subtegulum is uncontroversial. In both groups the latter sclerite contains the fundus of the sperm duct. However, the condition of the subtegular petiole is unknown among deinopoids; in some araneoids it is fused to the subtegulum. The deinopoid tegulum is a cylindrical sclerite that contains the reservoir of the sperm duct.

The deinopoid embolus characteristically curves in a clockwise direction (left palp, ventral view) and encircles the conductor. It may be either short or long, and it contains the ejaculatory portion of the sperm duct. A complete distal hematodocha is absent in both Uloboridae and Deinopidae. The course of the reservoir through the tegulum tends to be a simple spiral (Figures 34, 36; *Menneus, Deinopis*, pers. obs.).

Palp Homologies among Araneoidea

The following discussion treats the palp morphology of Araneoidea and its subsidiary groups in turn, and also discusses nongenitalic characters that bear on the cladistic placement of the group.

ARANEOIDEA

The presence of a paracymbium (Figure 108, character 4) on the ectal margin of the cymbium is apparently synapomorphic for Araneoidea (occurring in araneids, metines, nephilines, tetragnathids, theridiosomatids, linyphiids, and nesticids). A vaguely paracymbium-like structure occurs in some Theridiidae (Levi and Levi, 1962; Heimer, 1982), but in most genera it is highly modified from the basic araneoid condition, so that its homology to the araneoid paracymbium is doubtful. Not only is this structure not particularly similar to the paracymbium in other araneoid taxa, but it has a different function. In araneids (Grasshoff, 1968:50) and in linyphiids (van Helsdingen, 1965:38; 1969:22, 23; 1972) the paracymbium engages the median apophysis or the suprategular apophysis to stabilize the palpal bulb. In theridiids, however, the "paracymbium" locks the bulb in its unexpanded position. By criteria both of function and form, therefore, the theridiid paracymbium is unlike that of other araneoids. Levi (in litt.) has pointed out that in primitive theridiid genera (e.g., *Enoplognatha, Latrodectus, Steatoda*, as judged by retention of colulus), the "paracymbium" is more like that in other araneoids than it is for more derived theridiid genera. (It is coded as a paracymbium homologue in Table 1 (character 4, state 3: distal), but since it is autapomorphic, it has no effect on the cladogram topology.)

In nearly all araneoids, the labium is wider than long (character 33). In nephilines, as far as I know, it is longer than wide, but Figure 108 suggests that this is a reversal. In Deinopoidea and usually in more distant outgroups (cf. Forster, 1970; Forster and Wilton, 1973) it is longer than wide.

Also in nearly all araneoids, the lateral eyes are juxtaposed (character 61). The feature is reversed in some tetragnathines and *Latrodectus* among the theridiids, but overall it is quite general. In Deinopoidea and more distant outgroups the lateral eyes are usually separated by at least their diameter. The character of juxtaposed lateral eyes in araneoids corroborates the monophyly of Araneoidea. Certainly by outgroup compari-

son with deinopoids the feature is derived. All araneoid families that have been checked have aggregate and true flagelliform glands (characters 46, 47), two additional synapomorphies. Finally, if the previous five synapomorphies can be trusted, araneoids uniquely among Orbiculariae lack a cribellum and have true serrate setae (characters 42, 49). These characters, therefore, count as two more synapomorphies, although they are weaker because of frequent occurrence elsewhere among spiders. These seven characters at present constitute the morphological evidence for araneoid monophyly.

A simple helical route of the sperm duct reservoir through the tegulum is primitive, a more complex routing is derived. Complexity itself in the sperm duct is not synapomorphic, because, for example, "complex" reservoir trajectories occur in at least *Nephilengys* (pers. obs.), *Nephila* (Figure 52), *Metleucauge* (Figure 51), *Azilia* (Figure 53), *Meta* (Figure 54), *Leucauge* (Figure 55), and *Dolichognatha* (Figure 50); in the cyatholipid *Teemenaarus* (Figure 107), in the theridiid genera *Theridion* (Figures 92, 93), *Histagonia* (Levi and Levi, 1962, fig. 72), *Dipoena* (Figure 76), some *Euryopis* (e.g., Figure 77), *Phoroncidia* (Levi, 1964a, fig. 1), and *Episinus* (Figure 79), and also ubiquitously in the theridiosomatids (Coddington, 1986c). Convincingly similar switchbacks and turns can be recognized within some taxa (theridiosomatids; nephilines and metines) although not necessarily among them. Complex reservoir trajectories evidently have evolved several times. The character is promising at lower hierarchical levels.

On the other hand, a simple helix in the reservoir characterizes the metine genus *Metellina* (Figure 49), and the tetragnathines *Pachygnatha, Glenognatha, and Tetragnatha* (Figure 45); many theridiids, e.g., *Theridion* (Levi and Randolph, 1975, fig. 77; Levi, 1957a, fig. 153) and *Paidisca* (Levi, 1957a, fig. 395); some *Euryopis* (Levi and Randolph, 1975, fig. 43), *Achaearanea* (Levi, 1955a, fig. 25; 1963a, fig. 114), *Spintharus* (Figure 81), linyphiids, e.g., *Maro* (Figure 6), *Tapinocyba* (Merrett, 1963, fig. 80a); many other genera figured in Millidge (1977), most araneids (20 genera in Levi, from 1970 to 1978), nesticids (Lehtinen and Saaristo, 1980, fig. 2), as well as araneoid outgroups discussed herein.

ARANEIDAE-LINYPHIIDAE

The complex embolic division characteristic of linyphiids and araneids may be synapomorphic for these taxa alone. They share the following features: (1) articulation of the embolic division to the tegulum by a complete distal hematodocha or membranous stalk (the "column" of Millidge, 1980; Saaristo, 1971, fig. 6; Figure 108, character 21); (2) the insertion of the embolus on a basal sclerite, the radix (character 22); (3) the additional insertion on the radix of embolic apophyses. However, something similar to a column also occurs in *Nephila* at least (Table 1, Figure 108).

Gnathocoxal "sexual" glands (Legendre and Lopez, 1974; Lopez, 1977) occur only in the Linyphiidae and Araneidae

(character 34). Lopez (1977) did not find this unique gland type in any other spider group (35 families, 81 genera surveyed). Evidently, it is an additional synapomorphy of the two families. Lopez checked theridiids, araneids, linyphiids, metines, and *Nephila* among the araneoids, and *Uloborus* and *Zosis* among the deinopoids. He found that the glands were sporadically absent in some *Araneus* species and in *Cyrtophora*. He did not check nesticids, symphytognathids, mysmenids, anapids, theridiosomatids, or, for that matter, mimetids.

ARANEIDAE

Several years ago it was clear that if the orb web was a plesiomorphic araneoid feature, then the traditional argument for the monophyly of Araneidae in the old, broad sense had collapsed (Levi, 1980a; Coddington, 1982; 1986a:336). However, if nephilines, metines, and tetragnathines are removed, Araneidae becomes far more homogeneous and compact. Levi (1980b, 1981, 1983b, 1985, 1986) has done much to identify monophyletic subgroups of araneids, and the following discussion corroborates many of his conclusions. At present the family contains at least five subfamilies: Argiopinae, Cyrtophorinae, Mastophorinae, Araneinae, and Gasteracanthinae, although the number should probably increase. The best synapomorphy for the entire family seems to be the unusual tapetal structure of the posterior median eyes (Levi and Coddington, 1983; Table 1, character 59). In the plesiomorph araneoid condition the midline or "keel" of the canoe tapetum bisects the eye cup, and the rhabdoms and tapetum are equally displayed on both sides. In the derived condition, the canoe keel and the tapetum is much displaced towards the sagittal plane; on the ectal side the rhabdoms loop back and forth.

Figure 108 suggests additional synapomorphies for Araneidae, although some are an artifact of the taxa selected to represent Araneidae in Figure 108 (really equivalent to Araneinae). Coxal hooks (Table 1, character 50; Levi and Coddington, 1983), for example, are absent in the other subfamilies. Some representatives of those subfamilies do use a wrap attack to subdue prey (Robinson, 1975; Table 1, character 85). The ubiquitous presence of a wrap attack in Deinopoidea, however, casts doubt on its independent derivation in Araneidae. Presumption of homology in wrap attacks between the two superfamilies only adds one step of homoplasy to Figure 108.

In araneids, the sclerites also show a characteristic orientation to each other, or "conformation" (Millidge, 1977). In a mesal view of a left palp (Figures 8, 56–67), the median apophysis is centrally located. The tegulum is clearly visible below, and the embolus originates apically, and is usually protected by the conductor, lying above or to the side of the embolus. Nearly all araneids have a radix in the palp (Levi, 1986:94; Figures 56–67). The embolic division of araneines, if not all araneids, is consistent and synapomorphic.

A further problem in araneid palpal homology is the distal

hematodocha. In Comstock's (1910) original usage, the distal hematodocha was that between the tegulum and the embolic division. As it turns out, the araneid terminal apophysis is often set off from the embolic division by a hematodocha, and these hematodochae apparently sometimes are discrete structures (Grasshoff, 1968). At present the meaning of these terms remains ambiguous.

Levi (1983b:254) proposed that the median apophysis was a derived condition within Araneidae, but the evidence for that is at best equivocal. Figure 108 does not resolve the placement of the theridiid-nesticid lineage, but in four of the five most parsimonious solutions, the median apophysis is plesiomorphic for Araneidae (despite its absence in Linyphiidae). Only if theridiid-nesticids are the sister taxon to the rest of the araneoids, can the median apophysis be even an equivocal synapomorphy for araneids.

LINYPHIIDAE

The analysis of palp structure in Linyphiidae, and its relation to other araneoid groups remains difficult and ultimately ambiguous because the classification of the family is in flux. It is not, for example, at all clear that the family is a monophyletic group as presently constituted. Obviously there is a core group of genera that comprise a monophyletic group. However, one also gets the impression that enigmatic, non-orb-weaving araneoids have ended up by default in Linyphiidae (and also in Theridiidae). When one tries to write a diagnosis of the family that covers all such included groups, apomorphic characters may be entirely lacking.

In his diagnosis of Linyphiidae, many of the characters listed by Millidge (1977, 1980) as synapomorphies are clearly plesiomorphic by outgroup comparison to other araneoids, for example the basal hematodocha, subtegulum, tegulum, and the embolic division as a separate sclerite. Others, such as the radix and column, may also be present in Araneidae. At the time, Millidge (1977) equated simplicity with primitiveness and inferred derived features accordingly, a now widely recognized unreliable method. The argument for monophyly thus reduces to the suprategulum, which is a prong of the tegulum that bears the column, and through which the sperm duct passes (Figure 6). While this character is technically sufficient to define Linyphiidae, and does seems to be present in many erigonine and linyphiine taxa, no linyphiid specialist has really focused on the comparative morphology of the structure to assure homology in all groups. The generality of other potential familial synapomorphies, such as cheliceral stridulating files, or Fickert's gland, are also undocumented.

Leaving aside the question of monophyly, the subfamilial classification of linyphiids also remains unsettled and controversial. Millidge (1984) argued that epigynal design and tracheal morphology divide the family into four subfamilies and a paraphyletic group of miscellaneous genera. However, his most recent revision of that analysis concluded that paired spiracles are primitive for Linyphiidae (Millidge, 1986, figs. 12, 13). His discussion seems to imply that the posterior tracheal system of linyphiids arose directly from araneomorph posterior book lungs, which would not only deny linyphiids as Araneoidea, but even as Araneoclada. While paired spiracles may indeed result from direct transformation of posterior book lungs in some araneomorph groups (Forster, 1980), a single, slit-like spiracle is present in Uloboridae (Opell, 1979), and most araneoids with the exception of some linyphiids (Lamy, 1902) and symphytognathoids (Forster, 1959). Outgroup comparison and the cladogram (Figure 108), therefore, suggest that paired spiracles are derived, not primitive. This inference suggests that Millidge's polarization of this character should be reversed. That turns his most recent cladistic hypothesis for Linyphiidae on its head. Also, the classifications based on tracheal systems differ from those on epigynal characters, and these in turn differ from those based on male genitalia. Obviously these character systems are not concordant, and thus classifications based on single systems will conflict. Until these important issues are synthesized quantitatively and resolved by linyphiid specialists, one cannot judge the parsimony of existing "cladistic" schemes for the family. This in turn means that palpal variation such as that in the embolic division is difficult to interpret cladistically.

Linyphiids (Figures 68–75) apparently lack both a true median apophysis and a true conductor. The "embolic membrane" (Figure 6; Millidge, 1977, 1980) or "median membrane" (van Helsdingen, 1965) at times has been argued to be the homologue of either sclerite. As these structures, however, usually arise from the radix or column of the embolic division, and as their presence is sporadic in the family, homology is tenuous. Comstock (1910, fig. 70) did figure a tegular lobe that he labelled a "median apophysis" in *Pityohyphantes phyrygiana*. This structure, which seems to be the same as what Merrett (1963) labelled the "median apophysis" in linyphiids, does not seem to be the same sclerite as in theridiids, theridiosomatids, or araneids. Saaristo (1971, 1975) pointed this out, and later Millidge (1977, 1980) agreed with him. Saaristo renamed the part the "suprategulum" (Figure 6), tacitly recognizing its homology with the tegulum. Important evidence supporting Saaristo's hypothesis is that the sperm duct reservoir passes through the linyphiid suprategulum, which is never the case for the median apophysis. However, the median apophysis in Araneidae engages the female scape, and this is apparently true of the suprategulum in linyphiids as well (Grasshoff, 1968:49; van Helsdingen, 1965:38, 1969:15).

The possibility remains that the "suprategular apophysis" of those authors is the median apophysis homologue. The suprategular apophysis is a prolongation of the arm of the linyphiid tegulum beyond the point where the embolic division originates. However, it has never been clear whether the suprategular apophysis is articulated (and thus more like a true apophysis) or simply the elaborate (but fused) end of a tegular

projection. The literature suggests that the latter is most often the case.

Evidence for the existence of a linyphiid conductor is also equivocal. Many linyphiid genera have a distinctive apophysis that inserts on the radix, termed the lamella characteristica (Figure 6), which during copulation sometimes supports the embolic shaft (van Helsdingen, 1969:23). In the resting palp, long thin emboli are often enclosed in this structure. As such, the linyphiid lamella can function in a similar way to the nephiline, tetragnathine or theridiosomatid conductors (Figures 45–55, 104, 105). However, the linyphiid lamella is very clearly a part of the embolic division, and if one relies on the sequence of events outlined in Figure 4, homology between the lamella and the araneomorph conductor seems dubious. Obviously the linyphiid embolic division is complex, and it seems much more likely that the lamella is an autapomorphic modification in some genera of the complex embolic division that has come to serve the function of a conductor in some taxa. However, the level at which this feature is apomorphic remains undetermined.

Other linyphiid sclerites, such as the embolic membrane (Figure 6) also seem autapomorphic. If one wished to homologize this structure with a more general araneoid sclerite, again the obvious choice would be the araneoid conductor, because the araneoid conductor often inserts on the tegulum very close to the embolic division. Likewise the embolic membrane sometimes inserts on the column (Figure 6; Merrett, 1963), which itself inserts on the tegulum. The shift, perhaps, would not be too incredible a transformation. However, such speculations do not yield pragmatic benefits or analytical results. Even if the linyphiid embolic membrane were the conductor homologue, it would exhibit several apomorphic modifications. Mere presence of a conductor in Linyphiidae would increase the consistency of the character "conductor" on the cladogram in Figure 108 (Table 1, character 15), but would not affect the cladogram structure. Embolic membranes apparently are not a consistent feature of all linyphiid palps, most frequently being absent in "erigonine" taxa (Merrett, 1963). Thus if it is homologous with the conductor, its absence in erigonines is derived.

The other general linyphiid embolic sclerite is the terminal apophysis. It, along with the lamella characteristica and embolus, inserts on the radix. Until further detailed work is carried out to trace homologies within Araneidae and Linyphiidae, it is premature to claim homologies between the respective "terminal apophyses." One may note, however, that a complex embolic division, however one allocates its parts, is thus far unique to Araneidae and Linyphiidae among araneoids. The epigyna of the same taxa also tend to have scapes. Also the function of sclerites on complex linyphiid and araneid palps seems similar (Grasshoff, 1968:47–55; van Helsdingen, 1965:36–41, 1969:12–26). If this inference of homology is valid, then linyphiids with relatively simpler palps are derived. Those genera with simpler palpi tend to be smaller in size, and

to have modified tracheal systems (Millidge, 1984, 1986). Although the homology hypothesis thus has some support among other character systems, it really awaits a thoughtful analysis of all available data to produce an unrooted cladogram of linyphiid relationships. With that in hand, deciding where to root the cladogram, and thus the polarity of changes within Linyphiidae, should not be too difficult.

METINE-TETRAGNATHINE-NEPHILINES

The "metine-tetragnathines" have rather simple palpi, and are fairly generalized araneoid taxa. Many authors (see discussions in Levi, 1980a; Wunderlich, 1987) have suggested metines as the "stem taxon" of the araneoids. As always, however, the first question must concern the monophyly of the group. Essentially the problem has two parts: the monophyly of tetragnathids and whether any other taxa can be annexed to that group. *Tetragnatha*, *Pachygnatha*, and *Glenognatha* form a monophyletic group based on the characteristic shape of the paracymbium, the tegulum, morphology of the embolus, and shape of the conductor. The paracymbium is a thin, elongate lobe parallel to the cymbium and tegulum, not a hook, or a squat lobe (Table 1: character 4, state 4: long). The tegulum is smooth, globular, and the median apophysis is lacking. The embolus is apically placed, without apophyses (except some *Tetragnatha*), and to a greater or less extent is spiralled. The conductor inserts very close to the embolus, and spirals with the embolus. All these features characterize Tetragnathidae in the strict sense (together termed "tetragnathid conformation," character 2). Other genera that share these features are *Atelida*, *Hivaoa*, and *Hispanognatha*. Palmgren (1978a, b, 1979) also noted that *Tetragnatha* and *Pachygnatha* (he did not examine *Glenognatha*) uniquely share gastric caecae extending into the chelicerae. As he pointed out (Palmgren, 1979), the extent of the caecae is possibly an effect of the space occupied by other organs, such as muscles or poison glands. Perhaps his observation can be restated to say that tetragnathines have smaller poison glands.

Like the tetragnathines, the metine genera lack one tegular apophysis (probably the median apophysis), have a smooth and round (but not as globular) tegulum, an apically placed, more or less spiralled embolus, and a juxtaposed conductor that spirals with the embolus, although not to the extreme extent seen in tetragnathines. The paracymbium varies, but usually is short and robust (character 4, state 2: squat), not elongate and thin. The metines share, however, two additional features. They have a lobe extending from the embolus (character 17: metine embolic apophysis, MEA; Figures 49–51) and the course of the reservoir through the duct has a sharp switchback (character 7) soon after it enters the tegulum (Figure 50). Genera sharing these features include at least *Meta*, *Metellina*, *Chrysometa*, *Nanometa*, *Metleucauge* (N.B. sclerite apparently separate, Figure 51), *Azilia*, *Dolichognatha*, *Metabus*, as well as other old and new world taxa. *Azilia* lacks the embolic apophysis,

and has more than a single switchback in the reservoir routing. I thus agree with Levi (1980b, 1981, 1986) who argued that these genera, including *Azilia*, are related.

Levi has generally labelled the lobe of the metine embolus as the "terminal apophysis," which might imply homology with the araneine terminal apophysis. It seems to me that the araneid terminal apophysis is rather different from the metine structure, and instead is unique to some part of the Araneidae, or perhaps Araneidae + Linyphiidae. The araneine terminal apophysis (character 23) is often separated from the embolus by a hematodocha, is much larger and more elaborate, and, most important, is part of a consistent conformation of the embolic division, which the metines lack. In contrast, the metine embolic apophysis is a simple lobe from the base of the embolus. It does not resemble the araneid embolic division any more than it resembles the embolic apophyses of theridiosomatids (Coddington, 1986c). Viewed in the cladistic context of araneoids as a whole (Figure 108), one gains only homoplasy by supposing homology between these different structures in different groups. Thus the metine embolic apophysis becomes a synapomorphy for a group including tetragnathids, rather than merely the remnant or progenitor of the condition in araneines. Many *Zygiella* species (e.g., *Z. stroemi* in Levi, 1974) share the conformation of the araneine embolic division with the terminal apophysis and hematodocha. Other *Zygiella* species such as *Z. atrica*, may lack the terminal apophysis, but they still have the radix and associated distal hematodocha, which also characterizes araneids. Although Levi has placed *Zygiella* among the metines, it seems unlikely that the radix-distal haematodocha-terminal apophysis complex would have evolved twice. Thus the genus seems to be part of the araneine complex, at least based on palp structure.

The course of the sperm reservoir as a synapomorphy for metines is an intriguing possibility. The same switchback seems clearly present in *Dolichognatha, Leucauge, Metleucauge, Meta*, and such other metine genera as *Chrysometa*, and *Nanometa* (Levi, 1986). The course of the reservoir in *Azilia* is so complex that a detailed study would be required to locate the homologous switchback.

The homologous switchback appears to be present in *Herennia* and *Nephilengys* among the nephilines (the routing in *Nephila* is more complex), but they lack the embolic apophysis. With tetragnathines and metines, the nephilines share the absence of a median apophysis, and the apical, spiralled embolus and conductor. Nephilines are, of course, a monophyletic group on other grounds (Levi, 1980b; Eberhard, 1982; Coddington, 1986a:325).

In summary, then, the metine-tetragnathine assemblage seems to be monophyletic on the basis of four characters (1, 4 (state 2), 7, and 9), and to contain two lineages. One is the metine-tetragnathines, defined on the reservoir switchback and their resting posture (characters 7, 87; Coddington, 1986a; Levi, 1980b:7), and the other is the nephilines, defined by morphology, web architecture, and behavioral features (charac-

ters 33, 69, and 78). The nephilines appear to be the sister taxon of the metines, based on routing of the sperm reservoir, and the compact and complex form of the paracymbium (versus long and thin in tetragnathines, or a simple hook in the remaining araneoids). Nomenclaturally, they might either be subfamilies or separate families. Really reliable decisions on these matters must await more detailed work at the generic and species levels.

Three confusing metine-tetragnathine features deserve comment: the haplogyne or semi-entelegyne female genitalia in some genera (character 24), the femoral trichobothria in some genera (character 37), and the widely spaced lateral eyes in some genera (character 61). All of these feature are also present in some uloborids, and thus previous authors have expressed concern that they may be homologues. First, most metines are apparently entelegyne. As far as I know, only *Tetragnatha, Glenognatha*, and *Pachygnatha* are truly "haplogyne," but the morphological details of their haplogyne state vary considerably. Given that most araneocladan outgroups to the Orbiculariae are entelegyne, that deinopids are entelegyne, that other araneoids are entelegyne, and that many uloborids are entelegyne, it seems simplest to presume that haplogyny in some metines, and in some uloborids, is a convergent, nonhomologous similarity (character 24 has a C.I. of 0.33 (Table 1); but note that if *Polenecia* is correctly placed (Figure 108), its entelegyny is secondary).

Among metines and tetragnathines, the presence of femoral trichobothria (character 37) (e.g. in *Leucauge, Alcimosphenus, Glenognatha, Mecynometa, Pachygnatha*) and widely spaced lateral eyes (character 61) (*Azilia, Tetragnatha, Dolichognatha*) in some genera may seem to be primitive traits. However, the majority of metine genera apparently lack femoral trichobothria, and have juxtaposed lateral eyes (separated to some extent in *Clitaetra*, some *Nephila*, and *Nephilengys* (H.W. Levi, pers. comm.)).

For each of these three characters (24, 37, 61), then, the weight of evidence from other characters suggest that their sporadic conditions in metine-tetragnathines are convergences.

THERIDIIDAE

In 1961, Levi took the absence of tegular sclerites in some theridiids as primitive, although they occur elsewhere in Araneoidea. At the time, he warned that the terms he used probably did not indicate homologues. Levi (1983a) has since pointed out that the simpler theridiid palps are probably derived rather than primitive, but he did not comment on the homology of those sclerites. In many theridiid genera, the reservoir of the sperm duct passes through what has been called the "median apophysis," e.g., *Dipoena, Euryopis, Episinus, Spintharus, Chrosiothes, Stemmops, Theonoe, Robertus, Latrodectus*, and *Argyrodes* (Figures 76–88; see also Heimer, 1982, fig. 8). That sclerite is probably not the true median apophysis, but an autapomorphic outgrowth of the tegular wall, which, naturally, might contain a portion of the sperm duct reservoir. The

discrepancy was later realized by Levi (1968), and some sclerites were relabelled in later publications (Levi and Randolph, 1975), but the matter could use further emphasis and clarification. In no other spider taxa to my knowledge has the sperm duct reservoir been found to pass through the median apophysis (see "Linyphiidae"), whereas a trajectory along the periphery of the tegulum is quite normal. Ontogenetically, the median apophysis primordium in theridiids (the dorsal lobe) separates itself from the primordium, which contains the sperm duct before the sperm duct even forms, and certainly before the reservoir comes to occupy the tegulum (Figure 4). That segregation makes it less likely that the sperm duct would migrate into the median apophysis.

Further evidence comes from the observations of Levi (1961) and Heimer (1982) that this tegular process engages a notch in the cymbial margin so as to retain the unexpanded bulb inside the alveolus. Heimer (1982) theorized that the primitive function of the araneoid paracymbium was to arrest the rotation of the expanded bulb by engaging the "median apophysis," and cited this functional complex in theridiids as evidence. However, Levi (1961) wrote that this sclerite anchors the *unexpanded* bulb in the cymbium. Because palpal bulbs as they expand usually rotate at least 180 degrees, the claim that these two very different locking mechanisms are homologous seems unsupported, although that they both "lock" the bulb is a curious coincidence. No other araneoid taxon shows a similar morphological complex. In its functional role the feature is unique to theridiids, and along with lobed aggregate glands (Kovoor, 1977a) is probably synapomorphic for the family. Consequently the "median apophysis" of most theridiids is not the same as the median apophysis of other orb-weaving groups. In the latter the median apophysis articulates to the tegulum and does not contain the reservoir. The novel structure in theridiids thus needs a new name and has been labelled theridiid tegular apophysis (TTA) in Figures 76–100.

Hickman (1942) pointed out that Hadrotarsidae possess the same kind of locking mechanism as theridiids, one of the facts that led Wunderlich (1978b) to synonymize the two families. However, to support a sister group relationship between Theridiidae and Hadrotarsidae rather than merely subsuming hadrotarsids within theridiids, one would need evidence that Theridiidae, apart from Hadrotarsidae, are monophyletic. Theridiids are too heterogeneous to make that argument at present.

As already pointed out, the "radix" in its original sense (Comstock, 1910) referred to a distinct sclerite basal in the embolic division of linyphiids and araneids. If the distinction between the embolic and basal division of the palp is as fundamental as ontogenetic evidence suggests, homologues of the radix ought not to arise from the tegulum (Figure 4). However, a sclerite called a "radix" was figured in many theridiid genera, e.g., *Episinus* (Figure 79), *Spintharus* (Figure 81), *Chrosiothes* (Figure 83), *Argyrodes* (Figure 88), *Synotaxus* (Figure 89), *Enoplognatha* (Figure 90), *Theridion* (Figure 92),

Anelosimus (Figure 94), *Arctachaea* (Figure 95), *Thymoites* (Figure 96). (See also Levi and Levi, 1962, for his illustrations of *Comaroma* (fig. 294), *Craspedisia* (fig. 280), *Crustulina* (fig. 274), *Phoroncidia* (fig. 245), *Helvibis* (fig. 166), *Coscinidia* (fig. 149), *Dipoenura* (fig. 154), and *Coleosoma* (fig. 104).) The "radix" is absent in *Achaearanea* (Levi, 1955a). Like the "terminal apophysis" of nesticids, however, this tegular sclerite arises from the tegulum close to the conductor and is distinct from the embolus, just where one would expect a median apophysis to be. It does not contain the reservoir, and is usually some distance from the embolic division, neither basal to it nor part of it as is the true radix of the linyphiids and araneids. Probably the theridiid "radix" is actually either the conductor or the median apophysis (in a developmental sense).

The theridiid embolus generally arises from the distal, lateral portion of the tegulum, and inserts directly on the tegulum. It curves in a clockwise direction (left palp, ventral view): *Enoplognatha* (Figure 91), *Episinus* (Figure 78), *Thymoites* (Figure 96), *Spintharus* (Figure 80), *Theridion* (Figure 92), *Phoroncidia* (Figure 97), *Anelosimus* (Figure 94), *Helvidia* (Figure 99), *Steatoda* (Figure 98), but not some *Dipoena* (*D. abdita, D. daltoni*), *Theridula* (Levi, 1966, fig. 3), or *Achaearanea* (Levi, 1963a, figs. 43–49). This is the same as most uloborids, metines, and araneids. Complete distal hematodochae separating the embolus from the tegulum, as appear in linyphiids, nephilines, and araneids, are derived.

NESTICIDAE

Nesticidae is the sister taxon to Theridiidae (Coddington, 1986a, 1989), and, interestingly, Lehtinen and Saaristo (1980) found similar lobes on the tegulum of most nesticid genera (Figure 103). The homology of the nesticid tegular lobes with those in theridiids could be tested by finding the reservoir of the sperm duct in the lobes. Unfortunately, Heimer's (1982) diagram of nesticid palp function does not show the course of the reservoir. Nesticidae, as far as I know, do not exhibit the cymbial notches that form the other half of the functional complex that Levi (1961) described in Theridiidae. On the other hand, nesticids do have a basal paracymbium. In this respect, nesticids retain more plesiomorphic araneoid features than their sister taxon Theridiidae.

In Nesticidae, Lehtinen and Saaristo (1980:48) state that a sclerite, which they call a "terminal apophysis," arises close to the "conductor" or in some genera is fused to it. Ontogenetically and morphologically a terminal apophysis should be part of the embolic division (Figure 4), but the embolus of nesticids is a relatively simple sclerite (Figure 103). The nesticid "terminal apophysis" is the only other tegular sclerite besides the conductor and the embolus. Therefore, by ontogenetic and outgroup criteria, it seems simpler to suppose that it is the median apophysis. The remaining nesticid tegular lobe may be homologous to the theridiid tegular apophysis (Figure 103, TTA).

SYMPHYTOGNATHOIDS

The "symphytognathoid" families include Theridiosomatidae, Mysmenidae, Anapidae, and Symphytognathidae. Seven characters currently support their association.

Both theridiosomatids and mysmenids possess tiny denticles in the cheliceral fang furrow (character 35, state 1). One uloborid species and one nesticid are known to have small cheliceral denticles (Peters, 1982; Wiehle, 1963) but the states in these cases are probably convergent. Such denticles do occur in some anapids (N.I. Platnick and R.R. Forster, pers. comm.) but are absent in others and in all symphytognathids. The dentition in these groups is highly modified (character 35, state 2; Forster, 1959; Forster and Platnick, 1977; Platnick and Shadab, 1978a, b). By itself the character suggests that mysmenids are the sister group of theridiosomatids, but behavioral evidence suggests that mysmenids belong with anapids and symphytognathids. Consequently, the highly modified dentition of anapids and symphytognathids may be interpreted to be a further derivation of the state present in theridiosomatids and mysmenids. This interpretation can be refuted by ascertaining that the stem group of either Anapidae or Symphytognathidae had plesiomorphic cheliceral dentition, that is, two rows of simple teeth without denticles.

Both theridiosomatids and symphytognathoids (Anapidae, Mysmenidae, and Symphytognathidae) have acutely prolonged median claws on at least their fourth legs (character 40, pers obs.).

All four families have a tendency towards reduced female palpi, whether expressed as the lack of the claw (character 52), or actual reduction of segments (character 51, state 1). All four families modify the hubs of their webs in a unique way at the end of web construction, and have a tendency to leave primary radii (Coddington, 1986a:355-357) in the web so that the resultant orbs are three dimensional (characters 66, 76; Eberhard, 1981; Coddington, 1986a, figs. 12.15-12.18).

Plesiomorphic theridiosomatid genera such as *Ogulnius, Plato, Naatlo, Epeirotypus,* and the anapids *Anapis, Anapisona,* and the mysmenids *Mysmena* and *Maymena* retain their eggsacs at the hub of their webs and attach them by both ends of the eggsac (character 84). As far as I know, no one has ever seen a symphytognathid eggsac in the field. No other araneoids behave in the same way.

Finally, theridiosomatids and at least some symphytognathoid taxa all have a switchback in the course of the sperm duct reservoir just after it initially leaves the fundus (Figure 106; Table 1, character 8; Coddington, 1986c, figs. 62, 96, 147, 176).

All metid, tetragnathid, theridiosomatid, and symphytognathoid taxa use a forward tap of the inside first leg to locate the innermost loop of sticky spiral during web construction (character 78, state 1). Deinopids, uloborids, and araneids use a lateral tap of the outside first leg (Eberhard, 1982; Coddington, 1986a:345, 346). Nephilines use an outside fourth leg, hence they are autapomorphic, although Figure 108 suggests that the nephiline condition is derived from an inside first leg forward tap (Eberhard, 1982).

Primitive theridiosomatid genera seem to retain all the basic araneoid sclerites (i.e., conductor, median apophysis, and embolus, Figures 104, 105). The derived taxa, such as the subfamily Theridiosomatinae (Coddington, 1986c), show much modified conductors and emboli with various elaborate apophyses, but the conformation of the palp is unchanged.

The remaining symphytognathoid taxa show much more derived palps. Mysmenids, for example, always seem to have a characteristic "kink" in the reservoir (Figure 106). Emboli are often long, and many genera have lost one of the tegular apophyses. The cymbium is uniquely modified. The homology of the remaining tegular apophysis is uncertain, and indeed so little careful work has been done on these tiny araneoids that even hypothesizing homologues would be mere guesses. Anapidae and Symphytognathidae apparently have much less complex palps (Forster and Platnick, 1977), but one is forced to hypothesize secondary reduction in these cases.

OTHER "ARANEOID" TAXA

One of the greater issues in araneoid phylogeny at the moment concerns the inclusion or exclusion of Mimetidae in the superfamily. Their palp structure (Figures 101, 102), although complex, is basically an elaboration on the araneocladan ground plan and is not obviously homologous to that of any araneoid group. Shear (1981) identified the terminal element of the mimetid palp as a "terminal apophysis," and implied homology with the araneid terminal apophysis. I feel another interpretation is plausible (Figure 101), mostly because Shear's analysis does not account for the median apophysis, which is otherwise a fairly conservative araneomorph feature. Basically mimetid palpi, like those of most araneomorphs, have three tegular sclerites: the embolus, the mimetid "terminal apophysis," and the conductor. However, the mimetid "terminal apophysis," unlike that of araneids, inserts via an hematodocha directly on the tegulum, not on the embolic division (Shear, 1981, fig. 12). In araneines, the terminal apophysis is at least part of the embolic division. Thus one can also view the mimetid "terminal apophysis" as the modified second araneocladan tegular sclerite, the median apophysis (Figure 101). Insertion of the median apophysis on the tegulum via a flexible connection fulfills the classical definition of the median apophysis. The other tegular sclerite remains the conductor, as Shear (1981, fig. 8) pointed out. Under this interpretation, mimetids are derived araneocladans, but not necessarily derived araneoids. One of their tegular apophyses is more or less normal, but the other is elaborated, with hematodochae and sometimes a bipartite nature.

The single, stark, unarguable feature that mimetids share with Araneoidea is the paracymbium. At present, this character is over-ruled by the two synapomorphies suggested by Forster

and Platnick (1984:99–104) to place them in the Palpimanoidea, and the overall evidence is at best equivocal. Thus, despite the many "gestalt" similarities between mimetids and araneoids, I know of no hard evidence that convincingly refutes their placement among palpimanoids by Forster and Platnick, 1984:99–104).

Cyatholipidae is another group whose placement is uncertain. Like mimetids, cyatholipids have a prominent paracymbium (not shown in Figure 107), which therefore suggests that they are araneoids. Moreover, their lateral eyes are juxtaposed, their labium is broader than long, and they also have true serrate hairs. For Cyatholipidae to have gained independently each of these features, otherwise synapomorphic for araneoids, seems rather unlikely. However, at least one cyatholipid appears to lack flagelliform and aggregate gland spigots on their posterior lateral spinnerets (pers. obs.), and none are known to spin orb webs.

The one obvious place where at least some of the above characters occur is among palpimanoids, and, as I have said before (Coddington, 1986c:13), that may justify submerging all of Palpimanoidea within Araneoidea. At present we lack a critical estimate of the amount of homoplasy with other superfamilies within Araneoclada that such an hypothesis would entail.

Thus the best estimate is that cyatholipids are indeed araneoids. Griswold (1987) provided a good introduction to the group, but he did not place them more specifically than Araneomorphae. Wunderlich (1978a) placed them provisionally in Tetragnathidae, presumably because of palp structure and the advanced tracheal spiracle, but that theory has little in its favor (Coddington, 1986c:6).

An equally good case can be made to place Cyatholipidae as a derived group of linyphiids on the basis of three characters. The web form is an obvious, possibly synapomorphic similarity, and the tracheal system (Davies, 1978; Griswold, 1987) is not far from the *Tennesseellum-Microneta* pattern documented by Millidge (1986). The web sheet may be stretched and anchored ventrally by sparse, more or less vertical lines (Davies, 1978, fig. 16), which is characteristic of linyphiid webs and occurs in no other spider webs known to me. Also, a transverse duct links the widely spaced spiracles with their finely branched tracheal bundles in cyatholipids (Griswold, 1987). The same arrangement occurs in *Tennesseellum, Microneta,* and *Agyneta,* but a similar morphology is also characteristic of many erigonines (Blest, 1976; Millidge, 1986). Such an arrangement is only sporadically found, for example, in symphytognathoids (Forster, 1959:321–328), the other araneoid group that includes small spiders with modified respiratory systems. In these groups the anterior book lungs are often modified as well, but they are more or less normal in linyphiids and cyatholipids. The third feature is that the cyatholipid paracymbium, like many linyphiid paracymbia, consists of two processes; however, bifid paracymbia are also present in mimetids and nesticids. My impression is that the

evolution of the "paracymbium" is homoplasious and that close study will be required to detect homologous conditions.

On the other hand, cyatholipids differ in many respects from any known group of linyphiids. Cyatholipids show no trace of a suprategulum, although that characteristic structure is reduced in many erigonines (Millidge, 1977). Cyatholipid palps are rather simple, but then erigonine palps can be very simple also. As far as I know, no linyphiids ever have a complex reservoir trajectory, as occurs in *Teemenaarus* (Figure 107). The latter character might suggest possible placement within the metine-tetragnathine-nephiline lineage or, again, with the symphytognathoids. The parembolic apophysis (Figure 107, PA) of cyatholipids is clearly unique to a portion of the family. Likewise, the single, central tegular apophysis (Figure 107, CTA) is unlike anything else in araneoids, although it is superficially similar to that in Deinopidae, and somewhat less similar to that in Tetragnathidae. The former similarity is almost certainly convergent, and because (as far as I am aware) the cyatholipid apophysis does not spiral with the embolus, the condition is also different from tetragnathids. The placement of cyatholipids within araneoids remains moot, and, consequently, I have omitted them from the cladogram in Figure 108.

Alternative Cladograms for Orbiculariae

Wunderlich (1987:97, 99) recently proposed a cladogram to resolve the placement of Araneoidea within Araneoclada, and four alternative cladograms for Araneoidea. The first puts (Araneoidea, Uloboroidea) as the sister to Nicodamidae, and that triplet as sister to the triplet ((Palpimanoidea, Archaeoidea), Eresidae). The lineage including those six families is then linked to (Salticidae, Clubionidae, Zodariidae). His Uloboroidea is the same as Deinopoidea, but the latter name has priority (Koch, 1851). Likewise, Wunderlich's (Palpimanoidea, Archaeoidea) includes the same taxa as Forster and Platnick's (1984) Palpimanoidea (excepting Mimetidae), and for the sake of simplicity, I will use Palpimanoidea in the latter sense when discussing Wunderlich's hypotheses. Wunderlich offered no characters to support the sister relationship of Nicodamidae with Orbiculariae, and thus one cannot really discuss that suggestion.

These points made, Wunderlich's first hypothesis reduces to ((((Orbiculariae, (Palpimanoidea, Eresidae)), (Salticidae, Clubionidae, Zodariidae)). His linkage of Palpimanoidea and Eresidae is outside the subject of this paper, but Wunderlich links this inclusive group to Orbiculariae on the basis of a single metatarsal trichobothrium. As already noted (see "Cribellate Phylogeny") and in Figure 3, that character is apparently primitive for Araneomorphae. Wunderlich (1987:99) supports the grouping of all of these lineages with various characters: a canoe tapetum, the absence of male palpal tibial apophyses, a "space-web," tarsi without trichobothria and metatarsi with many trichobothria. However, all characters except the last, by outgroup comparison to the hypochilid and

austrochiloid families, are primitive for Araneomorphae. The last character would seem to define a lineage including Forster's Amaurobioidea (Forster et al., 1987), the lycosoid families, Oecobiidae, and Eresidae. Wunderlich (1987) ignores the divided cribellum in Eresidae, and thus presumably would derive it independently of other cribellate taxa. His diagram also calls for the loss of the cribellum at least three times, which seems unnecessary.

Within Araneoidea, Wunderlich's (1987:100) first alternative is the group (((Theridiosomatidae, (Araneidae-Tetragnathidae)), Anapidae sensu lato)) supported by the character "orb web," and that group as sister to the remaining araneoids that lack the orb web. This argument ignores the substantial homologies between the araneoid and deinopoid orb webs, which argue that his first group is symplesiomorphic. Wunderlich defines the non-orb-weaving araneoids by possession of a basal paracymbium and entelegyny. This argument also seems weak, because theridiosomatids, araneids, and tetragnathids also have a paracymbium, and they are also entelegyne, excepting a few secondary haplogynes (Table 1, character 24). Wunderlich's first alternative thus suffers from serious homoplasy in characters that he mentions, and also from lack of outgroup comparison. Using the data from Figure 108, and under the assumption of complete reversibility of character states (Fitch optimization), Wunderlich's proposed tree is eleven steps longer than Figure 108.

His second alternative (Wunderlich, 1987:101) for araneoid relations links Araneidae, Tetragnathidae, Theridiosomatidae, and Anapidae (as an unresolved group), with the Deinopoidea, on the basis of the orb web. This larger group is then linked to Linyphiidae, Nesticidae, Cyatholipidae, and Acrometidae, with Linyphiidae as sister to the latter three families. Besides sidestepping the issue of the orb web (as explained in the first alternative), this hypothesis also suggests either that the rather large set of impressively specialized characters that define Araneoidea (Coddington, 1986a) evolved twice, or Deinopoidea evolved all the neocribellate plesiomorphies in parallel. Either hypothesis imposes massive homoplasy on the data in Figure 108, and Wunderlich's second alternative is fifteen steps longer than Figure 108.

His third alternative (Wunderlich, 1987:102) is closest to the one presented in Figure 108, in that it recognizes the monophyly of Araneoidea and the sister group relationship between Araneoidea and Deinopoidea. Within Araneoidea, Wunderlich recognizes the group ((Anapidae, sensu lato), Theridiosomatidae), Theridiidae). His "Anapidae" plus Theridiosomatidae is essentially the same as the symphytognathoid families in Figure 108, and Wunderlich followed Eberhard (1982, 1986) and Coddington (1986a) in basing the group on specialized web construction behavior. Theridiidae, however, are then united by Wunderlich (1987:102) to that group by a "plate-shaped and elongated male palpal tibia." Linked to that entire group is ((Tetragnathidae, Araneidae), (Mimetidae, Malkaridae, Linyphiidae, Nesticidae,

Cyatholipidae, Acrometidae)), by the possession of a basal paracymbium. I have no evidence to contest the placement of Theridiidae, but I do not understand the "plate-shaped, elongated male palpal tibia" character sufficiently to agree that it decisively defines a lineage apart from other closely related araneoids, such as tetragnathines, metines, or araneids. Wunderlich's arrangement also ignores the substantial number of synapomorphies that link Nesticidae and Theridiidae (Coddington, 1986a, 1989). Using the same data from Figure 108, Wunderlich's third alternative is nine steps longer than Figure 108.

Wunderlich's (1987:103) fourth alternative emphasizes the placement of families not really discussed here (such as Mimetidae, Malkaridae, and Cyatholipidae), but it also places Anapidae as the sister group to the rest of the araneoids. This ignores the various characters that place Anapidae with the symphytognathoids, and also makes the various primitive characters of araneids (low clypeus, outside first leg lateral tap to locate next line during sticky spiral construction, silk wrap attack, various spinneret characters) homoplasious. Using the same data from Figure 108, this fourth alternative is also fifteen steps longer than Figure 108.

Although presenting alternative, equally parsimonious cladograms is a good idea, the five cladograms suggested by Wunderlich have rather little in common. A consensus tree of all five is, at best, a nine-way polychotomy. The only associations consistently supported by Wunderlich and also discussed here are Uloboridae-Deinopidae, and Araneidae-Tetragnathidae. I agree with the former, but the only feature that Wunderlich (1987:102) advances to support the association of Araneidae and Tetragnathidae is a low clypeus. That feature is primitive if anything remotely similar to the outgroup structure suggested by Figures 2, 3, and 108 is correct.

Wunderlich's third alternative does offer evidence to place Theridiidae, but at the cost of denying the family's relationship to Nesticidae. His suggestions generally conflict with each other. Because of the absence of explicit data presentation and analysis (e.g., a data matrix and consistency indices), one cannot easily decide which of his trees is better supported than the others. At the level of characters, one cannot easily decide which transformational hypotheses show least homoplasy across all of the trees he presents. Wunderlich's various suggestions seem as yet unrefined, and they lack formal justification, critical comparison, and analysis. Because Figure 108 quantitatively assesses most of the same evidence treated by Wunderlich, and some that he omitted, it offers some resolution to the various conflicting araneoid cladograms proposed by Wunderlich.

The remaining serious attempt at an araneoid phylogeny is that of Heimer and Nentwig (1982). Their arguments are outdated by now, partly because many of their assumptions, which they thought too obvious to require justification, have been shown to be either incorrect or at least questionable. A partial list includes the following: (1) *Wendilgarda* is a

mysmenid (verified as a theridiosomatid by Coddington, 1986c); (2) cyatholipids are theridiosomatids (rejected by Coddington, 1986c); (3) mimetids and archaeids are obviously araneoids (transferred to Palpimanoidea by Forster and Platnick, 1984); (4) mysmenids do not spin orb webs (orbs documented by Eberhard, 1986; Coddington, 1986a); (5) orb weavers are obviously not monophyletic, and thus neither deinopids nor uloborids are potential outgroups for Araneoidea (questioned in various ways and at various levels by Opell, 1979; Brignoli, 1979; Levi, 1980a; and Coddington, 1982, 1986a).

Even if these faulty assumptions are set aside, many of the characters Heimer and Nentwig (1982) listed as "synapomorphies" for araneoid subgroups are also questionable. Their character 1 ("upper part of tubuliform burrow built as a sheet") is, as near as I can tell, present in many non-araneoid spider families (Psechridae, Austrochilidae, Hypochilidae, Gradungulidae, Eresidae, Tengellidae, Amaurobiidae, Neolanidae, etc.). Without more precise description, it cannot be used as a synapomorphy for Araneoidea. Their character 4 ("catching area under the resident part of the web"), with which they ally Mysmenidae to Theridiidae-Nesticidae, is also factually incorrect, as far as I know. No mysmenid known to spin a web ever puts the sticky silk beneath the "resident part," if I understand their usage of these terms. The "gum-foot lines" architecture may work as an additional synapomorphy for Theridiidae-Nesticidae, but we do not yet know that the web-building behavior in these two families is plausibly homologous, and thus this architectural feature, which is a further step removed, could be only a superficial similarity. Their character 8 ("dorsal and lateral paracymbium are functioning together"), which they use to unite metine-tetragnathines with linyphiids, remains obscure to me, because I do not understand what is meant by a dorsal paracymbium. Biramous paracymbia occur sporadically among metines, linyphiines, and mimetids, but the distribution of the trait scarcely justifies the claim that it is plesiomorphic for all araneoids. Instead, the "ventral" paracymbium is more generally distributed among taxa thought to be primitive on other grounds, which would imply that it is the primitive state. Also biramous paracymbia are not universal either in metines, mimetids, or linyphiids. The biramous condition could well be derived within each of these groups, not primitive to all of them. Heimer's and Nentwig's character 10 ("catching area with radial-symmetric structure, radii and spiral threads are connected by material from glandulae piriformes"), which they use to ally cyrtophorines with *Nephila* and "other araneids," seems true of every other orb-weaving group. Cementing thread junctions with piriform silk is probably primitive for all araneomorph spiders (Kovoor, 1987). They offer no evidence for the inclusion of cyatholipids in Theridiosomatidae, and I know of none that support such a placement. Their character 11 ("chelicerae with spines or lobi, no teeth"), which they use to unite symphytognathids and anapids with mimetids and archaeids, has been discussed in some detail by Forster and

Platnick (1984:99–104), and there is no credible similarity between the cheliceral armature of these two groups.

I agree with Heimer and Nentwig (1982) on the linkage of theridiids and nesticids, of symphytognathids and anapids, and of metines and tetragnathines, although they often based their own conclusions on evidence I regard as plesiomorphies (such as the parallel acquisition of orb webs in the latter two groups). Indeed, they hypothesize that the orb architecture evolved six times within Araneoidea, and presumably once or twice in Deinopoidea, for a total of seven or eight times among spiders.

Despite the differences expressed here with the conclusions of Heimer and Nentwig (1982), their cladogram and arguments are fairly explicit, and so one can comment cogently on their ideas. The promulgation of alternative, competing hypotheses accompanied by detailed justification about araneoid phylogeny is to be encouraged, because it focuses debate, guides current research, and, one hopes, ultimately provides a fast route to the right answer.

Conclusions

On the whole, the habitual use of Comstock's terms (Comstock, 1910) for palpal sclerites in diverse families has impeded the recognition of monophyletic taxa. On the other hand sclerite patterns within taxa are often so consistent that homology is obvious.

One major result emphasized by this review is that araneoid taxa, like many other groups of organisms, are mosaics of primitive and derived characters. Thus the raging debate over which taxa are "most primitive" among araneoids is rather futile unless one specifies the character system under discussion, and one's notions of outgroups. On various occasions Levi has argued that metine palps may be primitive. Insofar as they have a relatively simple embolic division, the results of this review do not contradict that. Their lack of a true median apophysis, however, seems derived, not primitive. On the other hand, Coddington (1986a:360) argued that by outgroup comparison metines were derived in how they located the next attachment point during sticky spiral construction. Eberhard (1982) used inferred adaptive value to argue that the same trait was primitive. The early splitting of lineages in Figure 108 suggests instead that no known araneoid is an especially apt model for the araneoid stem lineage, and in particular that modern metines are probably substantially different from the earliest araneoid ancestors. They could well have primitive palps and derived behavior.

This review also documents how different the palpal sclerites of araneomorph families really are. The evidence seems to suggest that possession of three tegular sclerites is primitive for the infraorder. However, although that hypothesis is not refuted by other discordant characters, the pattern is very inconsistent from group to group, and thus even that mild generalization can be only weakly supported. Especially in the case of specialized sclerites (e.g., the oecobiid, eresid, dictynid, or cyatholipid

tegular apophyses), simplistic hypotheses of homology with sclerites in other families at this point do more to obscure the pattern than reveal it.

This lack of clear homology is also true of structures that seem ubiquitous, but that may be closely linked ontogenetically such as the median apophysis and conductor. If non-embolic tegular sclerites differ in position and shape, identifying conductors and median apophyses can be very difficult (e.g., mimetids, see "Other 'Araneoid' Taxa"). Another good example of this kind of problem is the orbicularian tegular apophyses or lobes (emboli excepted). Deinopids have one, some uloborids have two, and araneoids have anywhere from one to three. Homology of the apical tegular apophysis in deinopids and uloborids is relatively clear by positional and morphological criteria, but it has no obvious homologue in araneoids. If it has a homologue, positional criteria suggest that it is a conductor, but anatomical criteria might suggest that it is a median apophysis. Because concordance criteria do not dispute that, it seems advisable to call the deinopoid sclerite the conductor, but the assignation is only weakly supported. In truth, the question is not only hard to settle with current knowledge, but there is no reasonable prospect that future research will make it more clear.

From the point of view of stability of sclerite nomenclature, perhaps the most depressing result is the low consistency of the median apophysis in Figure 108 (character 9; CI = 0.12). Although in four out of five possible resolutions of the polychotomy in Figure 108 it remains most parsimonious to presume that the median apophysis was primitively present in the stem lineage of the orb weavers, one must still accept eight separate losses of the sclerite in different orbicularian groups. The only resolution in which convergent evolution of a "median apophysis" in Araneoidea is indicated has theridiid-nesticids as sister to the araneid-linyphiid lineage. However, how much confidence can one have in any character that shows so much homoplasy? Palp morphology, when judged in the light of all available information, apparently evolves more rapidly (and thus becomes more homoplasious) than somatic characters (Eberhard, 1985). The mean consistency of male genitalic characters in Table 1 is 0.77, but the mean consistency of the remaining characters is 0.89. Put another way, 48% of the male genitalic characters show homoplasy, but only 31% of the remaining characters show homoplasy. The bad news is that homologizing sclerites between families remains a frustrating, eternally unconvincing business. The good news is that the monophyly argument for many of those families is thereby strengthened.

This review begins to bring the Araneoidea—long regarded as spiders with intractably complex palpi—into an intelligible relationship with what appear to be their outgroups with simpler palpi. The Araneoidea as a group have a basic palp conformation, which can be homologized with their sister taxon Deinopoidea and potential orbicularian outgroups (Dictynoidea or Amaurobioidea, Figure 3).

A very conservative definition of a sclerite that has also been adopted and has caused much confusion is the "radix". This analysis suggests that a true radix occurs only in Linyphiidae and Araneidae and is actually absent in the other orbicularian taxa where it has been previously identified (Uloboridae and Theridiidae). Criteria of concordance (Figure 108) suggest that those sclerites mistakenly identified as median apophyses in Theridiidae and as radices in Uloboridae are autapomorphic, thus aligning the group they diagnose with the empirical distribution of each trait. In the Theridiidae the novelty is an outgrowth of the tegular wall that in many genera engages a cymbial notch to perform an apomorphic function. Whether any theridiid genera lack the trait is uncertain at this point, because the available illustrations do not include the critical information. If some genera do lack it, the analysis of the feature remains valid at a lower level of generality unless some other, more parsimonious, hypothesis of relationships among theridiid genera is proposed; no such hypothesis using shared derived characters is extant. In the Uloboridae the mesal apophysis of the embolus identified as a radix is apomorphic within the family.

The monophyly of Araneidae is becoming increasingly easier to justify as various less-related groups are removed. Derived araneids have a rather invariant conformation of the embolic division, which can be described as follows: the embolic division is separated from the tegulum by a stalk. The radix is the most proximal sclerite, a tubular or nearly tubular element through which the ejaculatory duct passes. The sclerite articulates either to the stipes, which seems to be simply either a subdivision of the radix or the enlarged base of the embolus, or directly to the embolus itself, in which case no stipes is present. The embolus bears a distal hematodocha, which is surmounted by a terminal apophysis. The conductor of the palp is variously shaped and situated, but almost always present. The median apophysis is nearly always on the mesal wall of the tegulum. Levi (1983b, 1985) has emphasized several other informative features. For example, many araneids have a peculiar locking mechanism on the first femora. This feature also substantiates the monophyly of a relimited Araneidae, although it apparently excludes the argiopids.

The remaining araneoid taxa are the theridiosomatids, anapids, mysmenids, and symphytognathids. These taxa have not received much mention in this discussion because they have been discussed elsewhere in their role as the sister taxon of theridiosomatids (Coddington, 1986c). In view of the outgroup and ontogenetic criteria outlined above, theridiosomatids are autapomorphic in having a sperm duct with its own consistently and uniquely complex trajectory, a consistent palpal conformation that is derived in having a tegulum much enlarged on the lateral margin and split on the mesal margin, a conductor that is hood-shaped and covers the embolus, a median apophysis located without exception at the end of the tegular split, juxtaposed to the conductor, and an embolus that curves in a counterclockwise direction (left palp, ventral view).

The group is perhaps especially interesting because unlike the araneoid taxa discussed previously (see Contents), the plesiomorphic sclerites are all still present, and in an orientation not markedly different from Deinopoidea, although their shapes are distinctively and consistently modified (Figures 104, 105). Because numerous characters support the position of the theridiosomatids as the basal group among the "symphytognathoid" taxa, the palp structure of the remaining symphytognathoid families may be interpreted as primarily a reduction series from the original araneoid ground plan (Figure 106).

Results of this review are summarized in the cladogram in Figure 108. The data from behavior, silk chemistry, and silk glands included in the analysis are discussed at greater length in Coddington (1986a, b). The theridiid-nesticid lineage (including hadrotarsids), although highly corroborated as a monophyletic group (characters 16, 39, 48, 79), still shows no characters that link it unambiguously to any single araneoid lineage. Consequently, the theridiid-nesticid lineage is placed on the cladogram at the lowest certain node, i.e., Araneoidea. With equal validity it may be placed as sister to the metine-nephilines, the symphytognathoids, the latter two together, or to the araneid-linyphiids. This is a total of five possible placements for this lineage. However, in every case, no unambiguous synapomorphies support its placement. Therefore, the ambiguity in Figure 108 is not due to equally parsimonious and fully resolved trees that are incompatible. Rather, the ambiguity is due to an appalling lack of character data that unambiguously links the theridiid-nesticid lineage to any other araneoid lineage. Thus, while theridiid-nesticids might well be the sister taxon to the symphytognathoids (my personal favorite), the node subtending such a lineage still has no characters to support it.

The character mappings reported in Figure 108 are those accurate for the placement of the theridiid-nesticids as sister to the remaining araneoids. The only palpal features whose mapping changes under the different resolutions of Figure 108 are the median apophysis, and the transformations among the various states coded for the paracymbium. Even among those changes, I have not been able to locate truly inconsilient mappings. The different mappings instead result from particular transformations switching from ambiguous mappings to unambiguous mappings and back again. Insofar as under one resolution a particular transformation becomes unambiguous, whereas under another it is ambiguous, the mappings are different, but the differences are not practically important.

Figure 108 is a more informative cladogram than that of Coddington (1986a, fig. 12.26) because it better resolves the relationships between araneids, tetragnathines, metines, nephilines, and linyphiids. The increase in resolution also allows more confident interpretation of otherwise homoplasious characters. For example, the many characters uniting theridiosomatids with symphytognathoids implies that the simplest interpretation of the absence of a median apophysis in the latter groups is loss rather than parallel gain in theridiosomatids. New information also rearranges the symphytognathoids so that symphytognathids now appear to be the sister group of anapids rather than mysmenids. The evidence, however, is evenly balanced and any of the possible sister relationships among these three taxa might be expected. Cyatholipids may also be araneoids (Wunderlich, 1978a), but no comprehensive anatomical work has been done; thus it does no good to include cyatholipids in this analysis.

It seems that the overall effect of this review has been to corroborate the monophyly of various taxa more fully, and to partition Araneoidea into a few large groups whose interrelationships are poorly established: symphytognathoids, araneid-linyphiids, theridiid-nesticids, and the metine-tetragnathine-nephilines. If the phylogenetic diagram can be trusted, theridiids can only be placed at one of five places. Further work is required to discriminate among those five, as well as to test the conclusions reached here.

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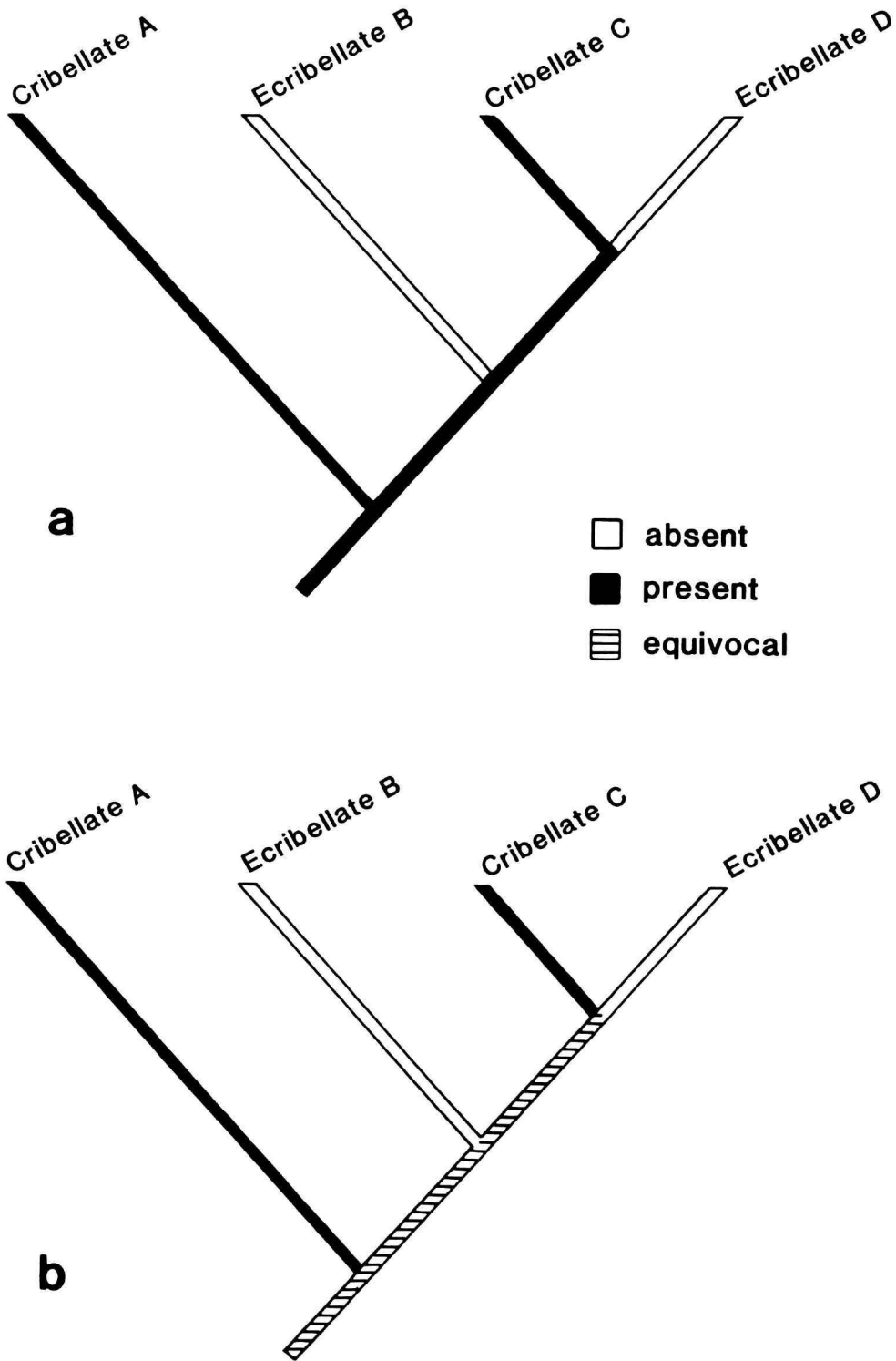
FIGURE 1.—Evolution of cribellum under assumption of irreversible loss (*a*) versus reversible change (*b*). Although hypothesis in *a* is more likely, no such cladogram has been proposed for any spider group. Hypothesis in *b*, with a different rooting, was proposed to place Filistatidae by Lehtinen (1986).

1. Gut: straight (vs. M-shaped)
2. Heart ostia: 2 or 3 (vs. more)
3. Cheliceral concavities present
4. Gut diverticulae cheliceral (vs. carapace)
5. Female bursa extension present
6. Bothrium base: crenulate (vs. notched)
7. Bothrium base: notched (vs. entire)
8. Clypeus ant. extension present
9. Serrula: single row (vs. many)
10. Dilator muscle from carapace (vs. rostrum)
11. Venom glands endocephalic (vs. cheliceral)
12. Paracribellum present
13. Ridged cuticle (vs. smooth)
14. Endosternite extensions lost
15. 5th endost. invagination lost
16. Maxillary glands clumped (vs. one row)
17. Chelicerae diaxial (vs. paraxial)
18. Single coxal gland (vs. 2 convoluted)
19. Ant. med. spinnerets as cribellum
20. Calamistrum present
21. Spinneret segments 1 to 2 (vs. more)
22. 17 suboesophageal neuromeres (vs. 12)
23. 1st abdominal sternite lost
24. Spinnerets posterior
25. 3 or 4 lateral spinneret segments (vs. more)
26. Spinnerets present
27. Modified pedipalps
28. Chelicerae with venom glands

Amblypygi · Liphistiomorphae · Mygalomorphae · Hypochilidae · Gradungulidae · Austrochilidae · Araneoclada

Neocribellatae
Araneomorphae
Opisthothelae
Araneae

FIGURE 2.—Cladogram of higher groups of spiders. Autapomorphies included only for araneomorph groups. Data mostly from Forster et al. (1987), and sources cited therein. Characters 12 and 13 are new hypotheses. (□ absent; ■ present; ? unknown)
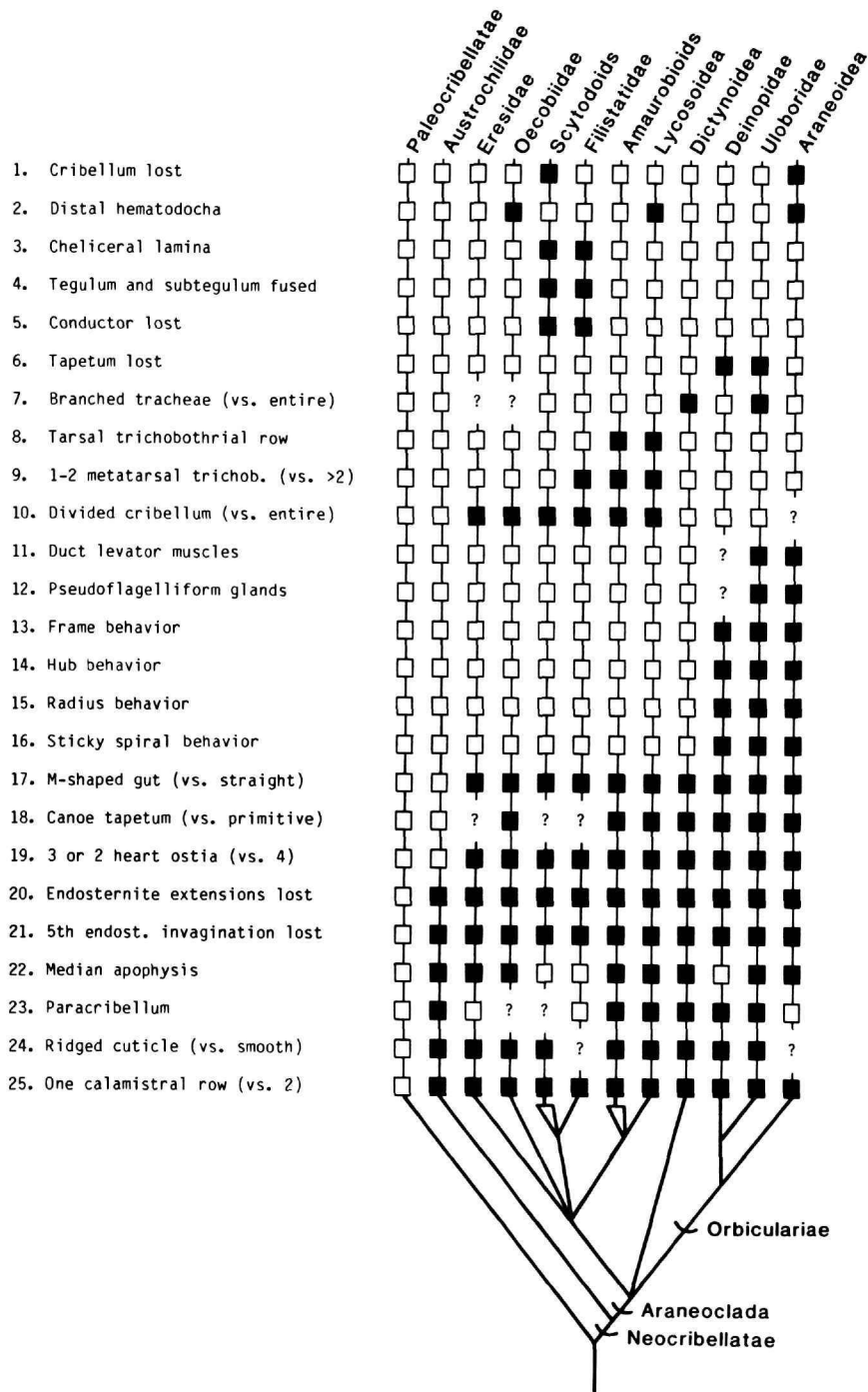
FIGURE 3.—Cladogram of cribellate Araneomorphae, emphasizing cribellate araneocladan subgroups. Sources for character data are given in text. Characters 13–16 represent the complex behaviors involved in orb-web construction, not merely the architectural features that result from the behaviors (Coddington, 1986a). See Figure 108 for other orbicularian synapomorphies. Austrochilidae represents Austrochiloidea. Amaurobioids and scytodoids are probably paraphyletic. Characters supporting Neocribellatae carried over from Figure 2. (□ absent; ■ present; ? unknown)
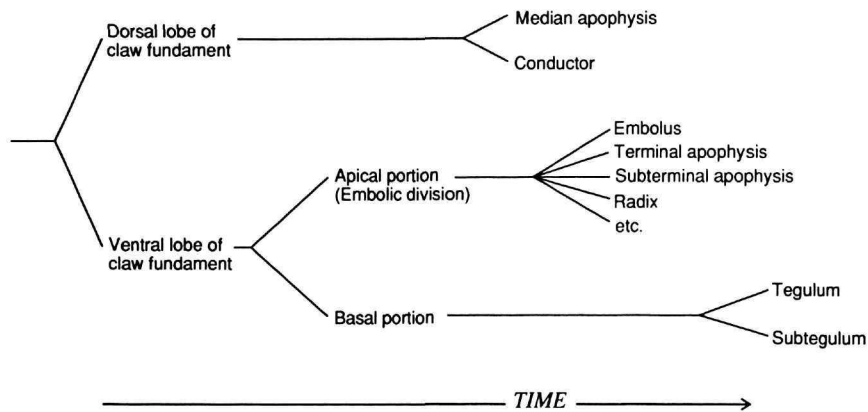
FIGURE 4.—Schematic of typical ontogeny of palpal sclerites. Synthesized from sources discussed in text.
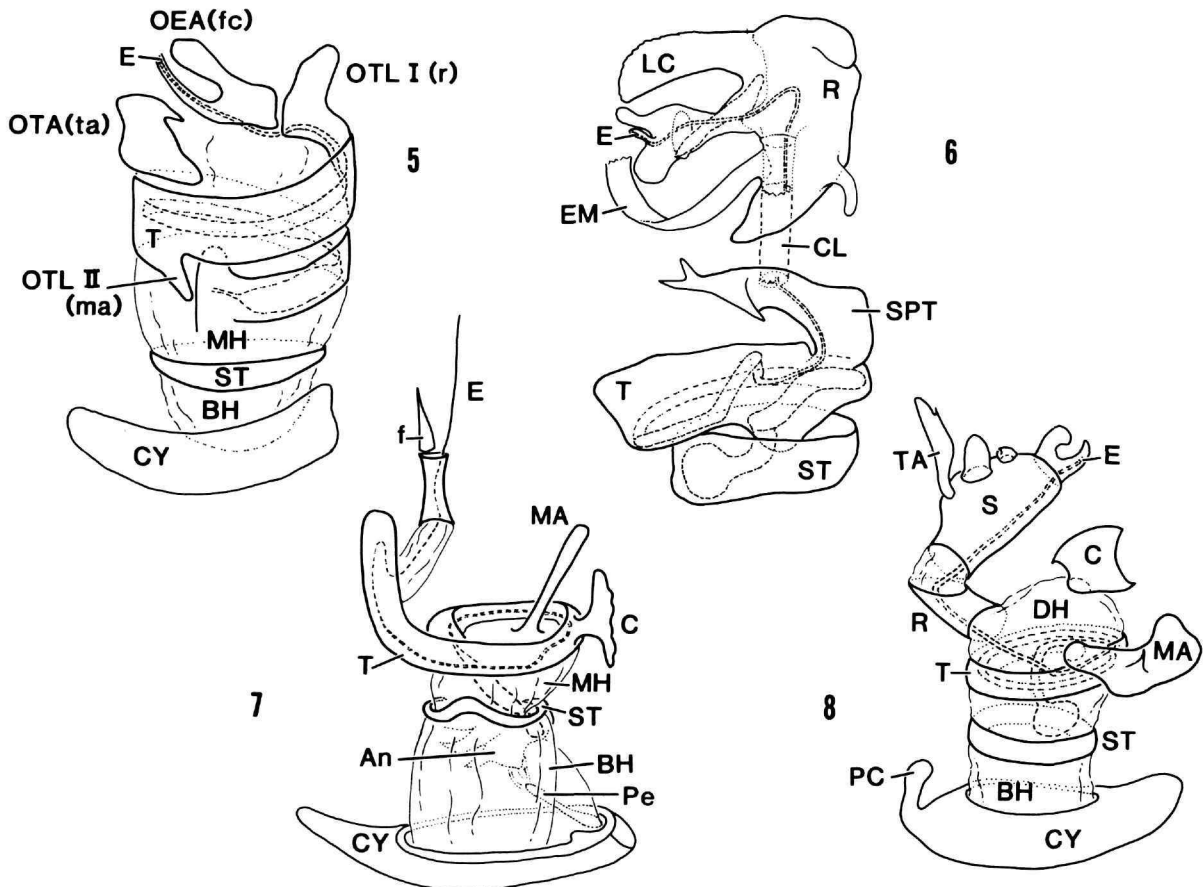
FIGURES 5–8.—Diagrammatic palp illustrations: 5, Oecobiidae, *Oecobius annulipes* (after Baum, 1972, fig. 62); 6, Linyphiidae, *Maro* schematic (ecribellate) (after Saaristo, 1971, fig. 1); 7, Pisauridae, generalized pisaurid palp (ecribellate) (after Sierwald, in press); 8, Araneidae, *Araneus diadematus* (ecribellate) (after Grasshoff, 1968, fig. 38).
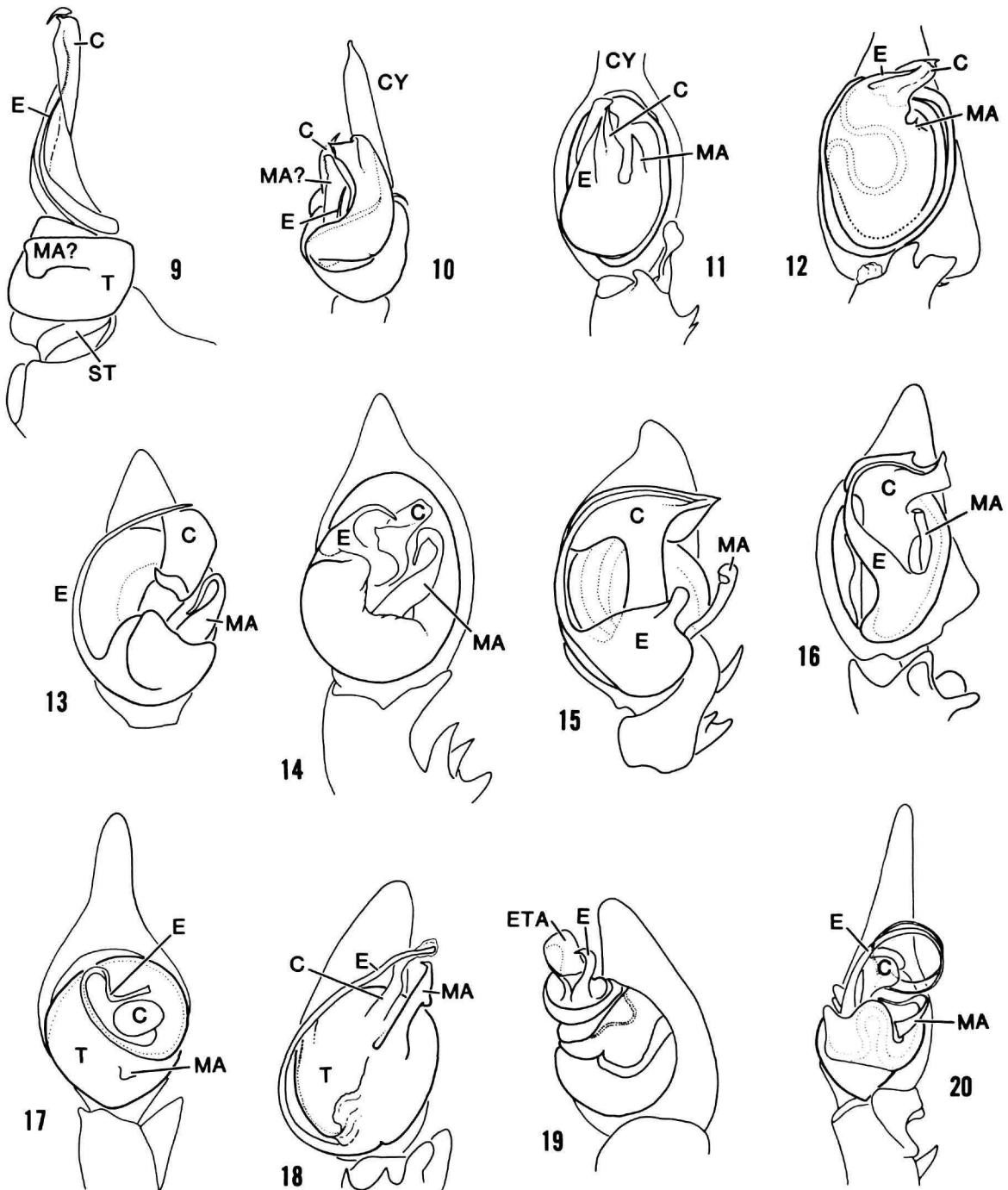
FIGURES 9–20.—Miscellaneous cribellate groups: 9, Hypochilidae, *Hypochilus coylei* (after Forster et al., 1987, fig. 49); 10, Austrochilidae, *Thaida peculiaris* (after Forster et al., 1987, fig. 156); 11, Stiphidiidae, *Cambridgea fasciata* (after Forster and Wilton, 1973, fig. 398); 12, Stiphidiidae, *Procambridgea cavernicola* (after Forster and Wilton, 1973, fig. 407); 13, Agelenidae, *Tararua puna* (after Forster and Wilton, 1973, fig. 231); 14, Agelenidae, *Neoramia margaretae* (after Forster and Wilton, 1973, fig. 364); 15, Agelenidae, *Mahura takahea* (ecribellate) (after Forster and Wilton, 1973, fig. 144); 16, Agelenidae, *Orepukia geophila* (ecribellate) (after Forster, 1970, fig. 90); 17, Neolanidae, *Neolana dalmasi* (after Forster and Wilton, 1973, fig. 956); 18, Psechridae, *Fecenia macilenta* (after Levi, 1982b, fig. 84); 19, Eresidae, *Magunia dumicola* (after Lehtinen, 1967, fig. 456); 20, Amphinectidae, *Amphinecta milina* (ecribellate) (after Forster and Wilton, 1973, fig. 480).
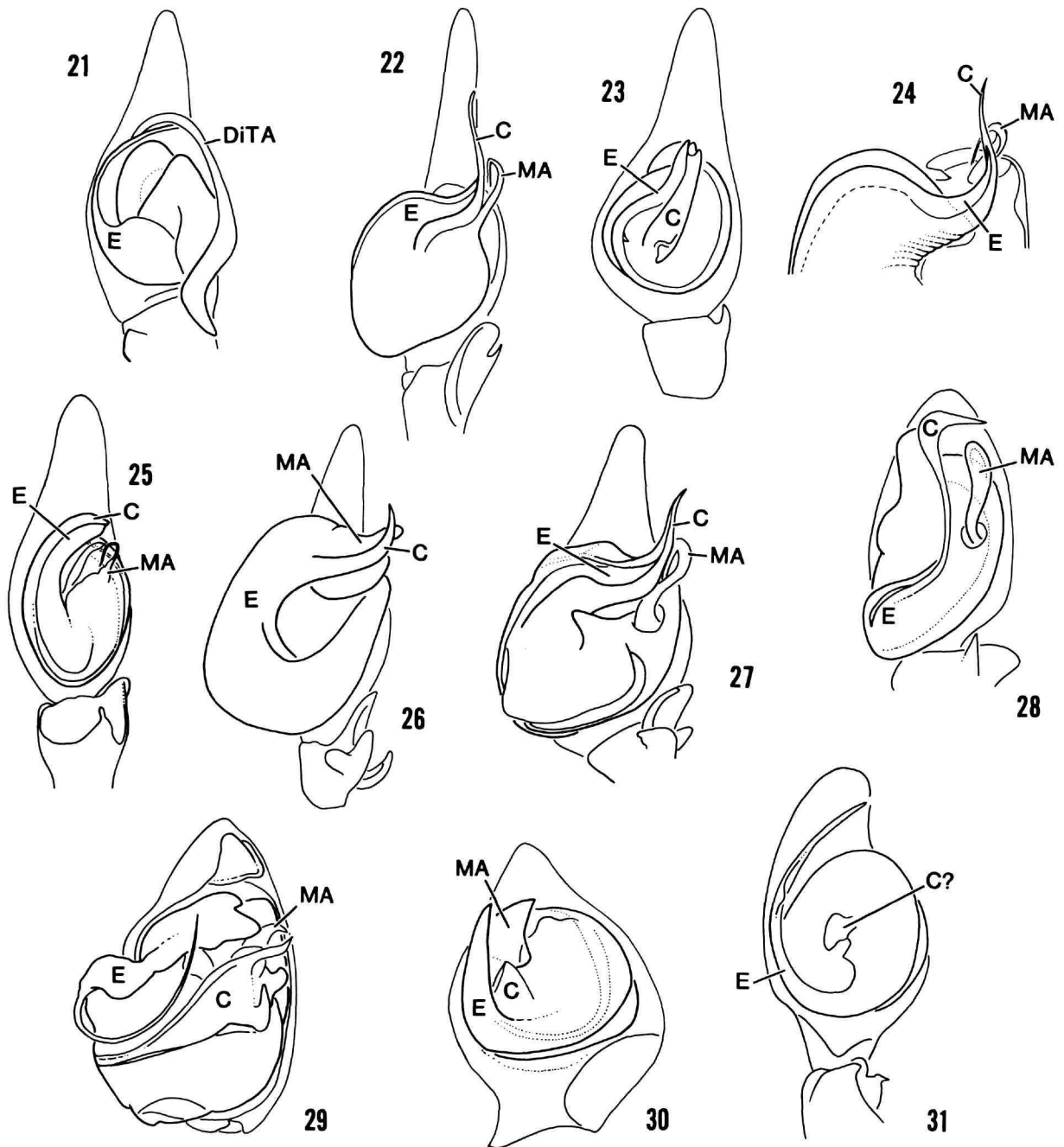
FIGURES 21–31.—Miscellaneous cribellate groups: 21, Dictynidae, *Paradictyna rufoflava* (after Forster, 1970, fig. 387); 22, Desidae, *Matachia marplesi* (after Forster, 1970, fig. 52); 23, Desidae, *Paramatachia tubicola* (after Forster, 1970, fig. 49); 24, Desidae, *Notomatachia hirsuta* (after Forster, 1970, fig. 66); 25, Desidae, *Desis marina* (ecribellate) (after Forster, 1970, fig. 38); 26, Desidae, *Goyenia electa* (ecribellate) (after Forster, 1970, fig. 99); 27, Desidae, *Tuakana wiltoni* (ecribellate) (after Forster, 1970, fig. 121); 28, Desidae, *Badumna robusta* (after Forster, 1970, fig. 147); 29, Anyphaenidae, *Amaurobioides maritimus* (ecribellate) (after Forster, 1970, fig. 475); 30, Nicodamidae, *Nicodamus bicolor* (ecribellate) (after Forster, 1970, fig. 510); 31, Megadictynidae, *Megadictyna thileniusi* (after Forster, 1970, fig. 525).
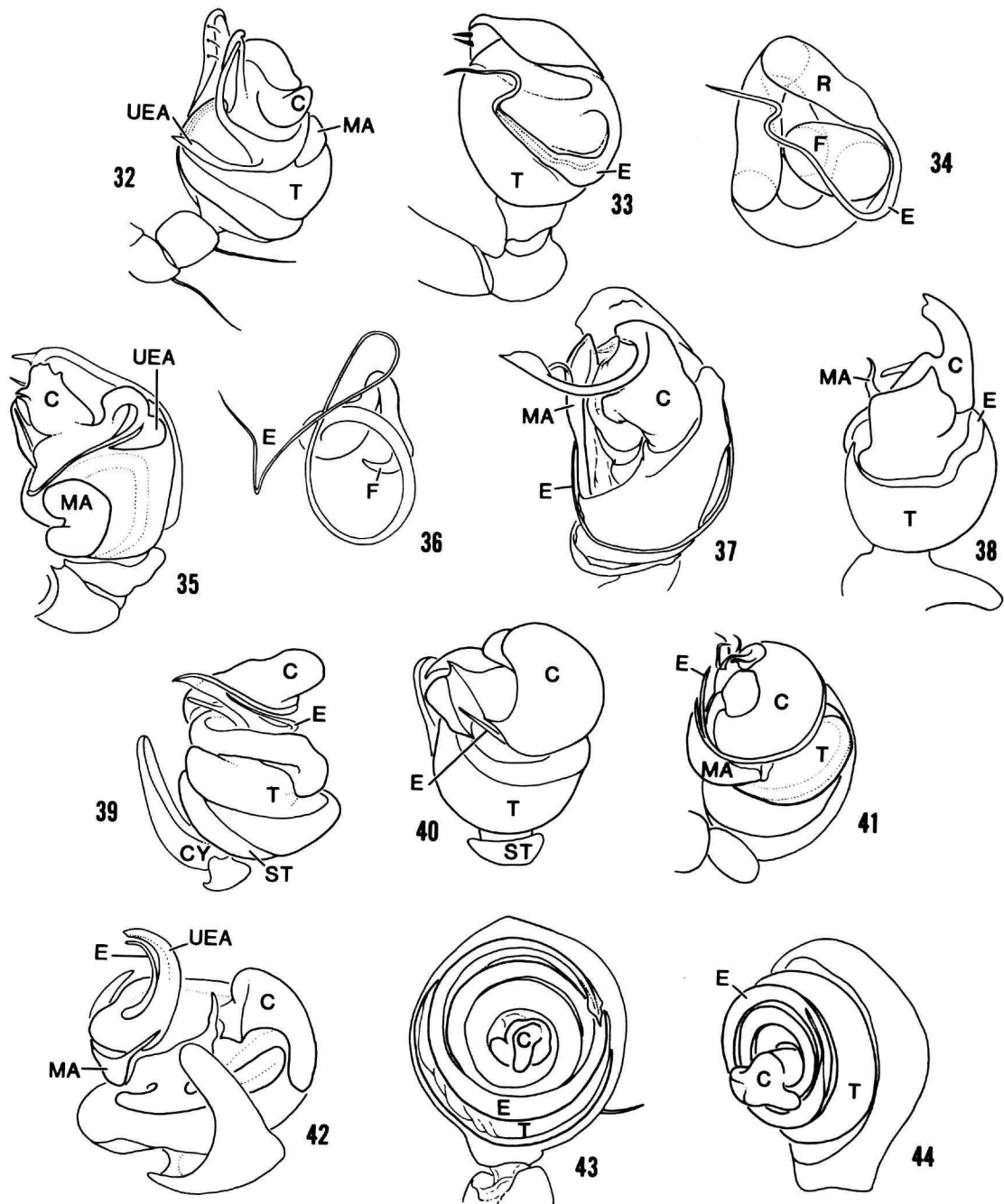
FIGURES 32–44.—Uloboridae and Deinopidae: 32, Uloboridae, *Waitkera waitkerensis* (after Opell, 1979, fig. 28); 33, Uloboridae, *Tangaroa tahitiensis* (after Opell, 1979, fig. 19); 34, Uloboridae, *Tangaroa tahitiensis* (reservoir) (after Opell, 1979, fig. 19); 35, Uloboridae, *Polenecia producta* (after Opell, 1979, fig. 46); 36, Uloboridae, *Polenecia producta* (reservoir) (after Opell, 1979, fig. 46); 37, Uloboridae, *Hyptiotes gertschi* (after Opell, 1979, plate 4A); 38, Uloboridae, *Miagrammopes latens* (after Opell, 1979, fig. 90); 39, Uloboridae, *Ponella lactescena* (after Opell, 1979, fig. 201); 40, Uloboridae, *Philoponella republicana* (after Opell, 1979, fig. 214); 41, Uloboridae, *Zosis geniculatus* (after Opell, 1979, fig. 173); 42, Uloboridae, *Siratoba referena* (after Opell, 1979, fig. 68); 43, Deinopidae, *Deinopis diabolica* (after Kraus, 1956, fig. 4); 44, Deinopidae, *Avella insularis* (after Lehtinen, 1967, fig. 38).
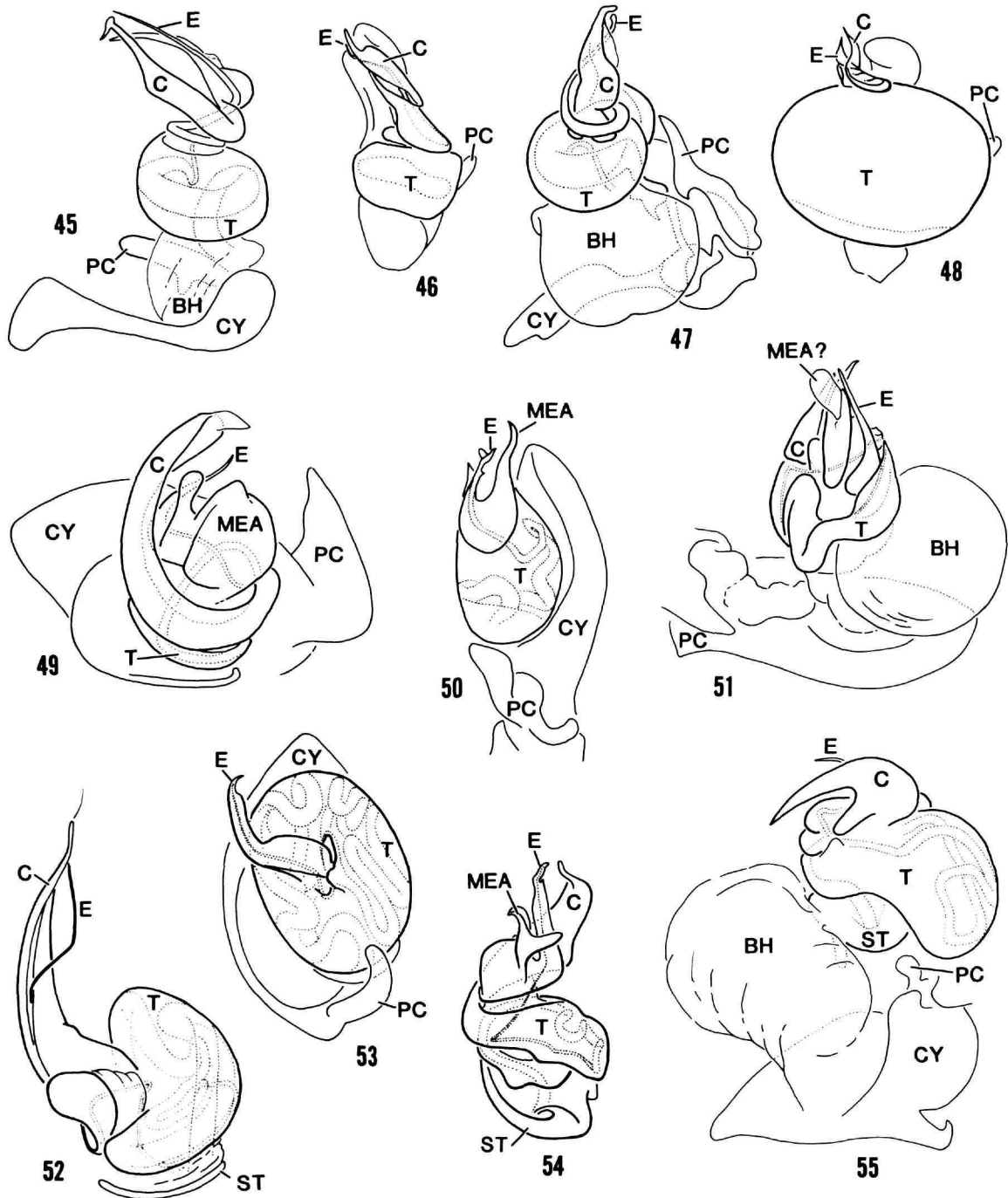
FIGURES 45–55.—Tetragnathidae: 45, *Tetragnatha laboriosa* (after Levi, 1981, fig. 20); 46, *Tetragnatha branda* (after Levi, 1981, fig. 174); 47, *Pachygnatha furcillata* (after Levi, 1980b, fig. 177); 48, *Glenognatha foxi* (after Levi, 1980b, fig. 278); 49, *Metellina segmentata* (after Levi, 1980b, fig. 99); 50, *Dolichognatha pentagona* (after Levi, 1981, fig. 13); 51, *Metleucauge eldorado* (after Levi, 1980b, fig. 149); 52, *Nephila clavipes* (after Levi, 1980b, fig. 25); 53, *Azilia affinis* (after Levi, 1980b, fig. 304); 54, *Meta menardi* (after Levi, 1980b, fig. 125); 55, *Leucauge venusta* (after Levi, 1980b, fig. 70).
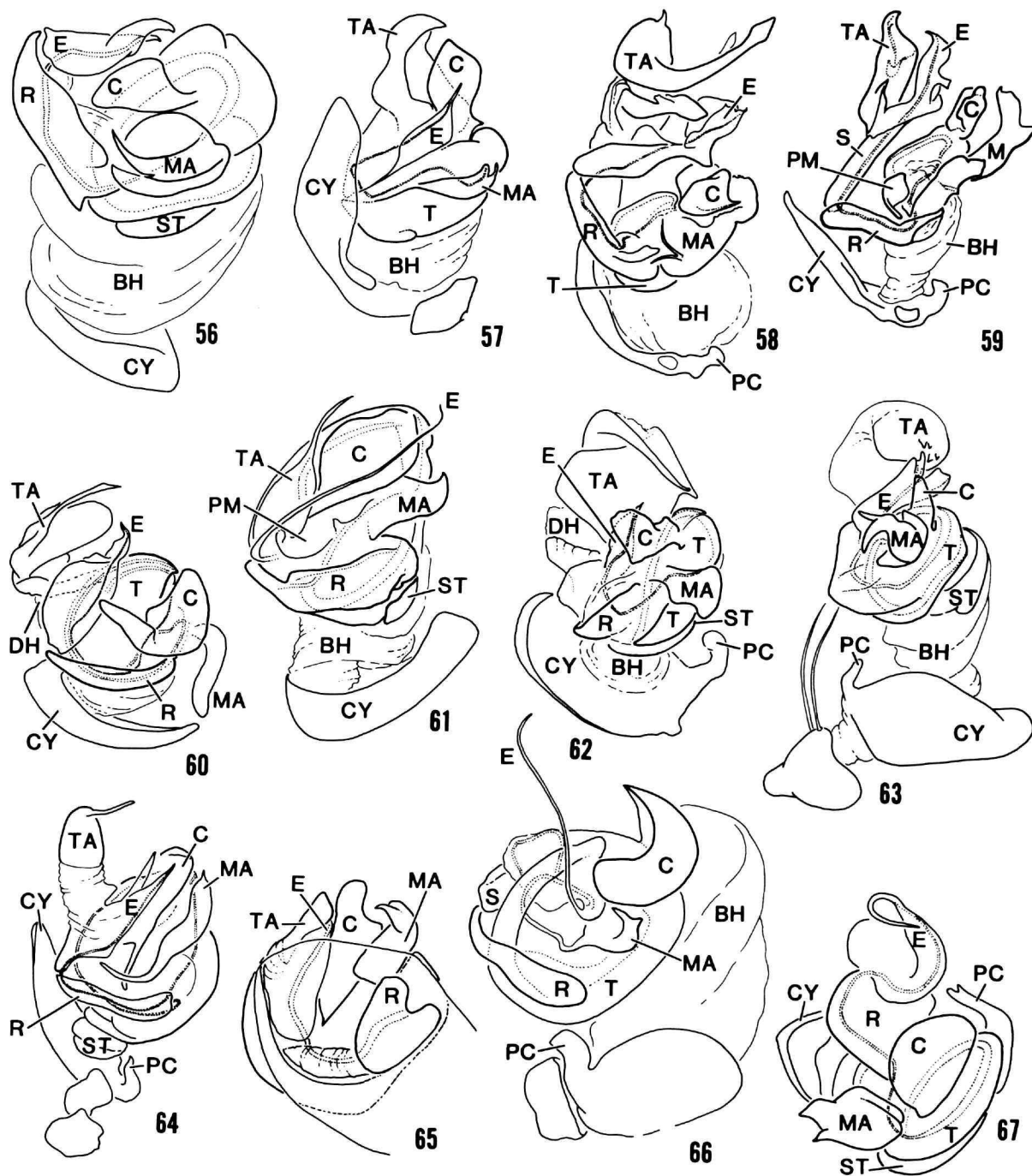
FIGURES 56–67.—Araneidae: 56, *Micrathena funebris* (after Levi, 1978, fig. 27); 57, *Colphepeira catawba* (after Levi, 1978, fig. 14); 58, *Aculepeira carbonoides* (after Levi, 1977a, fig. 173); 59, *Eriophora funebris* (after Levi, 1970, fig. 2); 60, *Eustala anastera* (after Levi, 1977b, fig. 232); 61, *Cyclosa turbinata* (after Levi, 1977b, fig. 20); 62, *Metazygia wittfeldae* (after Levi, 1977b, fig. 103); 63, *Metepeira labyrinthea* (after Levi, 1977a, fig. 10); 64, *Verrucosa arenata* (after Levi, 1976, fig. 9); 65, *Neoscona arabesca* (after Berman and Levi, 1971, fig. 4); 66, *Gea heptagon* (after Levi, 1968, fig. 20); 67, *Zygiella atrica* (after Levi, 1974, fig. 7).
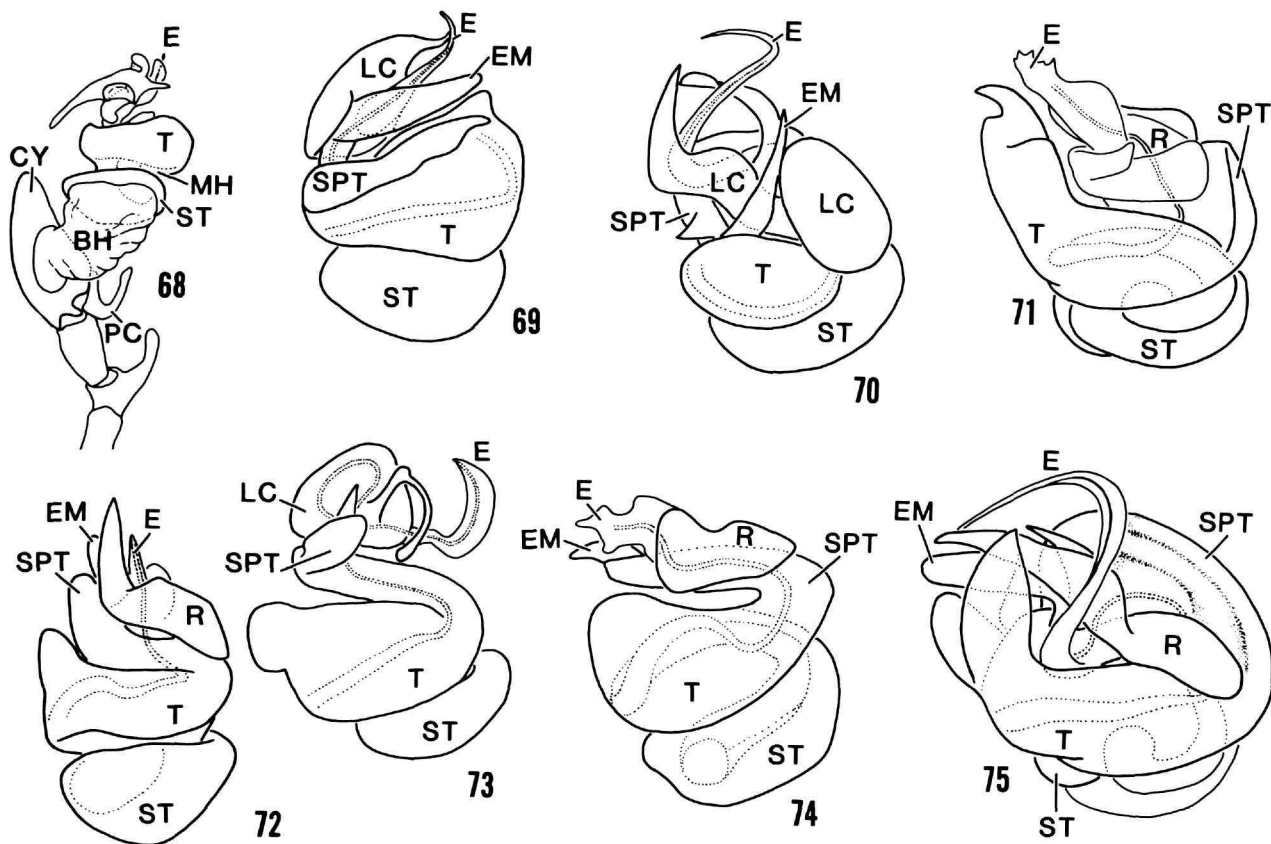
FIGURES 68-75.—Linyphiidae: 68, *Pityohyphantes phrygianus* (after Comstock, 1910, fig. 10); 69, *Porhomma pygmaeum* (after Merrett, 1963, fig. 34A); 70, *Mioxena blanda* (after Merrett, 1963, fig. 42A); 71, *Erigonidium graminicolum* (after Merrett, 1963, fig. 52A); 72, *Erigone vagans* (after Merrett, 1963, fig. 59A); 73, *Monocephalus fuscipes* (after Merrett, 1963, fig. 60A); 74, *Notioscopus sarcinatus* (after Merrett, 1963, fig. 73A); 75, *Dismodicus bifrons* (after Merrett, 1963, fig. 96A).

FIGURES 76-89 (opposite page).—Theridiidae: 76, *Dipoena alta* (after Levi and Levi, 1962, fig. 50); 77, *Euryopis emertoni* (after Levi, 1954b, fig. 37); 78, *Episinus erythrophthalamus* (after Levi, 1964b, fig. 90); 79, *Episinus truncatus* (after Levi, 1954a, fig. 3); 80, *Spintharus gracilis* (after Levi, 1963b, fig. 13); 81, *Spintharus flavidus* (after Levi and Levi, 1962, fig. 206); 82, *Chrosiothes jocosus* (after Levi, 1954c, fig. 1); 83, *Chrosiothes minuscula* (after Levi, 1954c, fig. 18); 84, *Stemmops bicolor* (after Levi, 1955b, fig. 17); 85, *Theonoe stridula* (after Levi, 1955a, fig. 3); 86, *Robertus riparius* (after Levi and Levi, 1962, fig. 291); 87, *Latrodectus mactans* (after Levi, 1959, fig. 1); 88, *Argyrodes elevatus* (after Exline and Levi, 1962, fig. 154); 89, *Synotaxus turbinatus* (after Exline and Levi, 1965, fig. 2).
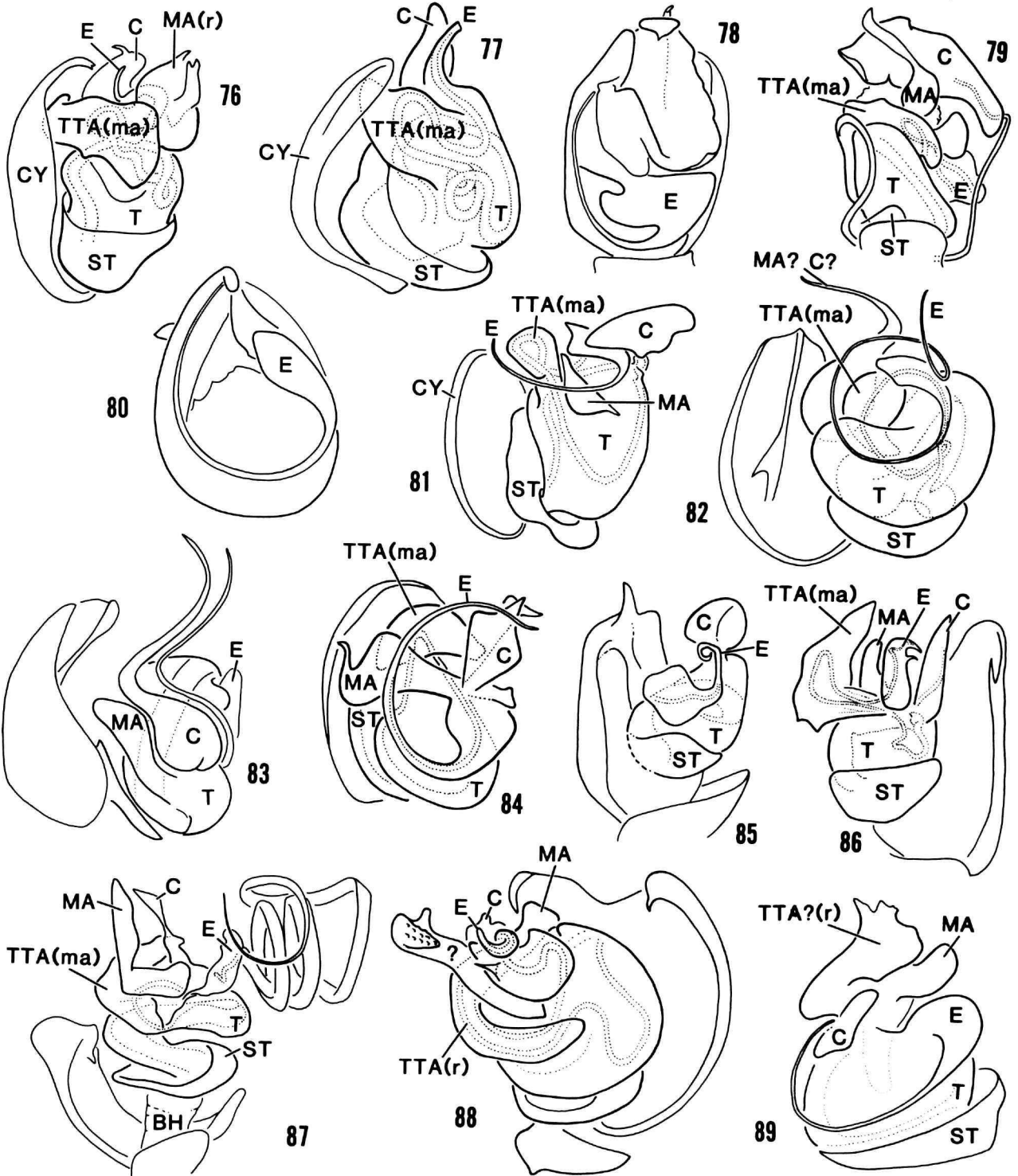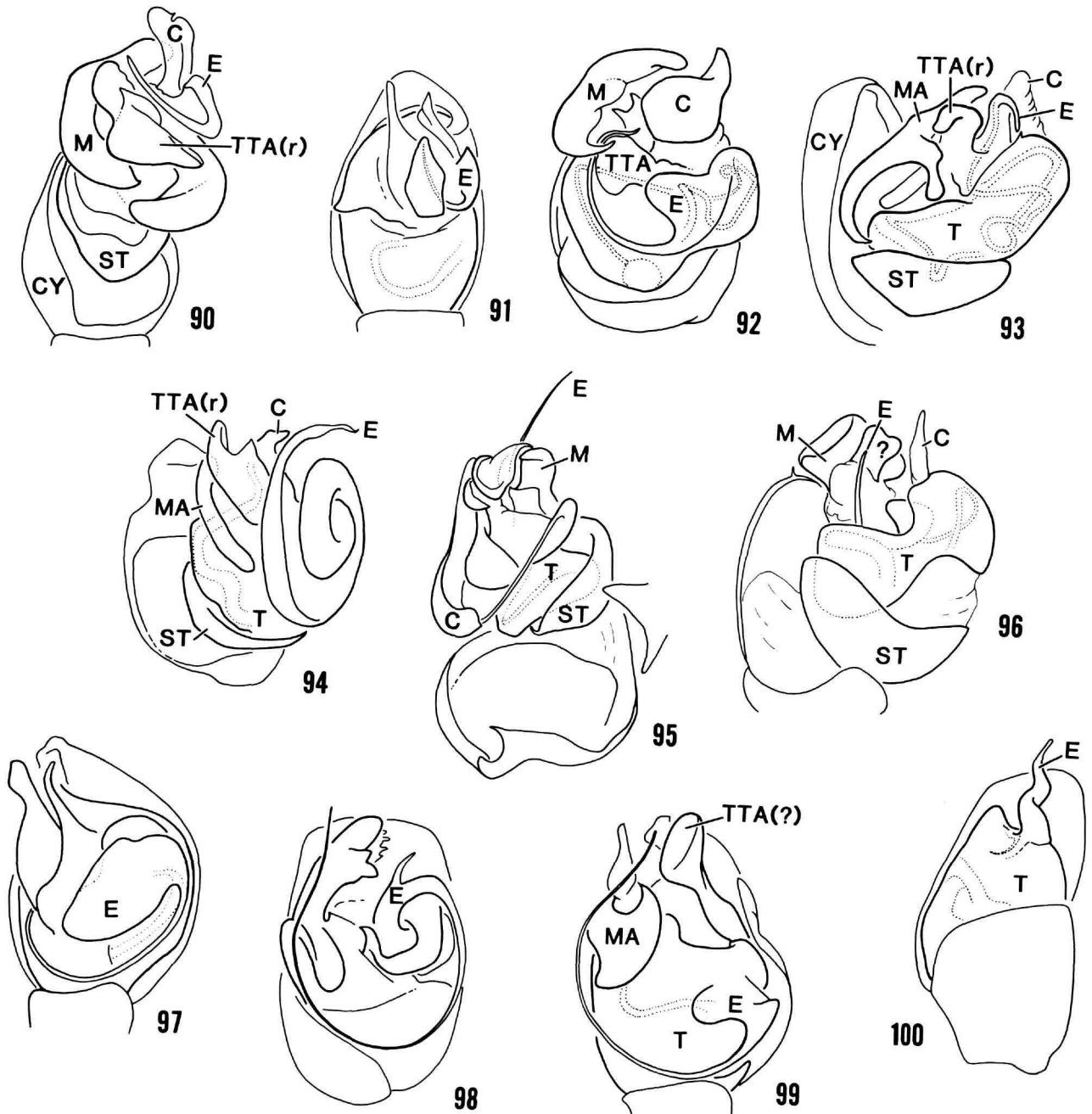
FIGURES 90–100.—Theridiidae: 90, *Enoplognatha ovata* (after Levi, 1957a, fig. 11); 91, *Enoplognatha joshua* (after Levi, 1957a, fig. 43); 92, *Theridion murarium* (after Levi, 1957a, fig. 62); 93, *Theridion pennsylvanicum* (after Levi, 1957a, fig. 307); 94, *Anelosimus eximius* (after Levi, 1956, fig. 17); 95, *Arctachaea nordica* (after Levi, 1957b, fig. 3); 96, *Thymoites marxi* (after Levi, 1957a, fig. 395); 97, *Phoroncidia tina* (after Levi, 1964a, fig. 35); 98, *Steatoda ancorata* (after Levi, 1962, fig. 47); 99, *Helvidia scabricula* (after Levi, 1972, fig. 8); 100, *Theridula nigerrima* (after Levi, 1966, fig. 3).
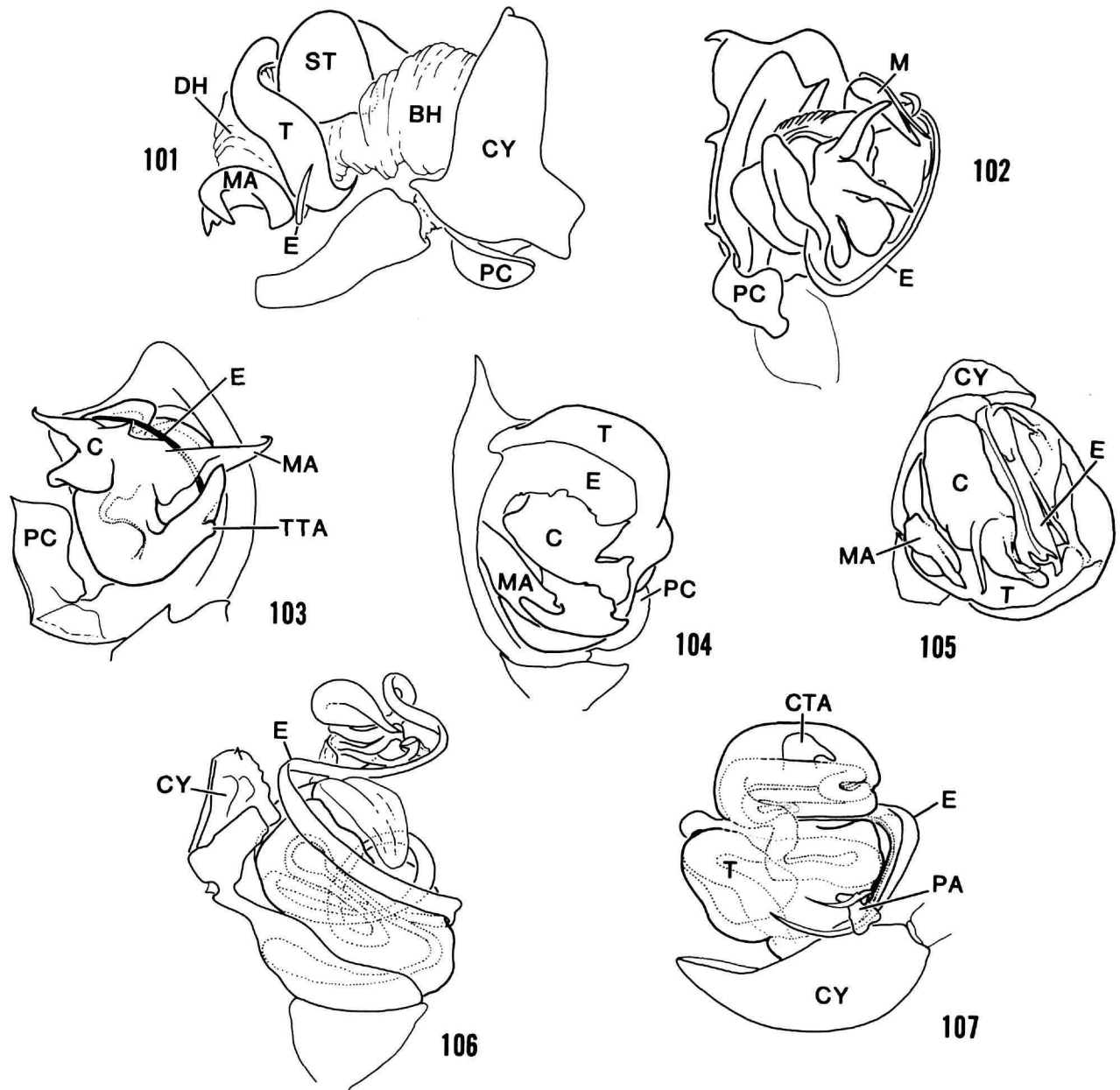
FIGURES 101–107.—Miscellaneous groups: 101, Mimetidae, *Ero furcata* (after Shear, 1981, fig. 11); 102, Mimetidae, *Mimetus puritanus* (after Shear, 1981, fig. 6); 103, Nesticidae, *Nesticus cellulanus* (after Lehtinen and Saaristo, 1980, fig. 1); 104, Theridiosomatidae, *Plato troglodita* (after Coddington, 1986c, fig. 10); 105, Theridiosomatidae, *Theridiosoma gemmosum* (after Coddington, 1986c, fig. 133); 106, Mysmenidae, *Mysmenella samoensis* (after Baert, 1984, fig. 26); 107, Cyatholipidae, *Teemenaarus silvestris* (after Davies, 1978, fig. 12).

FIGURE 108.—Cladogram of orbicularian taxa and potential outgroups. No characters unequivocally support either Dictynoidea or Amaurobioidea as the sister taxon of Orbiculariae, but these superfamilies are reasonable outgroups (see text). Little-known uloborid genera (*Astavakra, Conifaber, Lubinella*) are omitted. The placement of some character transformations is ambiguous (see text). The cladogram length is 154, and the consistency index is 0.72.

TABLE 1.—Character data for Figure 108. Characters are grouped by category. Each row represents one character, coded as "character: state" (0 = first state, 1 = second state, 2 = third state, etc.; dash indicates missing data). The last two columns give the consistency index (CI) of the character on the tree in Figure 108, and the transformation coding (Trans) used (a = 0-1-(3,2-4), b = 0-(2,1-3), o = ordered, r = reversible). Taxon abbreviations: Am = Amaurobioidea, An = Anapidae, Ar = *Araneus*, As = *Ariston*, Cy = *Cyclosa*, Da = *Daramuliana*, De = Deinopidae, Di = Dictynoidea, Gl = *Glenognatha*, Hy = *Hyptiotes*, Le = *Leucauge*, Li = Linyphiidae, Me = *Meta*, Mi = *Miagrammopes*, My = Mysmenidae, Ne = Nesticidae, Np = *Nephila*, Ny = *Nephilengys*, Oc = *Octonoba*, Or = *Orinomana*, Ph = *Philoponella*, Pl = *Polenecia*, Po = *Ponella*, Pu = *Purumitra*, Si = *Siratoba*, Sm = Symphytognathidae, Sy = *Sybota*, Ta = *Tangaroa*, Te = *Tetragnatha*, Th = Theridiidae, Ts = Theridiosomatidae, Ul = *Uloborus*, Wa = *Waitkera*, Zo = *Zosis*. For other abbreviations, see "Abbreviations."

Character: state	Am	Di	Ar	Cy	Li	Np	Ny	Me	Le	Te	Gl	Ts	My	An	Sm	Th	Ne	De	Ta	Wa	Pl	Si	As	Hy	Mi	Sy	Or	Ul	Zo	Oc	Ph	Po	Pu	Da	CI	Trans
MALE GENITALIA																																				
1. Metine palp conformation: absent; present	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.00	r
2. Tetragnathid conformation: absent; present	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.00	r
3. Uloborid cymbial macrosetae: absent; 3 setae; 2 setae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1.00	o
4. Paracymbium: absent; hooked; squat; distal; long	0	0	1	1	1	2	2	2	2	4	4	1	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.80	a
5. Median hematodocha: present; absent	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	1	-	-	0	0	0	0	0	-	-	0.50	r
6. Petiole fused to subtegulum: absent; present	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	-	-	-	0	0	0	0	0	0	-	-	1.00	r
7. Metine reservoir switchback: absent; present	0	0	0	0	0	1	1	1	-	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.50	r
8. Symphytognathoid reservoir switchback: absent; present	0	0	0	0	0	0	0	0	0	0	0	1	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.00	r
9. Separate median apophysis: present; absent	0	0	0	1	1	1	1	1	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	-	1	0	1	1	1	0	-	0.12	r
10. Median apophysis spur: absent; claw-like; concave	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	1	2	1	1	1	-	1.00	o
11. Median apophysis form: otherwise; large bulb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	1	0	1	1	1	-	0.50	r
12. Median apophysis extension: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0.50	r
13. Tegular spur: absent; small; large	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	2	0	0.67	b
14. Conductor-median apophysis fusion: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	-	0	1	1	0	0	0	0	1.00	r
15. Conductor: present; absent	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0.50	r
16. Tegular lobes: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.00	r
17. Metine embolic apophysis: absent; present	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.50	r

Table 1.—Continued.

Character: state	Am	Di	Ar	Cy	Li	Np	Ny	Me	Le	Te	Gl	Ts	My	An	Sm	Th	Ne	De	Ta	Wa	Pl	Si	As	Hy	Mi	Sy	Or	Ul	Zo	Oc	Ph	Po	Pu	Da	CI	Trans
18. Uloborid embolic apophysis: absent; present; wide w/loop; bifurcated	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	3	2	2	0	-	0	0	1	1	0	0	-	0.75	b
19. Uloborid embolic guide: not applicable; includes radix	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	-	0	0	0	0	0	0	-	1.00	r
20. Embolus cross-section: round; flat; crescent	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	1	0	0	2	2	0	0	0	-	0	0	0	0	0	0	-	1.00	b
21. Embolus stalk: absent; present	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.50	r
22. Araneoid radix: absent; present	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.00	r
23. Terminal apophysis: absent; present	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.00	r
FEMALE GENITALIA																																				
24. Female genitalia: entelegyne; haplogyne	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	-	1	-	0	0	0	0	0	0	0	0	0	0	0.33	r
25. Copulatory pore: posterior; ventral	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0.50	r
26. Female genital projection: absent; medium; lateral	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	2	2	2	2	2	2	2	0.67	o
27. Epigynal atrium: absent; undivided; divided	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	2	1.00	b
28. Accessory glands: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0.50	r
SOMATIC MORPHOLOGY																																				
29. Cephalon: wide; narrow	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1.00	r
30. Cephalic tracheal trunks: 2; 4; 0	-	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	0	0	0	0	0	0	0	1	0	2	2	2	2	2	2	2	1.00	b
31. Tracheoles: cephalic; abdominal	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0.50	r
32. Branched tracheae: absent; present	0	1	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	-	0	0	0	-	1	1	1	-	1	1	-	1	-	-	-	0.50	r
33. Labium: longer than wide; wider than long	0	0	1	1	1	0	0	1	1	1	1	1	1	1	1	0	1	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.50	r
34. Gnathocoxal glands: absent; present	0	0	1	1	1	-	-	0	0	0	0	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-	0	0	-	-	-	-	-	1.00	r
35. Cheliceral denticles: absent; present; modified	0	0	0	0	0	1	-	0	0	0	0	1	1	2	2	0	1	0	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	0.40	o
36. Poison glands: present; absent	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1.00	r
37. Femoral trichobothria: none; 1 row; 2 rows	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	-	2	1	1	2	2	2	2	2	2	2	2	2	2	0.40	o

Table 1.—Continued.

Character: state	Am	Di	Ar	Cy	Li	Np	Ny	Me	Le	Te	Gl	Ts	My	An	Sm	Th	Ne	De	Ta	Wa	Pl	Si	As	Hy	Mi	Sy	Or	Ul	Zo	Oc	Ph	Po	Pu	Da	CI	Trans
38. Tarsus IV macrosetal comb: absent; short; long	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	2	2	1	1	1	1	1	1	1	1	1	1.00	o
39. Tarsus IV tarsal comb (theridiid): absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.00	r
40. Tarsus IV median claw: normal; elongate	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.00	r
41. Tarsus IV: long; short	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	1	–	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	–	1.00	r
42. Cribellum: entire; divided; lost	1	0	2	–	2	2	2	2	2	–	2	2	2	2	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	1.00	b
43. Calamistrum: medium; long	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0	0	0	0	0	1	0	1	0	0	–	–	–	–	–	1.00	r
44. Duct levator muscle: absent; present	0	0	1	1	1	–	1	1	1	1	1	1	–	1	–	1	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1.00	r
45. Duct sphincter: absent; present	0	0	1	1	1	–	1	1	1	1	1	1	–	1	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.00	r
46. PLS gland: absent; pseudoflagelliform; flagelliform	0	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	–	1	1	1	–	1	1	1	–	1	1	1	1	1	–	–	–	1.00	o
47. Aggregate glands: absent; present	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	–	0	–	0	0	0	0	0	0	0	0	0	0	0	–	–	1.00	r
48. Modified aggregate spigot: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.00	r
49. Hair: plumose; pseudoserrate; serrate	0	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1.00	o
50. Coxal hook: absent; present	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.00	r
51. Female palp: normal; reduced/absent	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.00	r
52. Female palpal claw: present; absent	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.00	r
53. Male palpal femur: thinner; thicker	–	–	–	–	–	–	–	–	–	–	–	1	1	1	1	–	–	–	0	1	1	1	1	1	1	1	–	–	1	1	1	1	1	–	1.00	r
54. Male palpal tibia: small; w/extension	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0.50	r
55. Femoral tubercles: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1.00	r
56. Anterior lateral eyes: present; lost	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0.50	r
57. Anterior median eyes: present; reduced/absent	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0.50	r
58. Posterior median eye canoe tapetum: present; absent	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1.00	r

Table 1.—Continued.

Character: state	Am	Di	Ar	Cy	Li	Np	Ny	Me	Le	Te	Gl	Ts	My	An	Sm	Th	Ne	De	Ta	Wa	Pl	Si	As	Hy	Mi	Sy	Or	Ul	Zo	Oc	Ph	Po	Pu	Da	CI	Trans
59. Posterior median eye tapetum: otherwise; medial	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.00	r
60. Posterior lateral eye tubercle: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0.50	r
61. Juxtaposed lateral eyes: absent; present	0	1	1	1	1	1	1	0	0	1	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.00	r
62. Stridulatory apparatus: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0.50	r
63. Posterior abdomen extension: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0.50	r
BEHAVIOR																																				
64. Orb web: not applicable; normal; reduced	0	0	1	1	–	1	1	1	1	1	1	1	1	1	1	–	1	1	1	1	–	–	–	2	2	1	–	1	1	1	1	1	–	–	1.00	o
65. 2-dimensional frame: absent; present	0	0	1	1	–	1	1	1	1	1	1	1	1	1	1	–	1	1	1	1	1	1	1	1	1	1	–	1	1	1	1	1	1	1	1.00	r
66. 3-dimensional orbs: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	–	–	0	0	0	–	0	0	0	0	0	–	–	0.50	r
67. Frame construction: absent; araneoid; uloborid	0	0	1	1	–	1	1	1	1	1	1	1	1	1	1	–	1	1	1	1	2	1	1	2	1	1	–	2	2	1	1	1	1	1	1.00	o
68. Frame, radius construction inside NSSC: absent; present	0	0	1	1	–	1	1	1	1	1	1	1	1	1	1	–	1	1	1	1	–	1	1	–	1	1	–	1	1	1	1	1	1	1	1.00	r
69. Radii: absent; cut & reeled; doubled; nephiline	0	0	1	1	–	3	3	1	1	1	1	1	1	1	1	–	1	1	1	1	–	1	1	2	2	1	–	2	2	2	1	1	1	1	1.00	a
70. Radii lengthened: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	–	–	0	0	0	0	0	0	0	0	0	0	0	1.00	r
71. Radii with cribellate silk: absent; present	0	0	–	–	–	–	–	0	0	0	0	0	0	1	1	–	–	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0.50	r
72. Accessory radii: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	–	–	0	0	0	0	0	0	0	0	0	0	0	1.00	r
73. Hub construction: absent; present	0	0	1	1	–	1	1	1	1	1	1	1	1	1	1	–	1	1	1	1	–	1	1	–	1	1	1	1	1	1	1	1	1	1	1.00	r
74. Hub modification: absent; present	0	0	1	1	–	1	1	1	1	1	1	1	1	1	1	–	0	0	0	0	–	0	0	–	0	0	–	0	0	0	0	0	0	0	1.00	r
75. Final hub bite out: absent; present	0	0	1	1	–	1	1	1	1	1	1	1	1	1	1	–	0	0	0	0	–	0	0	–	0	0	–	0	0	0	0	0	0	0	1.00	r
76. Post-SS construction hub loops: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	1	–	–	–	0	1	1	–	1	1	1	1	1	1	1	1.00	r
77. Nonsticky spiral construction: absent; present	0	0	1	1	–	1	1	1	1	1	1	1	1	1	1	–	1	1	1	1	–	–	–	1	1	1	–	1	1	1	1	1	1	1	1.00	r
78. SS localization: absent; oL1; iL1; oL4	0	0	1	1	–	3	3	2	2	2	2	2	2	2	2	–	1	1	1	1	–	–	–	1	1	1	–	1	1	1	1	1	1	1	1.00	o

Table 1.—Continued.

Character: state	Am	Di	Ar	Cy	Li	Np	Ny	Me	Le	Te	Gl	Ts	My	An	Sm	Th	Ne	De	Ta	Wa	Pl	Si	As	Hy	Mi	Sy	Or	Ul	Zo	Oc	Ph	Po	Pu	Da	CI	Trans
79. SS wrap attack: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.00	r
80. iL4 push during SSC: absent; present	0	0	1	1	-	1	1	1	1	1	1	1	1	1	1	-	-	0	0	-	-	-	-	0	0	-	-	0	0	0	0	-	-	-	1.00	r
81. oL3,4 NS line grip: absent; present	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-	-	-	-	-	1	1	-	-	1	1	1	1	-	-	-	1.00	r
82. L4 switch during SS construction: absent; present	0	0	1	1	-	1	1	1	1	1	1	1	1	1	1	-	1	1	1	-	1	-	1	1	1	-	-	1	1	1	1	-	-	-	1.00	r
83. Cribellate silk puffed: absent; present	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	1	-	1	1	1	-	-	1	1	1	1	-	-	-	1.00	r
84. Eggsac doubly attached: absent; present	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.00	r
85. Wrap attack: absent; present	0	0	1	1	0	0	0	0	0	0	0	0	0	0	-	-	1	1	1	-	1	-	-	1	1	-	-	1	1	1	1	-	-	-	0.50	r
86. Juvenile web: absent; present	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	1	1	0	1	1	0	0	1	1	1	1	1	1	1	1	1	0.33	r
87. Metine resting posture: absent; present	0	0	0	0	0	-	1	1	1	1	1	0	0	0	0	0	1	-	-	-	-	-	-	1	1	-	-	1	1	1	1	-	-	-	0.50	r

Index

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