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## The Hypochiloid Spiders: A Cladistic Analysis, With Notes on the Atypoidea (Arachnida, Araneae)

NORMAN I. PLATNICK<sup>1</sup>

"The value of any classification rests on the soundness of the principles underlying it."

—A. Petrunkevitch, 1933, p. 303

"But I shall certainly admit a system as empirical or scientific only if it is capable of being *tested* by experience. These considerations suggest that not the *verifiability* but the *falsifiability* of a system is to be taken as a criterion of demarcation. In other words: . . . *it must be possible for an empirical scientific system to be refuted by experience.*"

—K. R. Popper, 1968, p. 40

### ABSTRACT

A hypothesis of interrelationships of the primitive araneomorph spiders based on shared derived characters is presented. The genera *Hypochilus* and *Ectatosticta* are regarded as sister groups and as constituting the sister group of all remaining araneomorphs. Three other genera (*Hickmania*, *Gradungula*, and *Thaida*) are sequentially considered plesiomorphic sister groups of the remaining araneomorphs. Sequenced and sub-

ordinated classifications derived from this cladogram are presented for purposes of comparison and evaluation. The family Ectatostictidae Lehtinen is newly synonymized with the Hypochilidae. Serrula morphology suggests that the superfamily Atypoidea is not monophyletic and that the Mecicobothriidae are more closely related to the Dipluridae than to the Antrodiaetidae or Atypidae.

### INTRODUCTION

The present paper represents an attempt to examine the higher classification of araneomorph spiders from the viewpoint of phylogenetic systematics. As such, it is primarily concerned (1) with the placement of the "hypochiloids," the most primitive of the true spiders, in monophyletic groups on the basis of shared derived characters with the methods developed by Hennig

(1965, 1966), and (2) with the establishment of a classification of these spiders that reflects the hypotheses of relationship thus generated. In addition, some data collected on mygalomorph spiders for purposes of out-group comparison, and relevant to a phylogenetic analysis of that group, are also provided.

One opinion occasionally expressed is that the

<sup>1</sup>Associate Curator, Department of Entomology, the American Museum of Natural History.

higher classification of many or most groups represents a consensus view based on consideration of many characters by many workers, and that no substantial improvements can be made in those classifications unless newly available or previously ignored characters are brought to bear on them. If previous classifications of the hypochiloid spiders are representative, and there seems to be no reason to suspect that they are not, this argument is indefensible. Although some new observations are added below, this information only corroborates hypotheses for which sufficient indicatory data have been available in the literature at least since the work of Marples (1968). That a satisfactory hypothesis of hypochiloid interrelationships has not yet been presented seems to indicate that arachnologists have lacked a satisfactory method of analyzing their data, not that they have lacked a sufficient data base on which to reach a consensus. Cladistic analysis provides that sorely needed methodology.

Taking to heart the statement Petrunkevitch made when he began his famous study on the internal anatomy of spiders, and which is quoted above, a brief discussion of the principles underlying this study is in order. The point of departure is the view expressed by Popper (1968) that the line of demarcation between science and non-science is falsifiability, that only a statement that can potentially be shown to be wrong by some possible observation of the real world qualifies as a scientific hypothesis. Thus if classifications are to be scientific they must be falsifiable hypotheses. Since the hypothesis involved in grouping a set of taxa together is one of relationship (namely that those taxa so grouped are more closely related to each other than to taxa excluded from the group), the process of constructing a scientific classification (as opposed to a classification designed only as a technique for information storage and retrieval) necessarily involves an attempt at reconstructing the interrelationships of the organisms concerned. If life on earth had a common origin, all organisms are related, and hypotheses of relationship must be comparative. The most explicit possible comparative hypothesis is a three-taxon statement: taxon A is more closely related to B than either of them are to C. For example, the circled area of figure

31 represents a hypothesis that liphistiids (*Mesothelae*) are more closely related to opisthothelines than either of those groups are to amblypygids. Brief inspection will show that phylogenies are merely interested series of such three-taxon statements that proceed from greater to lesser levels of universality in terms of the number of taxa they include.

As stressed by Hennig, the only evidence we can have that taxa A and B are each other's closest relatives is that they share a uniquely derived (synapomorphic) character state that they do not also share with C. For any three-taxon statement there are three possible explicit (dichotomous) hypotheses of relationship (A and B are closest relatives, A and C are closest relatives, or B and C are closest relatives) and one possible general (trichotomous) hypothesis of relationship (A, B, and C are closest relatives, as compared with D). If all we have available is a synapomorphic character state shared by A, B, and C, we must choose the general hypothesis. If we also have available a synapomorphic character state shared by only two of the three taxa, we can choose one of the three explicit hypotheses, not because we have demonstrated it to be true, but because we have falsified the two alternate explicit hypotheses (such falsifications are apparent and not absolute, of course; absolute falsification seems as theoretically unobtainable as absolute truth). Given a set of purportedly synapomorphic character states that do not have perfectly congruent distributions among the taxa considered, parsimony dictates that we must always choose the hypothesis that appears to have been falsified the least number of times. Thus if A and B share six purportedly synapomorphic character states, and A and C share two purportedly synapomorphic character states, we must choose the hypothesis that A and B are closest relatives, the implication being that the two incongruent character states are not actually synapomorphic. They may have been derived more than once by parallelism, they may be primitive rather than derived, or they may indeed not be homologous in all the taxa considered. The crucial point is that such a decision, once made, is always open to falsification by simply finding a larger number of purportedly synapomorphic character states in favor of one of the alternate hypotheses (Gaffney, MS).



Polarity judgments, statements that one given character state, such as paraxial chelicerae, is primitive (plesiomorphic) at a given level of universality and that an alternate character state, such as diaxial chelicerae, is derived at that level of universality, are thus themselves subsidiary hypotheses that can be falsified by incongruence with an otherwise corroborated hypothesis of relationship. Primitive character states shared by two out of three taxa cannot be used to choose between alternate three-taxon statements because they do not falsify any of the alternate hypotheses, but all shared primitive character states do represent synapomorphies at higher levels of universality. Shared character states derived separately in different lineages (i.e., parallelisms) cannot be used to choose between alternate three-taxon statements and do not represent synapomorphies at higher levels of universality; they can, however, be detected by incongruence with more numerous synapomorphy patterns.

Methods of arriving at a polarity judgment include, in roughly the order of their usefulness, out-group comparison, study of ontogenetic transformations, character correlation, and comparison of character-state frequency, but as with any hypothesis the criterion of its scientific acceptability is not the method by which it is reached, but its testability and potential for falsification (Popper, 1968). Like any science, phylogenetics does not now and never will provide us with the truth in any final sense, but only with a set of hypotheses that have not yet been falsified.

It is worth noting, primarily to forestall irrelevant criticism, that speciation has not been mentioned in this discussion, for the simple reason that although classical phylogenetic trees may purport to show speciation events, cladograms, in and of themselves, do not. Cladograms operate at a level of generality above that of phylogenetic trees; they function as sets of trees (Nelson, MS). In other words, a branch of a cladogram uniting two taxa says only that those two taxa are, comparatively, closest relatives. An ancestor and its descendant are more closely related to each other than either is to a third taxon not also a descendant of the same ancestor. Cladograms do not distinguish between ancestor-descendant relationships and sister-group relationships, because

there is no possible combination of shared derived characters that can falsify a hypothesized ancestor-descendant relationship (autapomorphic character states found in a purported ancestor but not in a purported descendant could be the result of character reversal within the lineage). Thus a cladogram uniting A and B may mean that they had a common ancestor (X) that underwent a speciation event, or it may mean that A is the ancestor of B, or that B is the ancestor of A. A cladogram containing fossil taxa may include branching points that represent no speciation events at all, but only ancestor-descendant relationships. Similarly, in a cladogram containing only Recent taxa a common ancestor may be identical with one of its descendants (if, for example, one parasitic species gives rise sympatrically to another by a host change without itself undergoing any genetic change) or not (if one species gives rise allopatrically to two or more others). It is for this reason that common ancestors in cladograms are always hypothetical and that no taxa are placed at the nodes of such diagrams. Certainly we may choose to regard all branching points in a cladogram as allopatric speciation events for the purposes of a biogeographic analysis, just as we may choose to regard all terminal taxa in a cladogram as biological species for the purposes of a reproductive analysis. Applications of such assumptions as axioms for some particular purpose involve converting the cladogram into one (and only one) of the numerous possible phylogenetic trees it represents, and such assumptions are not involved in the construction of cladograms or of classifications from them. Criticisms of cladistics as necessitating dichotomous speciation or equal (or unequal) evolutionary rates, and the like, are based on confusion between cladograms and phylogenetic trees.

What follows, then, is an attempt to develop a series of three-taxon statements reflecting the interrelationships of the hypochiloid spiders, five genera (*Hypochilus* Marx, *Ectosticta* Simon, *Hickmania* Gertsch, *Thaïda* Karsch, and *Gradungula* Forster) that have been placed in from two to five families and ranked at categorical levels as high as the suborder. The only consensus is that they do represent the most primitive of the known araneomorph spiders, as evidenced by

their retention of four pairs of heart ostia (in all five genera) and two pairs of book lungs (in all except *Thaïda*), both primitive character states as determined by out-group comparison with all other spiders. The term "hypochiloid" is therefore used here to indicate a grade, not a clade. The out-group comparisons made below are based on the subordinal classification argued by Platnick and Gertsch (1976).

*Hypochilus* contains four described and one undescribed (R. L. Hoffman, personal commun.) species from the southeastern United States, Colorado, and California, *Ectatosticta* a single species from China, *Hickmania* a single species from Tasmania, *Thaïda* (formerly *Austrochilus*) a single species from Chile and western Argentina, and *Gradungula* two described and several undescribed (R. R. Forster, personal commun.) species from Australia and New Zealand. *Gradungula* has been treated by Forster (1955) and Davies (1969), *Thaïda* by Zapfe (1955), and the other genera by Gertsch (1958, 1964).

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## HISTORY

The phylogenetic significance of the hypochiloids was recognized immediately when *Hypochilus thorelli* was discovered by Marx (1888); as Marx (1889, p. 166) said, the spider is "so anomalous that it appears like the representative of a prototype." As a result, we need be concerned here only with classifications proposed since 1888. With respect to the placement of the hypochiloids, four basically different views can be recognized.

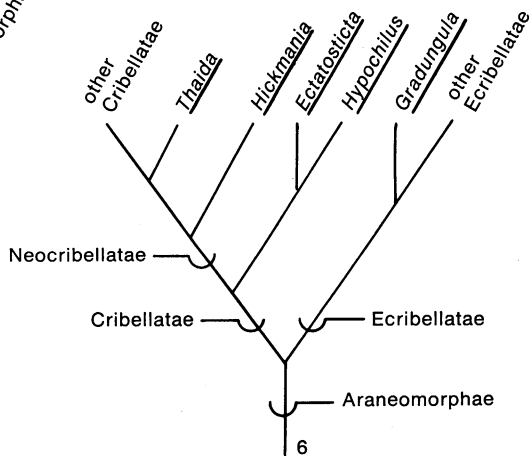
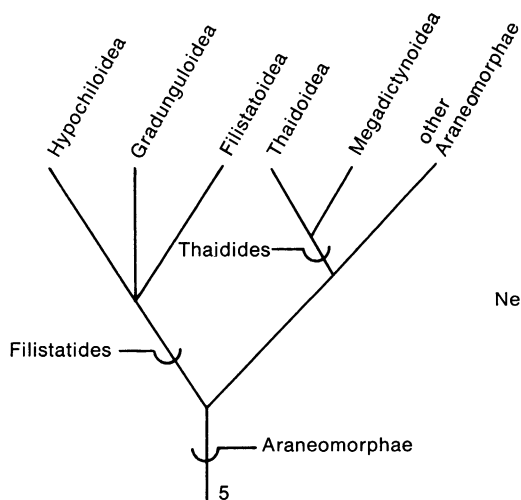
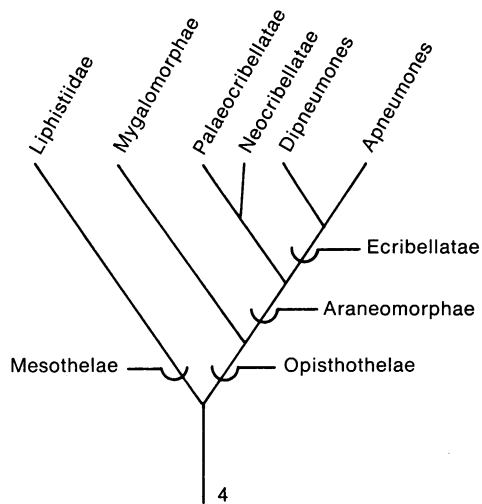
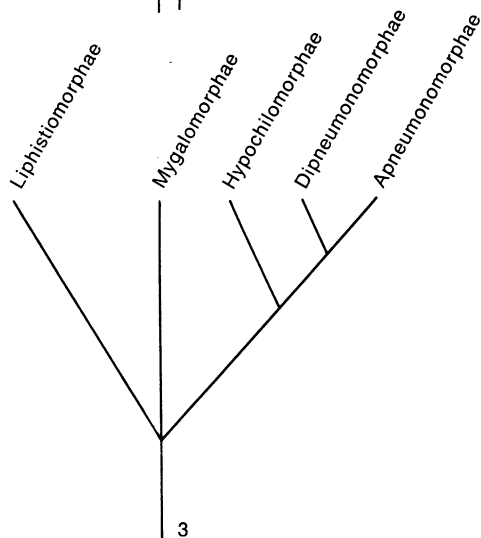
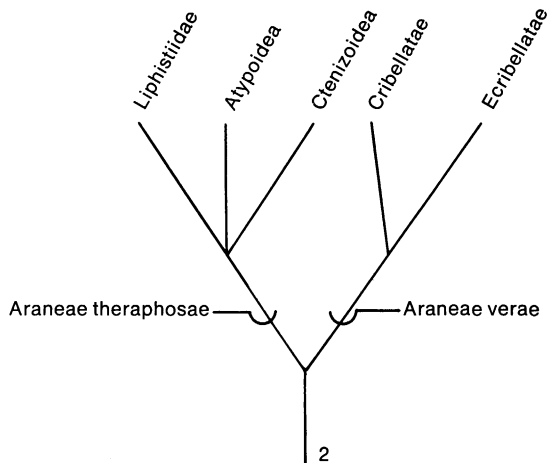
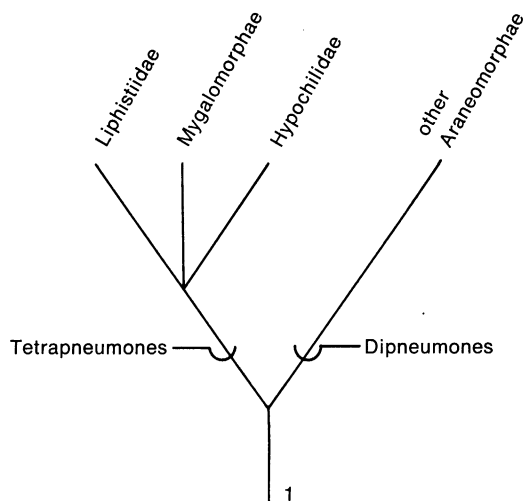
Thorell (1891) divided spiders into two groups, Tetrapneumones for those with two pairs of lungs and Dipneumones for those with a single pair of lungs (and presumably those few forms now known to be lungless); as a result he was forced to consider the hypochiloids more closely related to mygalomorphs and liphistiids than to the araneomorphs (fig. 1). Dahl (1904) excluded the liphistiids from Tetrapneumones but still placed the hypochiloids with the mygalomorphs.

Simon (1892) also divided spiders into two

groups, the "Araneae theraphosae" for those with paraxial chelicerae and the "Araneae verae" for those with diaxial chelicerae. The former group was divided into three families: the Liphistiidae, Atypidae (corresponding to the present-day superfamily Atypoidea), and Aviculariidae (corresponding to the present-day superfamily Ctenizoidea), whereas the latter group was divided into two sections, the Cribellatae for those true spiders with a cribellum and calamistrum (including the Hypochilidae) and the Ecribellatae for those true spiders lacking a cribellum and calamistrum (fig. 2). This basic division of araneomorph spiders into cribellate and ecribellate groups was maintained by Pocock (1900), Comstock (1912), and Bristowe (1938). A further refinement of this viewpoint was added by Caporiacco (1938), who divided the Cribellatae into two cohorts, the Palaeocribellatae, containing the four-lunged hypochiloids, and the Neocribellatae, containing all the other (two-lunged) cribellates (fig. 4). Gerhardt and Kästner (1938) and Bonnet (1959) followed Caporiacco in recognizing the Palaeocribellatae; Marples (1968) transferred *Hickmania* and *Thaïda* from the Palaeocribellatae to the Neocribellatae (fig. 6).

A third point of view is represented in an early proposal by Petrunkevitch (1923) in which the hypochiloids are considered more closely related to the Filistatidae and some haplogyne ecribellates than to the other cribellates; Petrunkevitch published a diagram in which the hypochiloids are considered the most plesiomorphic branch of a lineage including also (approximately in order of ascending apomorphy) the Filistatidae, Sicariidae, Ammoxenidae, Dysderidae, Oonopidae, Oecobiidae, Uroctidae, Leptonetidae, Prodidomidae, Caponiidae, and Telemidae. Among more recent authors, Lehtinen (1967) has presented similar views placing the hypochiloid genera in two separate plesiomorphic lineages of Araneomorphae. The first lineage, called Filistatides, is broken into three superfamilies: the Hypochiloidea (containing *Hypochilus* and the Leptonetidae, Ochyroceratidae, Pholcidae, and Scytodidae), the Gradunguloidea (containing *Hickmania*, *Gradungula*, and probably *Ectatosticta*), and the Filistatoidea (containing the Filistatidae, Plectreuridae, Caponiidae, Oonopidae, and Dysderidae); three families (Diguetiidae, Sicariidae, and Segestriidae) are *incertae sedis* within Filistatides (fig. 5). Lehtinen's sec-





FIGS. 1-6. Cladograms derived from previous classifications of spiders; names have been standardized wherever possible. 1. Thorell (1891). 2. Simon (1892). 3. Petrunkevitch (1933). 4. Caporiacco (1938). 5. Lehtinen (1967). 6. Marples (1968).

ond plesiomorphic lineage, called *Thaidides*, contains only the genera *Thaida* and *Megadictyna*, each placed in a separate superfamily.

Finally, a fourth point of view was first expressed by Petrunkevitch (1933), who regarded the hypochiloids as the sister group of all other araneomorphs; the cladogram representing his view (fig. 3) is taken not from his classification (which recognizes five separate lineages at the suborder level) but from a branching diagram provided in the same paper (1933, table 2). Forster (1955) followed Petrunkevitch's grouping when describing *Gradungula*, which he placed as the sister group of the other hypochiloid genera, an arrangement subsequently followed by Gertsch (1958) and Davies (1969).

### THE CRIBELLATAE

The following two sections are devoted to analysis of the classifications of hypochiloids that have been offered in the past. The question of the validity of the division of araneomorphs into cribellate and ecribellate groups is singled out first because there is certainly no other character that has caused more controversy in spider classification. Indeed, it is not uncommon even today to hear arachnologists speak of "the cribellate problem."

One of the insights provided by phylogenetic systematics is that when examining the status of any given character state at any given level of universality, there are only three possibilities: either the character state is symplesiomorphic in those taxa that share it or it is synapomorphic in them or it represents a parallelism (Hennig, 1965, fig. 1). Of course, Hennig's insight is not original; Pocock (1892) made this point quite clearly in his analysis of the Cribellatae, but many modern arachnologists (and other systematists) have ignored this crucial axiom of character analysis.

The first task of character analysis is identification of homologous character states. There is no problem here as all arachnologists since Thorell's time have agreed that both the cribellum (a broad platelike structure sometimes found in front of the anterior [lateral] spinnerets of araneomorphs) and the colulus (a smaller fleshy lobe found between or in front of the same spinnerets of other araneomorphs, and of which several degenerative forms are known) are homologous with the anterior median spinnerets of

liphistiids; these homologies have been well established by embryological studies (Dahl, 1901; Montgomery, 1909). Thus the only question is whether the cribellum and colulus are also homologous to each other; in other words, are there two separate transformation series (anterior median spinnerets to cribellum and anterior median spinnerets to colulus) or only one (anterior median spinnerets to cribellum to colulus, or alternately, anterior median spinnerets to colulus to cribellum)? If the first model holds, then cribellate and colulate spiders could both represent monophyletic groups; if the second model holds, one or both groups are not monophyletic.

In attempting to answer this question, the first difficulty encountered is that of clearly delimiting the cribellum and colulus (Lehtinen, 1967, pp. 398-403). Since some Agelenidae, Desidae, and Hersiliidae have a large and even platelike colulus, the only defining character of the cribellum seems to be the possession of functional spigots. However, a number of species of various groups are known in which the cribellum is functional in females, but not in males (which are thus colulate; Lehtinen, 1967). In other words, a colulus is simply a non-functional cribellum, and the two structures are therefore homologous.

Given that homology, is the presence of a functional cribellum in some araneomorphs a symplesiomorphy, a synapomorphy, or a parallelism? No one has argued seriously in favor of the last hypothesis, presumably because the cribellum is a complex structure and is associated with the calamistrum, one or two rows of setae on the fourth metatarsus used to comb silk from the numerous spigots on the cribellum. As pointed out in the last section, however, numerous authors over the last century have treated the presence of a functional cribellum as a synapomorphy. What is the nature of the evidence in favor of such a decision? Kaestner (1968), following Crome (1955), distinguished cribellates from ecribellates on the basis of the number of dorsoventral abdominal muscles (four pairs in cribellates, three or fewer in ecribellates). This character (1) does not seem to work, since Millot (1933) demonstrated that the abdomen of *Ectatosticta* has only three pairs of dorsoventral muscles, and Millot (1936) indicated that at least some Dictynidae, Psechridae, and Filistatidae resemble ecribellates in having three pairs of dor-



soventral muscles (plus anterior "latero-cardiac" muscles) rather than other cribellates such as the Eresidae, which have four pairs of dorsoventral (plus the latero-cardiac) muscles; (2) would not argue for the monophyly of the Cribellatae even if it did work, since out-group comparison with both *Liphisti* (Millot, in Bristowe, 1933) and *Heptathela* (Marples, 1968, fig. 4) indicates that the presence of four pairs of dorsoventral muscles is plesiomorphic; and (3) cannot, even disregarding the parallelisms in some mygalomorphs and cribellates, be regarded as synapomorphic for ecribellates, because it is not the same pair of muscles that is lost in all the ecribellate groups (Millot, 1936). Thus, although the abdominal musculature may provide useful data at lower levels of universality, it does not aid in analysis of the Cribellatae. It would appear that, to date, the advocates of this classification have not been able to discover any derived character shared uniquely by all the ecribellates; for that matter, other than the functionally associated calamistrum, no additional derived characters shared uniquely by all the cribellates seem to have been discovered either.

There is, moreover, voluminous evidence arguing against regarding the functional cribellum as synapomorphic for the Cribellatae. Lehtinen (1967), Forster (1970), Baum (1972), Forster and Wilton (1973), and Davies (1976) have presented numerous cases of families and genera that contain both cribellate and ecribellate (i.e., colulate) species and that are nonetheless each united by obvious synapomorphies. To view the cribellum as derived from the colulus is to require that within each of these groups a non-functional colulus has been converted into a functional cribellum, with the silk gland connections, the associated calamistrum, and the appropriate behavior patterns being re-evolved in each lineage. Since the number of incongruent characters provided by all these groups is vastly greater than the single character of the cribellum, parsimony dictates rejection of the functional cribellum as a synapomorphy. Further, character correlation also falsifies that hypothesis. Of the five genera of araneomorphs with four pairs of cardiac ostia, *Hypochilus*, *Ectatosticta*, *Hickmania*, and *Thaïda* are cribellate. *Gradungula* was described as ecribellate, and the fact that Marples (1968) knew only ecribellate gradungulids was certainly instrumental in his decision to accept

the functional cribellum as synapomorphic, a decision that ruined an otherwise impeccable analysis of hypochiloid interrelationships. The discovery of as yet undescribed cribellate gradungulids (R. R. Forster, personal commun.) should provide the final nail for the coffin of the Cribellatae.

Thus it appears that there is a single transformation series (anterior median spinnerets to cribellum to fleshy colulus to reduced colulus bearing setae to colular setae only to colular setae absent). If this view is correct, the cribellum is a synapomorphy, but a synapomorphy for all araneomorphs rather than just for those with a functional cribellum. That the homologue of the anterior median spinnerets is functional must obviously be primitive for spiders. Since the calamistrum disappears whenever the homologue of the anterior median spinnerets loses its function (even in males of species whose females have calamistra and a functional cribellum; Shear, 1970), the only derived character of the Cribellatae (fused anterior median spinnerets) is the same as one of the derived characters of the Araneomorphae. To put it baldly, all true spiders are cribellates; in some the cribellum has simply lost the function it primitively had. Moreover, the transformation to a colulus is clearly not a synapomorphy for all colulates; it has happened at least twice (independently in the Gradungulidae and in other araneomorphs) and in all probability a great number of times. The cribellate nature of Araneomorphae is reflected below in the enlargement of the Neocribellatae to include all araneomorphs other than *Hypochilus* and *Ectatosticta*.

## A CRITIQUE

Evolutionary systematists often maintain that the cladistic emphasis on shared derived characters is merely an explicit statement of what they have always done. To some extent this is true, since random chance will dictate that of any two groups distinguished by alternate states of the same character, one will be monophyletic and the other might be. But one has merely to look at past spider classifications to discern how frequently groups have been delineated by shared primitive characters only.

For example, Thorell and Dahl placed the hypochiloids with the mygalomorphs since both groups have two pairs of lungs. Thorell's Dipneumones is a group based on a purported synap-

omorphy, but out-group comparison with amblypygids shows clearly that the presence of four lungs is primitive for spiders and therefore cannot be used to demonstrate relationship between any two subgroups of spiders.

The division of araneomorphs into hypochiloids and non-hypochiloids (Dipneumonomorphae plus Apneumonomorphae) by Petrunkevitch (1933) is a parallel case; each of the character states listed by Petrunkevitch as characterizing the Hypochilomorphae (abdomen without tergites, cribellum present, four pairs of ostia, two pairs of lungs, diaxial chelicerae, endochelicer al poison glands, coxal glands with one outlet, endites present, maxillary glands unicellular, and three tarsal claws) that is still known to be accurate (the cribellum is lost in some gradungulids; *Hickmania*, *Gradungula*, and *Thaida* have endocephalic poison glands; the maxillary glands of all five genera are multicellular [see Marples, 1968]) is indicated on his own table as being plesiomorphic for araneomorphs. The monophyly of the Hypochilomorphae has been effectively disputed by both Lehtinen (1967) and Marples (1968).

The third view of hypochilomorph interrelationships, placing them with other haplogyne families, is more difficult to deal with. This view was presented by Petrunkevitch (1923) and repeated, with minor differences, by Lehtinen (1967). Although Lehtinen claimed to be presenting a phylogenetic classification, both his and the early Petrunkevitch arrangement are typical evolutionary classifications and share the fundamental flaw of such systems. Since neither author has presented a list of shared derived character states uniting such groups, it is not possible to falsify their proposals. Since we do not know how many (if any) synapomorphies support such groupings, we can never know whether we have found enough conflicting characters to have falsified those groupings. Any proposal that cannot be potentially falsified is unscientific. Both those authors have united *Hypochilus* with haplogyne ecribellates; I am unaware of any shared derived characters supporting that grouping, and there are several characters, discussed below, that support a closer relationship of those haplogyne families to other araneomorphs than to *Hypochilus*. Petrunkevitch (1933) eventually abandoned this view; if Lehtinen still accepts it, it is to be

hoped that he will present the shared derived characters needed to provide his groups with a basis that can be discussed and evaluated scientifically. It is unfortunate that Lehtinen's superb analysis of the evolution of the cribellum and the inadequacy of many classical groups was presented together with undocumented proposals of new groupings. Such undocumented groupings may be heuristic when offered as preliminary suggestions, but when used as the basis for entire classifications (as they frequently are by evolutionary systematists), they represent authoritarianism and not science.

## CHARACTERS

The distributions of the states of the following numbered characters are used to support a cladogram (fig. 7) in which a lineage containing only *Hypochilus* and *Ectatosticta* is shown as the sister group of all other Araneomorphae.

1. In *Ectatosticta* (Millot, in Bristowe, 1933) and *Hypochilus* (Marples, 1968) the thoracenteron (the prosomal portion of the midgut) has diverticula that extend into the base of the chelicerae. According to Millot (1933) who had earlier (Millot, 1931) studied the thoracenteron of numerous araneomorphs, *Liphistius* is the only other genus in which the diverticula are known to extend into the chelicerae. *Hickmania*, *Thaida*, and *Gradungula* lack the anteriorly extended diverticula (Marples, 1968). Immediate out-group comparison with mygalomorphs indicates that the absence of cheliceral diverticula is plesiomorphic. The presence of cheliceral diverticula in *Liphistius* might tend to contradict this polarity hypothesis, but both *Heptathela* (Millot, in Bristowe, 1933) and amblypygids (Millot, 1949, fig. 337) lack them. To consider the presence of cheliceral diverticula synapomorphic for Araneae (and therefore plesiomorphic for any spider) requires three separate cases of character reversal (in *Heptathela*, Mygalomorphae, and Araneomorphae other than *Hypochilus* and *Ectatosticta*) and is therefore a less parsimonious hypothesis than the polarity proposed here, which requires one case of parallelism in the acquisition of cheliceral diverticula (between *Liphistius* and *Hypochilus* plus *Ectatosticta*).

2. *Hypochilus* and *Ectatosticta* have distinct concavities on the median surface of the chelic-



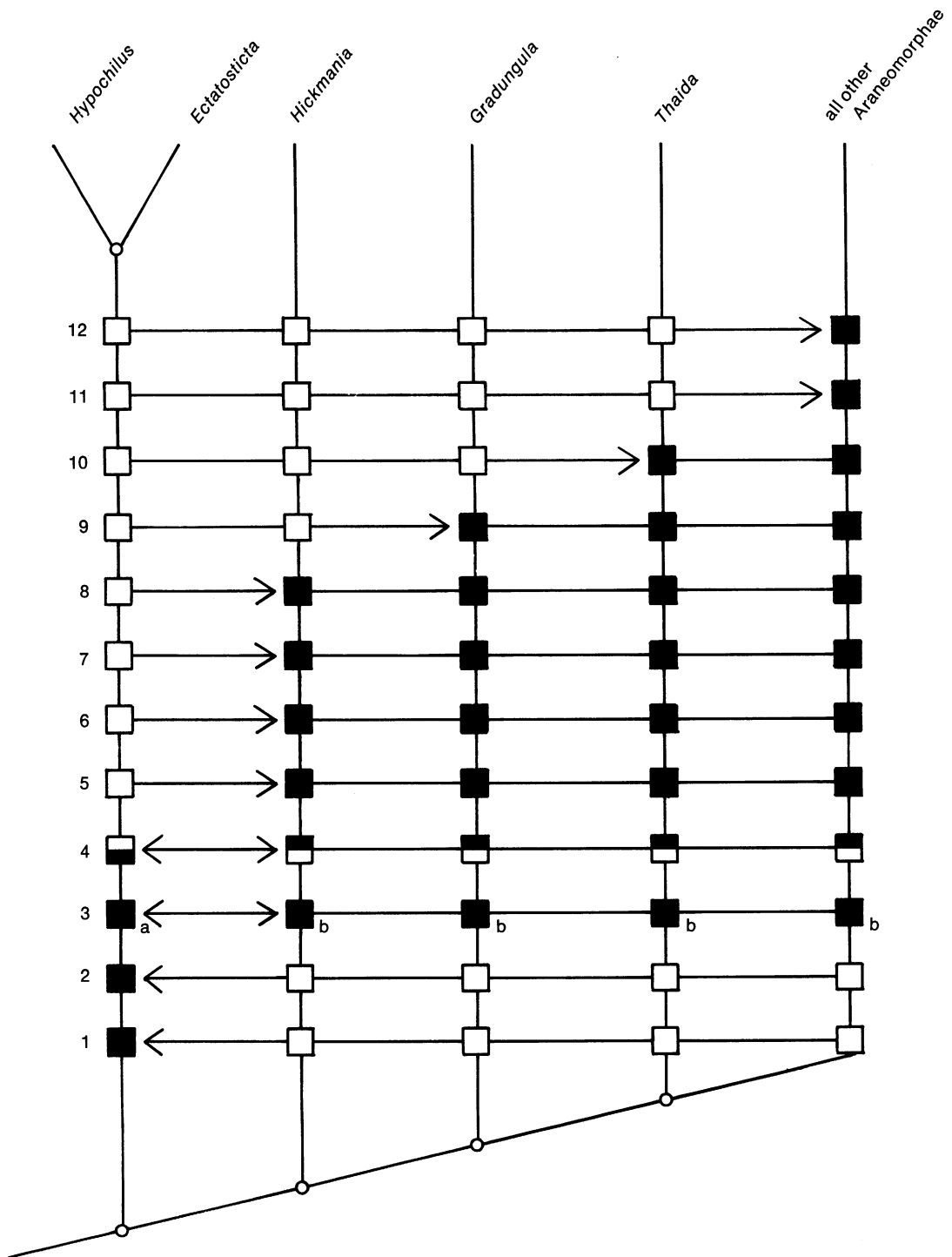
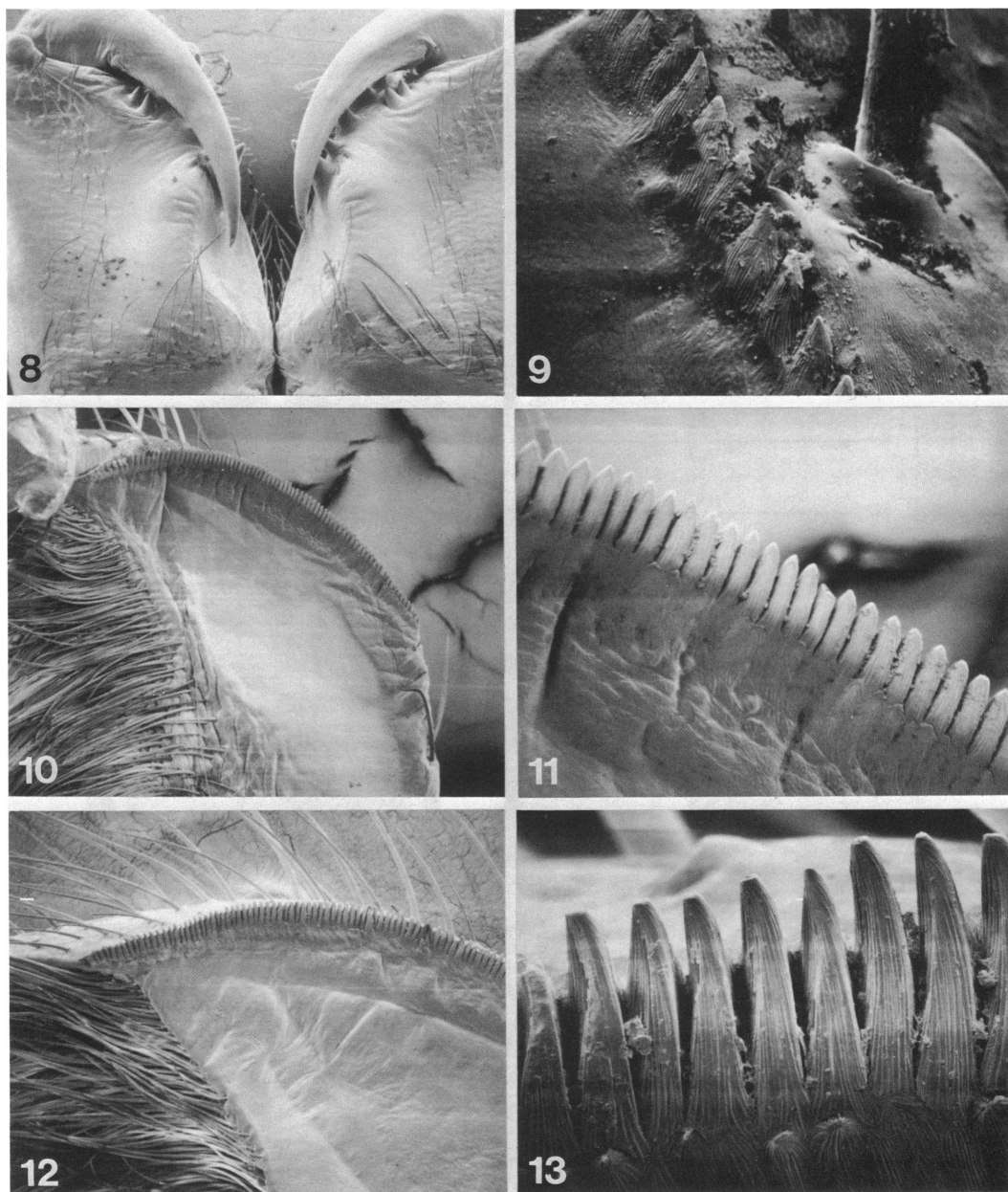


FIG. 7. Cladogram of hypochiloid interrelationships. Numbers refer to characters discussed in text. Dark squares denote apomorphic character states; partially darkened squares denote transformation series of uncertain polarity; subscript letters denote different, independently derived apomorphic states of a single character.



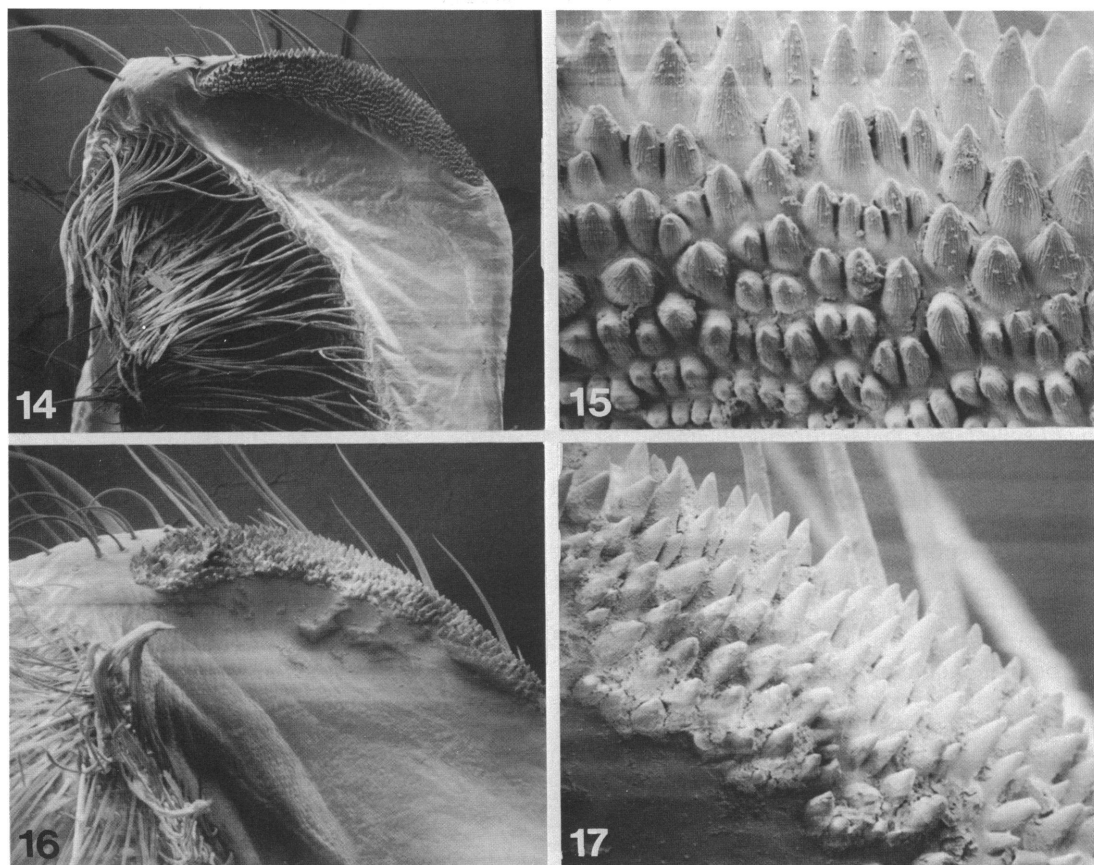
FIGS. 8-13. Scanning electron micrographs. 8. *Hypochilus* sp., chelicerae, posterior view, 60X. 9-13. Serrulae of females, anterior views. 9. *Gradungula* sp., 1300X. 10, 11. *Thaida* sp., 120X, 600X. 12, 13. *Hickmania* sp., 130X, 1300X.

erae (fig. 8) into which the tips of the long fangs fit when closed. These concavities are not found in the other hypochiloid genera nor, to my knowledge, in other spiders, and their presence is

regarded as autapomorphic for the lineage containing *Hypochilus* and *Ectatosticta*.

3. Marples (1968) noted that two types of serrula (a group of toothlike structures situated





FIGS. 14-17. Scanning electron micrographs of female serrulae, anterior views. 14, 15. *Hypochilus* sp., 120X, 1200X. 16, 17. *Ectatosticta* sp., 130X, 650X.

at the ventral tip of the anterior surface of the palpal endites) are found in araneomorph spiders. Most have a single row of closely spaced teeth; *Thaïda* (figs. 10, 11), *Gradungula* (fig. 9), *Hickmania* (figs. 12, 13), and the non-hypochiloid araneomorphs (including the other cribellates and the haplogyne ecribellates) have this type of serrula. In *Hypochilus* (figs. 14, 15) and *Ectatosticta* (figs. 16, 17), however, the serrula consists of a plate bearing several parallel rows of teeth. To judge which state is derived, a wide variety of mygalomorphs (listed below) were examined with light and scanning electron microscopy. Most mygalomorphs lack serrulae, and those that have been found generally consist of a patch of scattered teeth not aligned in distinct rows (as in fig. 18). Further comments on mygalomorph serrulae will be found in the section on Atypoidea

below. Since neither type of araneomorph serrula is found in mygalomorphs or liphistiids, both the multiple row type of *Hypochilus* and *Ectatosticta* (character 3a) and the single row type of all other araneomorphs (character 3b) are regarded as apomorphic.

4. Marples (1968) examined the musculature associated with the cuticle-lined foregut of a wide variety of spiders (although he did not provide a complete list of examined taxa) and noted that in most mygalomorphs and araneomorphs the dorsal dilator muscles of the pharynx originate dorsally on the carapace and insert on the pharyngeal lobes (a pair of dorsally directed cuticular folds situated at the juncture of the pharynx and esophagus); the anterior dilator muscles of the pharynx also originate dorsally on the carapace but insert on a groove of the phar-

ynx anterior of the pharyngeal lobes. Among the hypochiloids, *Hickmania*, *Gradungula*, and *Thaïda* have muscular systems of this type. In *Hypochilus* and *Ectatosticta*, however, the pharyngeal dilators have the same insertions but originate anteriorly on an apodeme of the rostrum. Immediate out-group comparison with the Mygalomorphae suggests that a carapace origin is the plesiomorphic state of the character, but both the liphistiid genus *Heptathela* (Marples, 1968) and amblypygids (Millot, 1949, fig. 334) have a rostral origin for at least the anterior dilators. As a result, the polarity of this transformation series seems indeterminable; if the rostral origin is plesiomorphic for opisthothelina spiders, one case of parallelism is required (between Mygalomorphae and araneomorphs other than *Hypochilus* and *Ectatosticta*), whereas if the carapace origin is plesiomorphic for opisthothelina spiders, one case of character reversal is required (in the lineage containing *Hypochilus* and *Ectatosticta*). Although parallelism may in fact be more common in evolutionary sequences than character reversal, both polarity hypotheses are equally parsimonious and there is no compelling reason to prefer one over the other. Thus the distribution of the states of this character supports the dichotomy between *Hypochilus* plus *Ectatosticta* and all other Araneomorphae, and the monophyly of one group or the other, but we do not know which.

This character could also be used to support an alternative cladogram in which *Hypochilus* and *Ectatosticta* constitute the sister group of all other Opisthothelae rather than of all other Araneomorphae, but a much larger number of synapomorphies (the presence of modified anterior median spinnerets, fewer than three articles in the posterior lateral spinnerets, diaxial chelicerae, coxal glands with a single opening, and maxillary glands opening on a sieve; Platnick and Gertsch, 1976) unite those genera with the other araneomorphs.

5. The venom glands of *Hypochilus* (Petrunkévitch, 1933) and *Ectatosticta* (Millot, 1933) are endocheliceral and do not extend into the cephalothorax; the venom glands of *Hickmania* (Marples, 1968), *Gradungula* (Forster, 1955), *Thaïda* (Zapfe, 1955), and the other araneo-

morphs that have such glands (Petrunkévitch, 1933) do extend into the cephalothorax. Mygalomorphs and liphistiids have endocheliceral poison glands, and the endocephalic glands of araneomorphs other than *Hypochilus* and *Ectatosticta* are regarded as synapomorphic.

6. In liphistiids and most mygalomorphs the endosternite has ventral extensions that reach the cuticle of the labium and sternum and are attached there at rounded sigilla. Gertsch (1958) noted that *Ectatosticta* have sternal sigilla, and Marples (1968) demonstrated that both *Ectatosticta* and *Hypochilus* have a pair of labial sigilla. In the other hypochiloids and araneomorphs, the ventral extensions of the endosternite do not reach the cuticle (Marples, 1968), and the shortening of both the sternal and labial endosternite extensions is regarded as synapomorphic for araneomorphs other than *Hypochilus* and *Ectatosticta* (with a parallel shortening being found in some mygalomorphs). Lehtinen (1967) indicated that some Filistatidae appear (externally) to have sigilla; this needs to be confirmed by internal examination of the endosternite.

7. Marples (1968) examined the coxal glands of the hypochiloids and confirmed that all five genera resemble araneomorphs rather than liphistiids and mygalomorphs in having a single outlet at the base of the first coxae and lacking an outlet at the base of the third coxae. However, he also noted that although *Hickmania*, *Gradungula*, and *Thaïda* have the simple inverted U-shaped ducts of other araneomorphs, *Hypochilus* and *Ectatosticta* have highly convoluted ducts like those of mygalomorphs (Buxton, 1913, diagram B3) and liphistiids (Millot, in Bristowe, 1933). Thus out-group comparison indicates that acquisition of the inverted U-shaped duct is apomorphic.

8. Millot (1933) indicated that all spiders have four ventral abdominal invaginations of the cuticle forming short endosternites and representing the posterior margins of the anterior abdominal segments (bearing the anterior and posterior respiratory organs and spinnerets), and that *Liphistius* retain in addition five extra posterior endosternites reflecting the primitive abdominal segmentation. Marples (1968) indicated that *Heptathela* also retain the five extra abdomi-

nal endosternites, and that *Hypochilus* and *Ectatosticta* (but not the other hypochiloids) retain the most anterior of the extra invaginations. Since the endosternites reflect abdominal segmentation that is primitive by both ontogenetic evidence and out-group comparison, the loss of the fifth endosternite is regarded as a synapomorphy for Araneomorphae other than *Hypochilus* and *Ectatosticta* (paralleled in the Mygalomorphae).

9. It has been argued elsewhere (Platnick and Gertsch, 1976) that the presence of two pairs of spermathecae is primitive for spiders; among the Araneomorphae, only *Hypochilus*, *Ectatosticta*, and *Hickmania* retain two pairs of spermathecae. The loss of the second pair of spermathecae is regarded as a synapomorphy for *Gradungula*, *Thaida*, and all other araneomorphs (with parallelism in some mygalomorphs). Some non-hypochiloid araneomorphs have two longitudinally interconnected receptacles on each side of the internal female genitalia, but these are clearly different from the side-by-side, non-interconnected spermathecae of liphistiids, atypoids, and some hypochiloids, and are presumably specializations of single spermathecae. The single median receptacles of some other araneomorphs are presumably specializations acquired by fusion. Kraus and Baur's (1974, figs. 42-44) observations of what may be a strongly reduced single median receptacle in some *Atypus* may provide evidence against the polarity adopted here; ontogenetic studies might help to resolve the question.

10. The posterior respiratory organs of *Hypochilus*, *Ectatosticta*, *Hickmania*, and *Gradungula* are book lungs, whereas those of *Thaida* and all other Araneomorphae are tracheae. Out-group comparison with Mygalomorphae, Mesothelae, and Amblypygi indicates that the presence of posterior book lungs is plesiomorphic, and replacement of the posterior pair of lungs with tracheae is regarded as a synapomorphy for *Thaida* plus the non-hypochiloid araneomorphs.

11. Millot (1933) pointed out that *Ectatosticta* resembles mygalomorphs rather than araneomorphs in having the opisthosomal portion of the midgut M-shaped in lateral view rather than straight, and Marples (1968, fig. 4) has shown that all five hypochiloid genera resemble mygalomorphs rather than the other araneomorphs in having an M-shaped intestine.

Consideration of the straight intestine as a synapomorphy for the non-hypochiloid Araneomorphae is also supported by the presence of an M-shaped intestine in both *Liphistius* (Millot, in Bristowe, 1933) and *Heptathela* (Marples, 1968).

12. Most araneomorphs have only two or three pairs of heart ostia. Among the hypochiloid genera, however, *Thaida* (Zapfe, 1955), *Gradungula* (Forster, 1955), *Hickmania* (Marples, 1968), *Ectatosticta* (Millot, 1933), and *Hypochilus* (Petrunkévitch, 1933) all have four pairs of ostia. Mygalomorphs have three or four pairs of ostia, but the presence of five pairs in *Liphistius* (Petrunkévitch, 1933) and six pairs in *Amblypygi* (Millot, 1949) provides ample evidence that the direction of the transformation series is toward reduction in number. The presence of three or fewer pairs of ostia is regarded as synapomorphic for the non-hypochiloid Araneomorphae (with parallelism in some mygalomorphs).

H. W. Levi has argued (*in litt.*) that the presence of four pairs of cardiac ostia and two pairs of book lungs are necessarily correlated with each other for physiological reasons, and that the two features therefore cannot be considered separate characters. That *Thaida* has four pairs of cardiac ostia but only a single pair of lungs seems to be a sufficient refutation of that contention.

There are a few other characters not included in figure 7 that may serve to support the dichotomy between *Hypochilus* plus *Ectatosticta* and all other Araneomorphae. First, the male palpi of *Hypochilus* and *Ectatosticta* are peculiar in that the alveolus and bulb are situated at the apex of a long cymbium (Gertsch, 1958, figs. 17, 27). In the other hypochiloids the bulb has its normal (for most araneomorphs) basal placement. Out-group comparison with mygalomorphs and liphistiids is not particularly useful in this case since the cymbium in those groups is generally so short that the bulb cannot be judged to be either basal or apical. Second, *Hypochilus* and *Ectatosticta* have calamistra composed of two rows of hairs; the other hypochiloid genera and, to my knowledge, all cribellates other than a few Amaurobiidae have calamistra consisting of a single row of hairs. It is tempting to regard the biseriate cala-

mistrum as derived on the basis of frequency alone, but since out-group comparison is inoperative (because mygalomorphs and liphistiids have no calamistrum) and ontogenetic evidence is lacking, no well defended polarity judgment is possible. Third, Marples (1968) reported that the anal tubercles of *Hypochilus* and *Ectatosticta* (but not the other hypochiloids) have multicellular glands known elsewhere in araneomorphs only in the Oecobiidae (including Urocteinae); a polarity hypothesis on this character must await study of the anal tubercles of mygalomorphs and liphistiids.

Finally, there are derived characters defining each of the hypochiloid genera. *Hypochilus* has false articulations in the tarsi and a spine-bearing cymbial apophysis on the male palp (Gertsch, 1958, fig. 17) not found in the other genera, *Ectatosticta* a uniquely serrate cymbial tip (Gertsch, 1958, figs. 26, 27), *Hickmania* an apically twisted male embolus (Gertsch, 1958, figs. 34, 37), *Gradungula* elongated proclaws on legs I and II (Forster, 1955, fig. 2), and *Thaida* a raised, semicircular, flangelike embolus (Gertsch, 1958, fig. 41).

### THE ATYPOIDEA

Recent workers, following the lead of Simon (1892), have often divided the Mygalomorphae into two groups, the Atypoidea (containing the families Atypidae, Antrodiaetidae, and Mecicobothriidae) and the Ctenizoidea (containing the remaining families). The monophyly of these superfamilies has been defended by Chamberlin and Ivie (1945) and Coyle (1971, 1975), even though this hypothesis requires parallelism in the acquisition of a rastellum and trapdoor burrowing habits between the Antrodiaetidae and Ctenizidae, and in the acquisition of elongated posterior lateral spinnerets and sheet-web building behavior between the Mecicobothriidae and Dipluridae.

Six characters have been used to support this dichotomy: (1) atypoids generally have six spinnerets, rarely four, and ctenizoids generally have four spinnerets, rarely six; (2) the anal tubercle is moderately separated from the spinnerets in atypoids, approximate to the spinnerets in cteni-

zoids; (3) the abdomen of atypoids bears tergites lacking in ctenizoids; (4) the penultimate male has a swollen palp in atypoids but not in ctenizoids; (5) atypoid females have two pairs of spermathecae, ctenizoid females usually a single pair; and (6) the male palp of atypoids has a conductor lacking in most ctenizoids.

Out-group comparison with liphistiids indicates that the larger number of spinnerets, the separated anal tubercle, the presence of abdominal tergites, a swollen pedipalp in the penultimate male, and two pairs of spermathecae are the plesiomorphic character states. It has been argued elsewhere (Platnick and Gertsch, 1976) that a homologue of the palpal conductor is probably present in liphistiids and that the presence of a conductor is historically associated with the presence of two pairs of spermathecae in females and therefore a necessary step in the evolution of the ctenizoid palp. If this argument is correct, and the presence of a palpal conductor and doubled spermathecae in the most primitive ctenizoids and araneomorphs argues strongly for it, the Atypoidea are not united by any known shared derived character.

For purposes of out-group comparison in connection with character 3 above, the endites of a variety of mygalomorph genera were examined: *Atypus* and *Calomimata* (Atypidae); *Antrodiaetus*, *Aliatypus*, and *Atypoides* (Antrodiaetidae); *Hexura* and *Megahexura* (Mecicobothriidae); *Ummidia*, *Galeosoma*, *Bothriocyrtum*, and *Nemesia* (Ctenizidae); *Actinopus* and *Missulena* (Actinopodidae); *Migas*, *Micromesomma*, and *Calathotarsus* (Migidae); *Euagrus*, *Atrax*, *Accola*, and *Hexathele* (Dipluridae); *Psalistops* (Barychelidae); *Ischnocolus*, *Eurypelma*, and *Grammostola* (Theraphosidae); *Paratropis* (Paratropidae); and an unidentified genus of Pycnothelidae. Of these, only the Mecicobothriidae and Dipluridae have a serrula. The typical diplurid serrula is found in *Hexathele* and *Euagrus* (figs. 20-22; see also Marples, 1968, fig. 5), and consists of a broad patch of more or less scattered teeth; this patch is greatly reduced in size in *Atrax* (fig. 23), and modified into a row of sharply pointed teeth that resembles that of araneomorphs (but is sinuous and subapical rather than evenly curved and apical) in *Accola* (figs. 24, 25). Both *Hexura*



(figs. 18, 19) and *Megahexura* have serrulae like those of typical diplurids.

To determine whether or not the presence of a serrula in the Dipluridae and Mecicobothriidae should be regarded as a synapomorphy, *Liphistius* and *Heptathela* were examined. No structure resembling a serrula was found in *Heptathela*, even under scanning electron microscopy. *Liphistius* has a structure that might be regarded as a precursor of a serrula; the cuticle of the anterior surface of the endite is scalelike (fig. 26), and toward the lateral side of the endite the tips of the cuticular scales become more elevated and toothlike (fig. 27). Even if this structure is regarded as a serrula, it is clearly quite different in position and morphology from that found in *Hexura* and *Hexathele*, and the latter structure can be considered derived.

Thus on the basis of two characters, serrula morphology and the length of the posterior lateral spinnerets, the Mecicobothriidae appear to be more closely related to the Dipluridae than to the Antrodiaetidae or Atypidae (and might well be regarded as merely the most plesiomorphic members of the Dipluridae), and the superfamily Atypoidea, at least as currently delimited, appears not to be monophyletic.

### CLASSIFICATION

According to Petrunkevitch (1923, p. 145), "Taxonomy is the mirror of evolution." What is the meaning of this poetic phrase? In what way can the taxonomic hierarchy of organisms "mirror" evolution? Numerous authors, including Hennig (1966), have argued at length that a hierarchical classification can include all the information found in a cladogram, that is, that it can accurately "reflect" both the content of branches and their sequence. It has not been sufficiently stressed, however, that a hierarchical classification can reflect *only* that information (Cracraft, 1974).

What evolutionary information is conveyed when a reference is made to, say, the family Xidae? All we can say is that (1) there is a purportedly monophyletic group containing the genus *Xus* and perhaps other genera as well, and (2) that the sister-group of the Xidae, whatever it

is, will also be a family (Yidae). In other words, given the following classification:

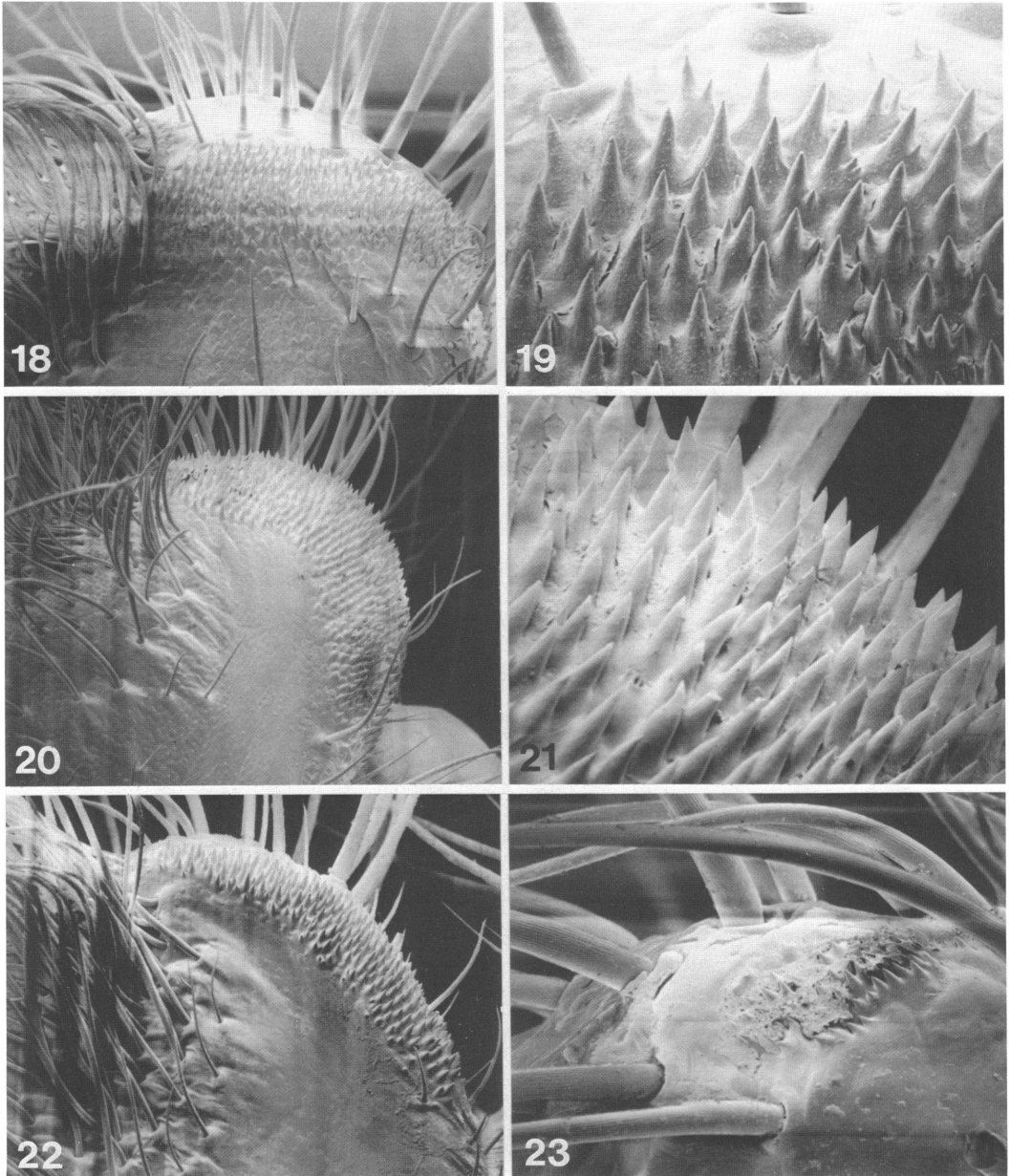
- (1) Order Araneae
  - Suborder Mesothelae
  - Suborder Opisthothelae
    - Infraorder Mygalomorphae
    - Infraorder Araneomorphae
      - Section Cribellatae
        - Cohort Palaeocribellatae
        - Cohort Neocribellatae
      - Section Ecibellatae
        - Cohort Dipneumones
        - Cohort Apneumones

the only evolutionary information we can obtain is the system of interrelationships portrayed in figure 4. Thus, what the taxonomic hierarchy "mirrors" is a hypothesized phylogeny.

Evolutionary systematists argue that additional information can be included in a classification that reflects the amount of change that has occurred in different branches. Disregarding the empirical difficulty of measuring the amount of change, such a systematist might argue that "Yes, the branching sequence is like that in figure 4, but the Mygalomorphae are very similar to the Mesothelae in appearance and biology. The Araneomorphae, however, are very different; they have been able to fill a greater variety of niches because of their increased reliance on silk, and have therefore radiated and become tremendously diverse. This diversity and shift into a new adaptive zone should be recognized at a higher taxonomic level, as in the following classification:

- (2) Order Araneae
  - Suborder Mesothelae
  - Suborder Mygalomorphae
  - Suborder Araneomorphae
    - Section Cribellatae, etc."

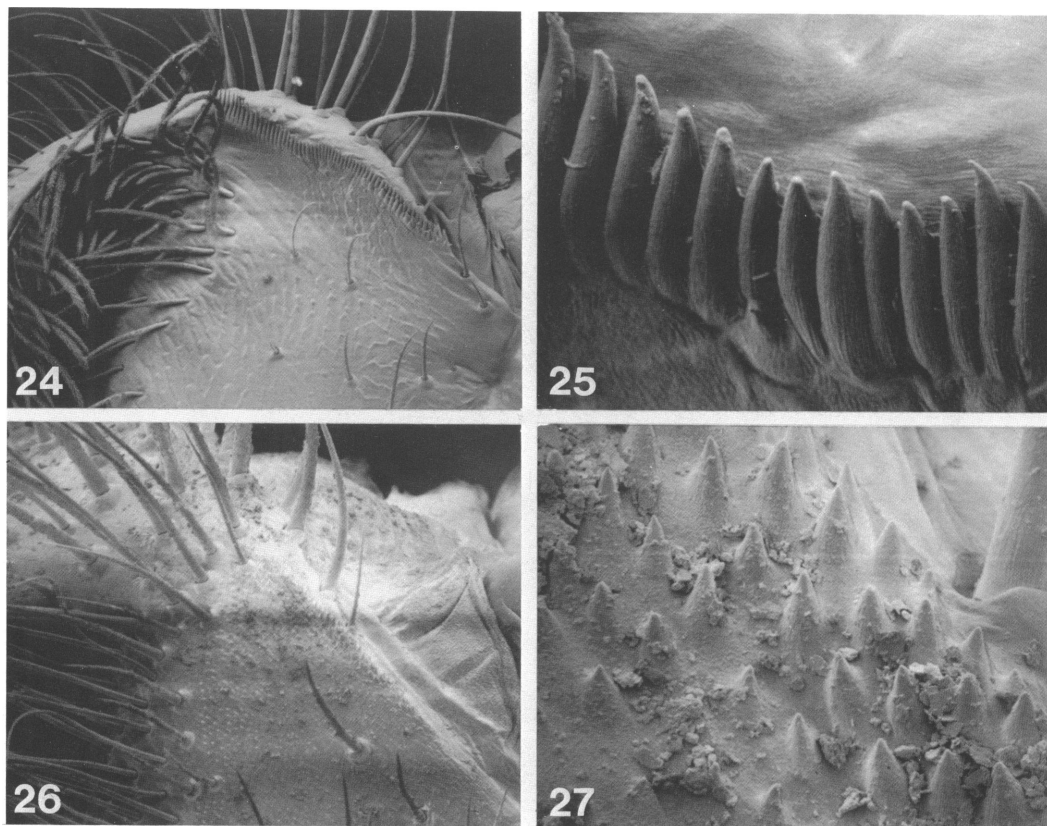
But what evolutionary information is contained in this hierarchy? If we use the hierarchy to construct a scheme of interrelationships like that of figure 4, we find that we get a different tree, resembling that of figure 3 in having three basal branches. In other words, where at first the hierarchy did convey some limited evolutionary in-



FIGS. 18-23. Scanning electron micrographs of female serrulae, anterior views. 18, 19. *Hexura* sp., 240 $\times$ , 1200 $\times$ . 20, 21. *Hexathele* sp., 125 $\times$ , 625 $\times$ . 22. *Euagrus* sp., 240 $\times$ . 23. *Atrax* sp., 260 $\times$ .

formation, it no longer does, because that small amount of information that it did include has now been distorted. In this case, the distortion is an omission of the information that mygalo-

morphs are more closely related to araneomorphs than to liphistiids. Had the argument been carried further and the Araneomorphae treated as equal in importance (in diversity, adaptive zone,



FIGS. 24-27. Scanning electron micrographs of female serrulae, anterior views. 24, 25. *Accola* sp., 240X, 2400X. 26, 27. *Liphistius* sp., 130X, 1300X.

or the like) to all other spiders, as in the following classification:

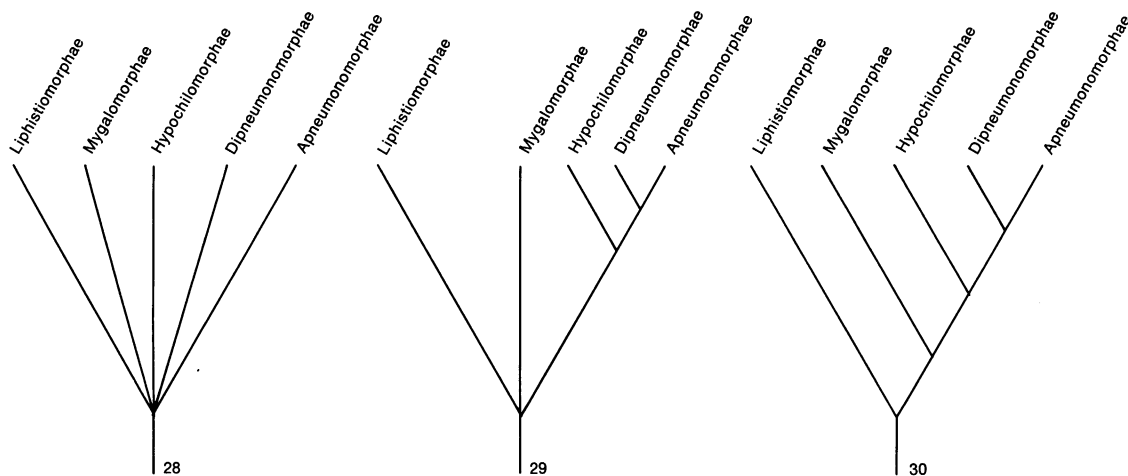
- (3) Order Araneae
  - Suborder Orthognatha
  - Infraorder Mesothelae
  - Infraorder Mygalomorphae
  - Suborder Labidognatha
  - Infraorder Araneomorphae

the distortion would be replacement of the intended hypothesis of relationships with an incorrect one. The question then is whether we want the taxonomic mirror to be flat, and reflect exactly the information put into it, or curved, and distort the information put into it. Since systematists have gone to considerable effort to compile the information in the first place, a flat mirror seems to be required.

How can we construct classifications that do reflect exactly the information put into them? Two methods have been suggested. One (subordination) requires that we name every monophyletic group (i.e., every inclusive taxon); the other (sequencing) does not. Take, for example, the classification proposed by Petrunkevitch (1933):

- (4) Order Araneae
  - Suborder Liphistiomorphae
  - Suborder Mygalomorphae
  - Suborder Hypochilomorphae
  - Suborder Dipneumonomorphae
  - Suborder Apneumonomorphae

In a subordinated classification, the number of immediate subtaxa within a group reflects the number of branches originating at that point, so if Petrunkevitch's classification was a subordi-



FIGS. 28-30. Cladograms and classifications, or, what did Petrunkevitch mean? 28. Petrunkevitch (1933) spider classification if subordinated. 29. Petrunkevitch (1933) branching diagram. 30. Petrunkevitch (1933) spider classification if sequenced. See text for explanation.

nated one, his cladogram would look like figure 28. In a sequenced classification, equally ranked taxa represent branches that arise in the order they are listed, so if Petrunkevitch's classification was a sequenced one, his cladogram would look like figure 30. Petrunkevitch provided his own branching diagram, like that of figure 29 (the dichotomy between Dipneumonomorphae and Apneumonomorphae represents his taxonomic grouping of what his diagram shows as four separate lineages). Clearly, Petrunkevitch subordinated the Liphistiomorphae and Mygalomorphae but sequenced the remaining three suborders, thereby eliminating two inclusive taxa (Araneomorphae, and an unnamed taxon for Dipneumonomorphae plus Apneumonomorphae). Millot (1933) criticized the Petrunkevitch system *because* it excluded the inclusive taxon Araneomorphae (and also because he doubted, with good reason, the monophyly of the Apneumonomorphae).

Marples (1968) presented a classification based on a cladogram like that in figure 6 and in which some of the groups (Cribellatae and Ecribellatae; Palaeocribellatae and Neocribellatae) are subordinated and some (the families of Neocribellatae and Ecribellatae) are sequenced. The cladogram shows that there are monophyletic groups containing all Neocribellatae except *Hick-*

*mania*, all Neocribellatae except *Hickmania* and *Thaïda*, and all Ecribellatae except *Gradungula*, but these inclusive taxa were not named by Marples.

Given, then, that there are three ways to construct a classification (subordination, sequencing, or a system combining the two), which is best? To answer the question, of course, one must know: best for what? If classifications are to be used by comparative biologists in general (including those who may be unfamiliar with the techniques of constructing them), we must presumably use either subordination or sequencing consistently throughout our classifications, as it is unlikely that the subtleties of a combined system will be understood by non-systematists. The use of sequencing eliminates some inclusive taxa, so the question is really, do we need inclusive taxa (i.e., names) for every monophyletic group? Given an infinite expansion of biological knowledge, every monophyletic group will eventually be found to have important generalizations true only of its members, and names for each such group will presumably be needed. The time when most genera of spiders will be so well known that every monophyletic subgrouping of species has important biological meaning is clearly very far off, yet at some level inclusive taxa are necessary for purposes of communication. For example,



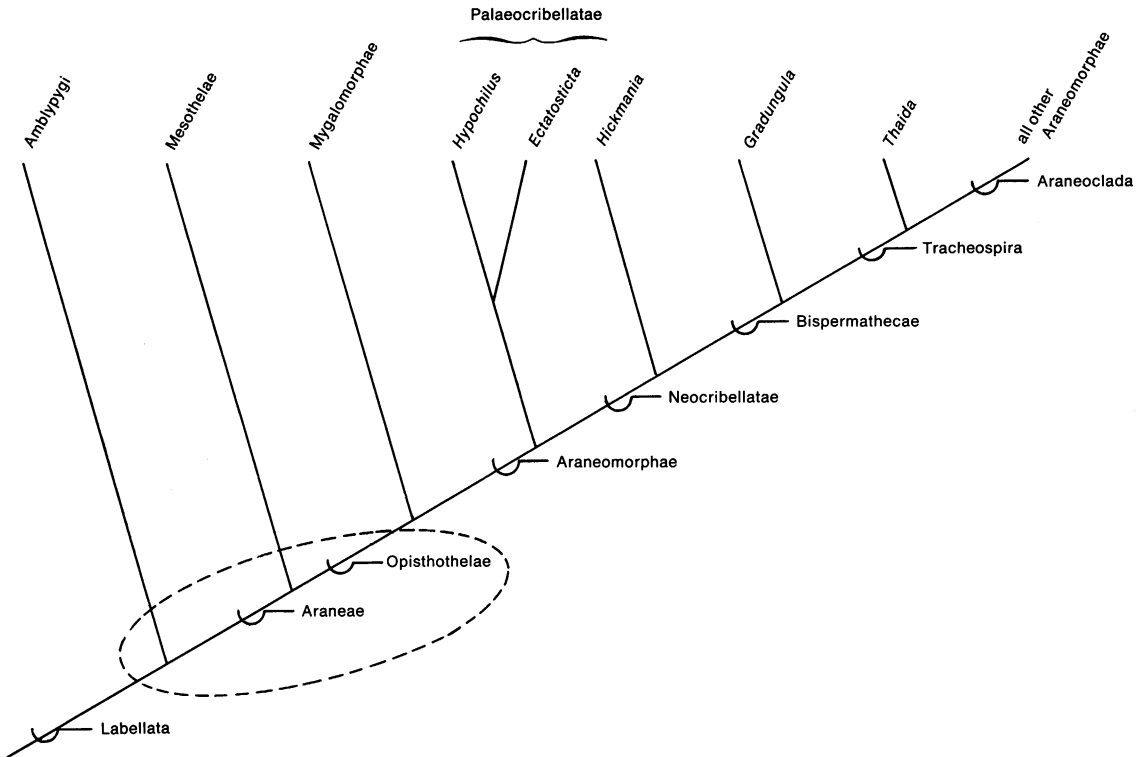


FIG. 31. Cladogram of hypochiloid spiders with inclusive taxa indicated. Circled area at lower left represents a single three-taxon statement.

given the cladogram shown in figure 31 and defended earlier, and the fact that the rank of Araneae has been, for our purposes, preset at the ordinal level, we could construct the following sequenced classification:

- (5) Order Araneae
- Suborder 1 Mesothelae
  - Suborder 2 Mygalomorphae
  - Suborder 3 Hypochilomorphae
  - Suborder 4 Hickmaniomorphae
  - Suborder 5 Gradungulomorphae
  - Suborder 6 Thaidomorphae
  - Suborder 7 [all other spiders]

Note that we must include the number of the suborder to indicate both that it has been sequenced and that the sister group of any one suborder is represented by all other suborders with a higher number taken together. Two points are clear: (1) we have lost some inclusive taxa (like Araneomorphae) whose names we now use fre-

quently, and (2) as the interrelationships of the non-hypochiloid araneomorphs are worked out, we may end up with numerous additional suborders. The choice of when to stop sequencing and shift to a categorical level lower than the suborder appears to be an arbitrary one, and it seems better to have (temporarily) useless names than not to have names for which there is a need. Those workers who do prefer a sequenced classification could relimit the Araneomorphae and use that name for suborder 7, without great damage to the present concept; they would have to be prepared, however, to relimit the group again when further divisions of the cladogram are established.

Since sequenced classifications omit important and unimportant inclusive taxa (at least by the standard of current usage) and combined systems are unlikely to be understood by the non-initiate, subordinated classifications seem best for use by comparative biologists in general.

In subordinated classifications, categories (rather than equally ranked taxa) are proliferated. Some authors, notably McKenna (1975), have provided new category names to deal with this problem, but such names are a source of confusion in that one must always turn back to the classification to determine which of two ranks (say, sublegion and magnorder) is higher. Farris (1976) has provided an ingenious mechanism of generating easily understood categories, and his system is followed in the classification presented below. The Farris method allows an infinite increase in the number of categories by proliferating their prefixes, of which only eight easily memorizable forms are used. To avoid nomenclatural complications from the International Code, it seems best to retain all the new names proposed below at the ordinal (rather than familial) level, so single prefix names are used down to the lowest ordinal rank (the picoorder), where the use of double prefix names is initiated.

Some comments on the classification proposed below are in order. The family Ectatostictidae Lehtinen is placed as a junior synonym of the Hypochilidae (NEW SYNONYMY); the sister-group relationship between *Hypochilus* and *Ectatosticta* can be expressed at the generic level without requiring redundant monotypic family names; a similar case is the purported sister-group relationship between *Liphistius* and *Heptathela* within the Liphistiidae. New names are introduced for three inclusive taxa (Bispermathecae, Tracheospira, and Araneoclada) that will prob-

ably become increasingly useful if the cladogram is corroborated as our knowledge grows. The corresponding new names for individual branches (Hickmanithecae, Gradungulospira, and Thaidoclada) will certainly be less used, because they are redundant with available generic and family names. Farris (1976) has proposed deleting such redundant names from classifications; they are included here because not to do so eliminates half of the information content of any taxonomic name, i.e., the knowledge that the sister group of a given taxon will have the same rank as that taxon.

Finally, to those who may find both the sequenced and subordinated classifications presented here intolerably radical (and certainly both have their drawbacks), I can only reply (1) that although no previously proposed classification is consistent with the cladogram shown in figure 31, numerous classifications that are consistent with it are possible; (2) that whether we recognize all monophyletic groups is of less importance than whether all the groups that we do recognize are monophyletic; and (3) that those workers who prefer to combine subordinated and sequenced systems are therefore free to do so. The two classifications presented here for purposes of comparison and evaluation can be ignored with impunity, but the cladogram proposed here cannot, because it is only by the use of such hypotheses of relationship that classifications can be falsifiable and that systematics can be a science.

## PROPOSED CLASSIFICATION

- Superorder Labellata Petrunkevitch, 1949
  - Order Amblypygi Thorell, 1900
  - Order Araneae Clerck, 1757
    - Suborder Mesothelae Pocock, 1892
      - Family Liphistiidae Thorell, 1869
    - Suborder Opisthothelae Pocock, 1892
      - Infraorder Mygalomorphae Pocock, 1892
        - [other families]
      - Infraorder Araneomorphae Smith, 1902
        - Microorder Palaeocribellatae Caporiacco, 1938, new rank
          - Family Hypochilidae Marx, 1888
        - Microorder Neocribellatae Caporiacco, 1938, new rank
          - Gigapicoorder Hickmanithecaceae, new
            - Family Hickmaniidae Lehtinen, 1967
          - Gigapicoorder Bispermathecaceae, new
            - Megapicoorder Gradungulospira, new
              - Family Gradungulidae Forster, 1955
            - Megapicoorder Tracheospira, new
              - Hyperpicoorder Thaidoclada, new
                - Family Thaididae Lehtinen, 1967
              - Hyperpicoorder Araneoclada, new
                - [other families]

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