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The Suborders of Spiders: A Cladistic Analysis (Arachnida, Araneae)

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"What, for instance, shall we do if we find fossils that are typical of the Mygalomorph and Arachnomorph forms save for the presence of segmentation? It is well within the bounds of possibility and we shall then have to decide whether a 'grandfather' is to be grouped with his descendants or 'his cousins'."

—W. S. Bristowe, 1933, p. 1033

"The synthetic or evolutionary method of classification . . . agrees with cladistics in the postulate that as complete as possible a reconstruction of phylogeny must precede the construction of a classification . . ."

—E. Mayr, 1974, p. 95

ABSTRACT

The methods of phylogenetic systematics are applied to the problem of the subordinal classification of spiders. Synapomorphies in external morphology, internal morphology, embryology, and karyology indicate that the Liphistiidae represent the sister group of all other Recent spiders. The two currently prevailing subordinal classifications of spiders (those of Bristowe and Gertsch) are rejected because they imply sister group relationships (between the Liphistiidae and, in the first case all of, and in the second case some of, the mygalomorph spiders) documented only by symplesiomorphic characters. A return to the earlier classification of Pocock, recognizing two suborders (Mesothelae and Opisthothelae) and two infraorders of Opisthothelae (Mygalomorphae and Araneomorphae), is advocated.

INTRODUCTION

The present paper represents an attempt to examine the higher classification of spiders from the viewpoint of phylogenetic systematics. The principles involved are that all named taxa must be strictly monophyletic (i.e., must contain all species assumed to be descendants of a hypothetical ancestral species; Nelson, 1971, 1973) and that such groups can be recognized only by

[1] Assistant Curator, Department of Entomology, the American Museum of Natural History.
[2] Curator Emeritus, Department of Entomology, the American Museum of Natural History.

the presence of shared, derived (synapomorphic) characters and not by the presence of shared, primitive (symplesiomorphic) characters (Hennig, 1966). By this means, the reconstruction of phylogeny is placed on an objective basis, as it involves character analysis only, and not (as seen in one recent classification of araneomorph spiders) the subjective recognition and evaluation of "basic patterns and evolutionary trends" (Lehtinen, 1967, p. 204). The cladograms produced differ from phylogenetic trees in that they do not attempt to specify unknowable ancestor-descendant relationships or unmeasurable differences in genetic similarity; they are, however, predictions of general synapomorphy and are thus testable and potentially falsifiable (and therefore scientific) hypotheses (Wiley, 1975).

As Schaeffer, Hecht, and Eldredge (1972) have pointed out, character analysis involves two separate processes, the recognition of transformation series of homologous character states and the determination of the polarity (primitive to derived sequence) of those transformation series; the first process presents no real difficulties for the characters described below. To determine which of two or more homologous states is primitive and which derived, we have used two sources of evidence, immediate out-group comparison and ontogeny; where such evidence is unavailable we have refrained from establishing polarities and merely indicate that the character distribution supports the monophyly of one or the other of two taxa even though we do not know which. The use of out-group comparison requires knowledge of the closest relative of the entire group under consideration, which in this case we suggest is the arachnid order Amblypygi. The hypothesis that spiders and amblypygids are sister groups is supported by at least two apparently autapomorphic characters: they are the only arachnids with subchelate chelicerae and with both a pumping pharynx and a pumping stomach (Kaestner, 1968). We thus hypothesize that any character state found in some but not all spiders and also in amblypygids is plesiomorphic, and its homologs apomorphic; this hypothesis can be falsified in any particular case by incongruence with more numerous synapomorphy patterns, but only one such incongruence has been detected in the characters used below. If

it can be shown that amblypygids and spiders are not each other's closest relatives, much of our analysis may be falsified; we would point out, however, that several authors who have recently addressed the problem of the interrelationships of the various arachnid orders (Petrunkevitch, 1955; Savory, 1971; Firstman, 1973; Yoshikura, 1975) have supported this hypothesis.

We thank Dr. Mohammad U. Shadab for providing the illustration of *Liphistius*, Mr. Robert J. Koestler for assistance with the scanning electron microscope, and Dr. Herbert W. Levi of the Museum of Comparative Zoology, Harvard University, for the loan of specimens. Drs. W. S. Bristowe, R. R. Forster, H. W. Levi, and R. T. Schuh read and commented on the manuscript.

HISTORY

Since the time of Pocock (1892) it has been recognized that the basic problem in the higher classification of spiders centers around the family Liphistiidae and its relationships; as he summarized it (pp. 307-308), "In the presence of chitinous plates on the upper surface of the abdomen and of two sternal plates on the anterior extremity of its under surface, in the extreme narrowness of the sternum, but above all in the position and structure of its spinning-mammillae, *Liphistius* differs from all known spiders; and no gradational forms are known which would lessen the value of these peculiarities. . . . The isolated position that *Liphistius* occupies with respect to other spiders can perhaps be best expressed by setting it apart by itself in a group equal in value to a group containing all the others. For these I propose the names Mesothelae and Opisthothelae, the terms being derived from the position of the spinning-organs." A cladogram can be easily derived from Pocock's strictly subordinated classification (fig. 1).

Petrunkevitch (1923, pp. 150-152) reacted to this classification: "Pocock's idea in separating the Liphistiidae in a special sub-order Mesothelae is undoubtedly sound, although the name chosen by him is misleading and therefore objectionable. . . . To correct this error and to make the names more uniform, I shall call this first sub-order Liphistiomorphae. . . . One might regard all spi-
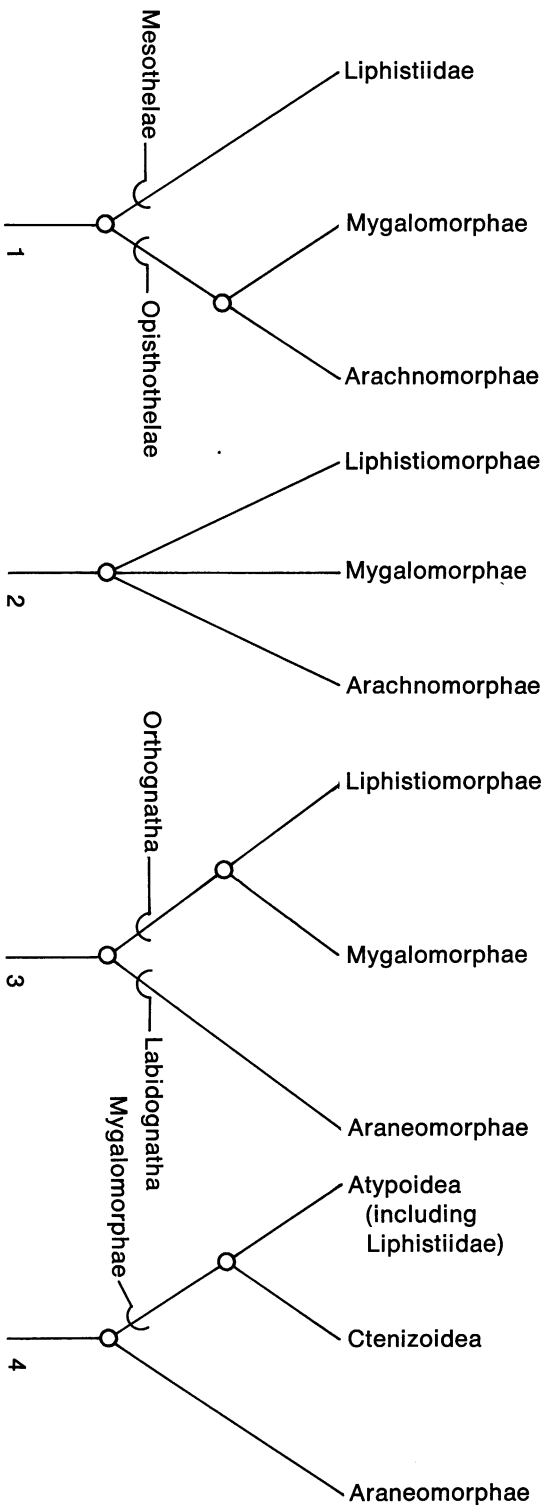
FIGS. 1-4. Cladograms derived from previous subordinal classifications of spiders. 1. Pocock (1892). 2. Petrunkevitch (1923). 3. Bristowe (1933), inclusive taxa from Millot (1949). 4. Gertsch (1949). Arachnomorphae and Araneomorphae are equivalent.

ders with an unsegmented abdomen as belonging to a sub-order equivalent in value and opposed to the Liphistiomorphae. Without calling such a group a sub-order, Pocock has applied to it the name Ophisthothelae. This, however, seems to me objectionable for two reasons: First, it would necessitate the creation of divisions under the sub-order, and, second, it would be reasonable only if the composition of the abdomen in all non-segmented spiders were the same. This, however, is not only far from being certain, but may altogether not be true. It is, for example, known that the heart in Arachnomorph spiders has three pairs of ostia, while in Mygalomorph spiders it has four pairs." From these comments and the classification he presented, it is evident that in 1923 Petrunkevitch accepted the monophyly of Liphistiomorphae, Mygalomorphae, and Arachnomorphae, but not of Opisthothelae; thus his scheme must be presented as a trichotomy (fig. 2). Among recent authors, Lehtinen has evidently accepted this scheme, as his dendrograms of the higher taxa of spiders (1967, figs. 1-7) all include a basal trichotomy for these three groups.

Bristowe (1933), after a detailed study and revision of the Liphistiidae, concluded (p. 1015) that "(a) the Liphistiids are more primitive than any other living spiders; (b) the Liphistiids are more closely related to the Mygalomorphae than to the Arachnomorphae, but they are not their direct ancestors; [and] (c) the Liphistiids deserve to rank as a suborder, Liphistiomorphae, equal in importance to the Mygalomorphae and the Arachnomorphae (for which the name Araneomorphae is substituted)." Expressed as a cladogram (fig. 3), Bristowe's second conclusion represents a prediction of general synapomorphy between Liphistiomorphae and Mygalomorphae, but Bristowe did not name an inclusive taxon for this clade. Most recent authors who have presented classifications involving three suborders have not provided cladograms or phylogenetic trees, and it is therefore difficult to determine whether they postulate phylogenies like that of Petrunkevitch (fig. 2) or Bristowe (fig. 3). One recently published diagram (Levi and Levi, 1968, p. 7) apparently adopts Bristowe's scheme, and Millot (1949, p. 719) explicitly accepts it by using an inclusive taxon (Orthognatha) for Liphistiomorphae plus Mygalomorphae.

Finally, Gertsch (1949) presented a classification accepting only two suborders (Mygalomorphae and Araneomorphae) in which the Liphistiidae are associated with the mygalomorph families Mecicobothriidae, Antrodiaetidae, and Atypidae in the superfamily Atypoidea and the other mygalomorph families are associated in the superfamily Ctenizoidea (fig. 4). This scheme has since won widespread acceptance by authors such as Archer (1948; although published prior to Gertsch's classification Archer credits Gertsch for the changes relevant here), Kaston (1972), Lehtinen (1975), and recently even Bristowe (1976). Gertsch's classification appeared in a popular book, and the justification of it was intended for publication as part of a revision of the North American Atypoidea that, for various reasons, has not yet been published. As the adoption of this classification has never been adequately defended in print, we have thought it best to begin the present analysis with a summary of the arguments presented in that unpublished manuscript. Sections in quotation marks are taken directly from the manuscript and represent a viewpoint prior to the application of cladistic principles to the problem.

THE ATYPOIDEA

In the following discussion, all references to the Atypoidea refer to the concept of the group held by Gertsch (1949): Liphistiidae, Mecicobothriidae, Antrodiaetidae, and Atypidae.

"It was mainly on the basis of dorsal segmentation and unique spinneret features that the liphistiids were first separated widely from other spiders. This separation belies the close relationship of the group to the other mygalomorph spiders. When associated with the Atypoidea the liphistiids still remain the most generalized representatives, separated by a substantial gap from the other families. Most of the features contributing to this gap are now known to be intergradient to those of other atypoids. The remaining ones seemingly exclusive to the liphistiids were enumerated by Bristowe (1933, p. 1016) and largely pertain to internal details of the brain (which shows evidence of 16 or 17 neuromeres, rather than 12, in the subesophageal nerve mass of the cephalothorax) and the heart (which in *Liphistius* at least has five pairs of

ostia) and in other internal features of the body. Since the Liphistiidae are obviously the most generalized of living spiders, it is to be expected that they should retain more primitive features than the families derived from their prototypes. All the spiders with orthognath chelicerae are here viewed as a closely related series from liphistiid to atypid, ctenizid, and theraphosid.

"The following alternative classification of the suborder Mygalomorphae emphasizes the similarities of the liphistiids to the other atypoid families and maintains them with the other orthognath families. It postulates that from Paleozoic liphistiines have been developed the following elements: A. the Atypoidea, all of which still retain some abdominal tergites, and B. the Ctenizoidea, coming from the atypoids as derivative types that have lost the abdominal tergites and revised many other characters. The living liphistiids have morphological features that suggest they are representative of the direct precursors of all orthognath spiders.

"The presence of sclerotized tergites on the dorsum of the abdomen is one of the prime features of all the Atypoidea. The 12 basic tergites are discernible in most liphistiids but the caudal ones are reduced or obsolete in some of the species. Most of the other atypoid families retain in the adult only the three or four at the base of the abdomen. The original caudal sternites cannot be detected in any living species but the segmental appearance of the venter is clearly apparent in the Liphistiidae and in most of the other families by at least modest sclerotization of the transverse lung plates and spinneret areas.

"When the group name Atypoidea was proposed to designate this series of mygalomorph spiders (Gertsch, 1949) with distinct marks of primary segmentation in the form of hardened tergal plates, the term 'segmented' had been explicitly restricted to members of the family Liphistiidae. In his paper on the liphistiids Bristowe (1933, p. 1034) stated that 'one would describe all other spiders as being unsegmented in the adult stages (though of course spinnerets represent segments just as much as in the Liphistiidae).' Although well marked tergites in *Antrodiaetus* and other genera were noticed by a few students, they were passed over swiftly as something only analogous to the plates of the liphistiids. Many years ago and on several occasions I

discussed this matter with Dr. Alexander Petrunkevitch, and in 1939 (p. 150) he modified his definition of the suborder Mygalomorphae (which excluded the liphistiids) to admit that the abdomen of some were 'very imperfectly segmented, at most with two or three anterior tergites.' Since that time it has become plain that the tergites of the liphistiids and the other atypoid families are homologous structures marking the basic dorsal segmentation of the abdomen.

"The tarsus of the pedipalp of the immature male atypoid is distinctively swollen in the penultimate stadium, a condition not yet noted for any of the Ctenizoidea. The swollen tarsus of *Heptathela kimurai* Kishida (Liphistiidae) was mistakenly believed by Kishida (1923), and his thesis for a time accepted by others, to signify that the species lacked the typical copulatory organ of other spiders. Bristowe's conclusion (1933, p. 1024) that the swollen condition merely represented immaturity is the correct one, and the swelling is a normal condition of the penultimate stadia of males of all four families.

"The pedipalp of the mature male bears a terminal intromittent organ of simple design in all families of the Atypoidea. The bulb is mostly subterminal in position and bears two usually evident terminal elements, the embolus and conductor. The palpus of the Liphistiidae is often described as being specialized but its simple design is evident in spite of development of various accessory processes. The presence of an elemental conductor is postulated here in spite of the failure of students who have described and illustrated these organs to precisely identify the various parts with modern nomenclature. Just when the doubled condition of these elements of the male and the complementary ones of the female genitalia were established is a subject for speculation. I prefer to believe that this is an ancient condition established during an early period when spiders were first beginning to pass the spermatophore to the female by means of their palpal appendages.

"In this connection it can be mentioned that the male palpi of the most generalized araneomorph spiders, the Hypochilidae and recently established related families, have conductors as sheaths for their emboli, and these are paralleled in the females by the presence of doubled seminal

receptacles. Some students believe that such araneomorph spiders were possibly contemporaneous with Carboniferous spiders, presumably already at that time derived from them and sharing many of their features. If this were to be verified, it would strengthen the thesis that the doubled condition of the accessory genital structures was of early origin.

"When ancient arachnids became free of an aquatic habitat, it was necessary to make provision for safe transfer of the male sex products to the female in a terrestrial environment. Direct transfer by means of a spermatophore probably was a first invention of scorpions and this method or slight modifications of it was adopted by all arachnids. The ancient male spider at first voided a spermatophore upon a handy substratum; only later was a web evolved to receive it. He then picked it up in his pedipalps for transfer to the female genital orifice. Both pedipalps were simultaneously pressed with force into the front face of the ectodermal lining of the vulva where the seminal products were then released. Eventually there were produced two pouches opening directly into the vaginal area, each representing the introduced portion of a pedipalp, allowing for advantageous storage of the seminal products. It is my belief that at this early period each of these pouches was of double nature, pressed into two distinct receptacles on each side by the complementary elements of the male palpus, the basic embolus and its accompanying process or conductor. The double nature of each side is easily seen in the thick pouch of glandular material enclosing the sclerotized receptacles of present-day atypoids. At this time the conductor was not an accessory shield for the embolus but of equal status in that it pressed its own imprint into the wall of the vulva. Two receptacles on each side is the standard number for the liphistiids, the three other atypoid families, the most generalized of the diplurids (*Scotinoecus* and *Hexathele*), and the primitive araneomorph spiders, the Hypochilidae and related families. The pattern was apparently set early; thus, in *Hexathele* the paired receptacles persist on each side even though a single embolus is now present.

"In recapitulation of the above discussion, we come up with the various tenets on which the present classification is based. The generalized

liphistiines during the Carboniferous Period became widespread in the northern hemisphere and probably during the Mesozoic Era, from which we have little or no fossil spider records, gave rise to the Atypoidea. These still retain few or all of the original abdominal tergites, more numerous spinnerets, and doubled elements in the palpus and epigynum. It is postulated that the doubled condition of both male and female genitalia was standard for the liphistiines and then was passed on to the Atypoidea. The living liphistiids are considered to be representative of the generalized liphistiines from which the Atypoidea originated but at the same time closely enough related to the other families, as exemplified by the Antrodiaetidae, to be contained within a single grouping."

A CRITIQUE

It is an unfortunate but unescapable fact that analysis of a problem such as the one considered here involves a certain amount of criticism of the work of others, in this case of Petrunkevitch and Bristowe, both of whom have had long and honorable careers and added much valuable data to the literature of arachnology. However, it is our opinion that "The expectations of theory color perception to such a degree that new notions seldom arise from facts collected under the influence of old pictures of the world. New pictures must cast their influence before facts can be seen in different perspective," and that "Science progresses more by the introduction of new world-views or 'pictures' than by the steady accumulation of information" (Eldredge and Gould, 1972, pp. 82, 86). In applying the new world-view of cladistics, we hope we have been as critical of our own previous opinions as of those of others, and we remain aware that this worldview is equally subject to criticism and eventual replacement. It is none the less historically interesting that by the use of this methodology we have come to precisely the same conclusions as did Pocock (whose knowledge of orthognath spiders has never been surpassed) in 1892; this suggests to us that the methods of phylogenetic systematics are basically sound and were grasped, even if only intuitively, by the best of early taxonomists.

The conception of Petrunkevitch (fig. 2) is

rather easily dealt with; it is, in essence, an expression of defeat, and implies that the question "Are the mygalomorph spiders more closely related to araneomorphs or to liphistiids?" cannot

be answered. In phylogenetic terms, this question is equivalent to "Do the mygalomorphs and araneomorphs share a hypothetical common ancestor not also shared with the liphistiids?"
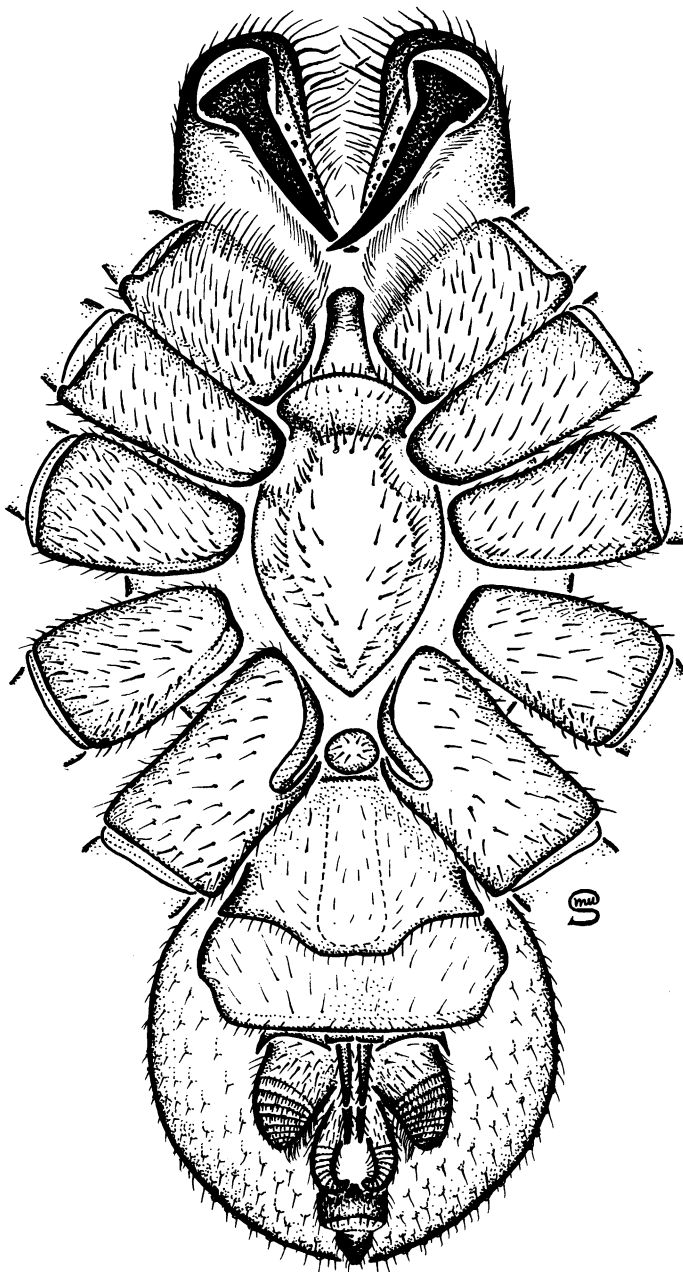
FIG. 5. *Liphistius* sp., ventral view. Note invagination of coxae IV, rounded first abdominal sternite in front of first lung plate, and the number, position, and segmentation of the spinnerets.

and in operational terms it is equivalent to "Do the mygalomorphs and araneomorphs show shared, derived characters not also shared with the liphistiids?" We believe this question is answerable (see below) and therefore reject Petrunkevitch's classification. Note that his scheme is not automatically rejected because it is not dichotomous; it is not a requirement of cladistic analysis (as has been claimed by its opponents) that all speciation be dichotomous, but only that it be assumed to be so if the question "Is taxon A more closely related to B than to C?" can be answered by reference to synapomorphic characters.

The conception of Bristowe (fig. 3) is much more explicit, and requires that at least one derived character shared by the Liphistiidae plus Mygalomorphae (Orthognatha), but not by the Araneomorphae (Labidognatha), be found. So far as we can determine, no such character has yet been brought forth by adherents of this view. Early arachnologists used some characters to distinguish orthognaths and labidognaths that are now known to be invalid: the hypochilids (Labidognatha) share with the orthognaths endocheliceral poison glands, two pairs of book lungs, and the absence of tracheae, and the number of heart ostia has been shown to vary from five to three pairs in orthognaths and from four to two pairs in labidognaths; interestingly, the orthognath state of each of these characters except for the first is also found in amblypygids, and can therefore be considered plesiomorphic (poison glands are not found in amblypygids). The orientation of the chelicerae does serve to distinguish the groups, being paraxial in orthognaths and diaxial in labidognaths, but amblypygids also have paraxial chelicerae and that state is also presumed plesiomorphic. Orthognaths have two pairs of coxal glands and labidognaths a single pair, but both states occur in amblypygids and the polarity of this transformation series appears indeterminable at this level.

Gertsch's association of the liphistiids and atypoid mygalomorphs (fig. 4) was based primarily on recognition of the homology of the abdominal tergites in the two groups; out-group comparison shows the presence of tergites to be plesiomorphic (although incongruence with other synapomorphy patterns indicates that the loss of the tergites is not a synapomorphy but a parallelism, having occurred independently in Mygalomorphae and Araneomorphae). The union of these groups may also be supported by possible genitalic homologies, although functional analyses are needed to document such homologies; since comparison with amblypygids indicates that primitive spiders probably did transfer a spermatophore (for a behavioral defense of this hypothesis, see Alexander and Ewer, 1957), and since it is difficult to imagine a male spider manipulating a spermatophore with palpi consisting only of a terminal embolus (even if both palpi cooperate in the attempt, a behaviorally unlikely possibility), the arguments presented above seem sufficient to indicate that even if these homologies do exist, the genitalic similarities between liphistiids and atypoids must be considered symplesiomorphic.

In short, we have been unable to find any shared, derived characters that would support the association of the Liphistiidae with either all or some of the Mygalomorphae; the similarities of the two groups seem to be restricted to shared, primitive characters, and while these transformation series provide good evidence for the monophyly of the Araneomorphae, they tell us nothing of the interrelationships of the various orthognath groups. Unless we maintain a purely phenetic classification, for either Bristowe's (1933) or Gertsch's (1949) groupings to be adopted it would have to be shown not only that there are synapomorphic characters uniting the orthognaths, but that there are more of them than we have been able to demonstrate below between mygalomorphs and araneomorphs.

CHARACTERS

The distributions of the states of the following numbered characters are used to support a cladogram (fig. 6) in which the Liphistiidae are shown as the sister group of all other Recent spiders. Although there are enough external morphological characters available to support this hypothesis, we have used in addition characters taken from internal morphology, embryology, and karyology. It might be objected that too few species have been examined to allow generalizations on these other characters; we

reject this argument because (1) there is no reason to suspect that these characters are any more variable than is external morphology, and they may well be more conservative and homeostatic than is external morphology, and (2) if we insist on having all the "facts" before constructing hypotheses, we shall always have only "facts" and never hypotheses. Further, we suspect that most such objections have their root in a belief that a classification is a permanent statement of truth about the world, when it is in actuality only a hypothesis and as such is potentially testable (by studying the distributions of character states other than those used to originally construct it) and falsifiable.

1. The fourth coxae of both *Liphistius* and *Heptathela* have peculiar invaginations at their posteromedian corners (fig. 5); so far as we are aware these invaginations are found neither in other spiders nor in amblypygids, and their presence is considered autapomorphic for the Liphistiidae.

2. Suzuki (1954) has shown that the Japanese liphistiid *Heptathela kimurai* has a haploid chromosome number of 48; all other spiders, including atypoid and ctenizoid mygalomorphs, that have been examined (now approaching 200 species) have haploid numbers of 24 or fewer; since Millot and Tuzet (1934) reported a haploid number of 24 for the amblypygid *Sarax sarawakensis*, the high chromosome number of liphistiids is considered apomorphic.

3. The morphology of the trichobothria on the dorsal surface of the distal leg segments appears to differ in liphistiids and other spiders. A wide variety of mygalomorph genera have been investigated. Most have a base consisting of a rounded dome covered on one side by a flattened plate (figs. 13, 15, 17); genera with this type of structure include *Hexura* (Mecicobothriidae); *Antrodiaetus* and *Atypoides* (Antrodiaetidae); *Atypus* (Atypidae); *Ummidia*, *Cyclo-*
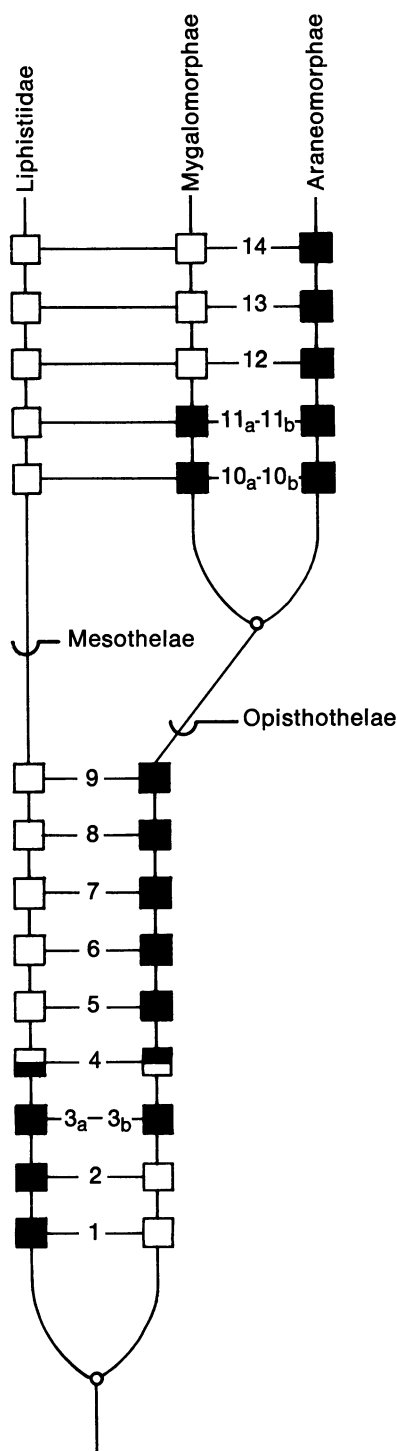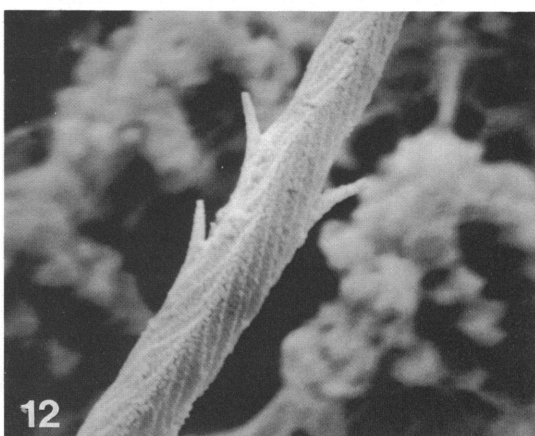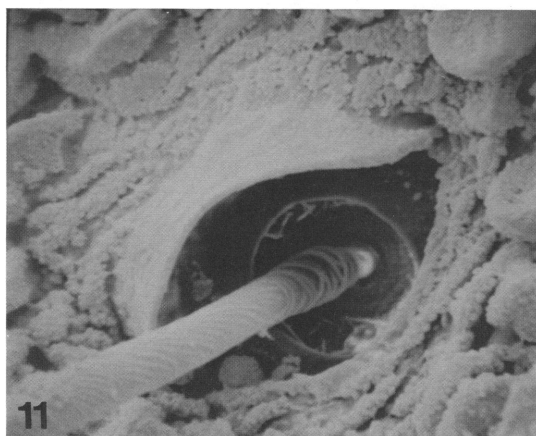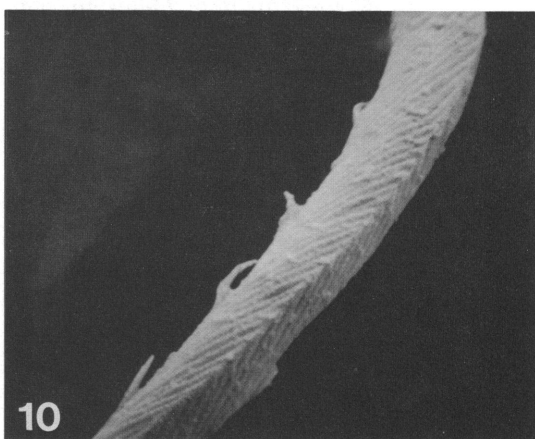

FIG. 6. Cladogram of the major groups of spiders. Numbers refer to characters discussed in text. Dark squares denote apomorphic character states; partially darkened squares denote transformation series of uncertain polarity; pairs of numbers denote different, independently derived apomorphic states of a single character.
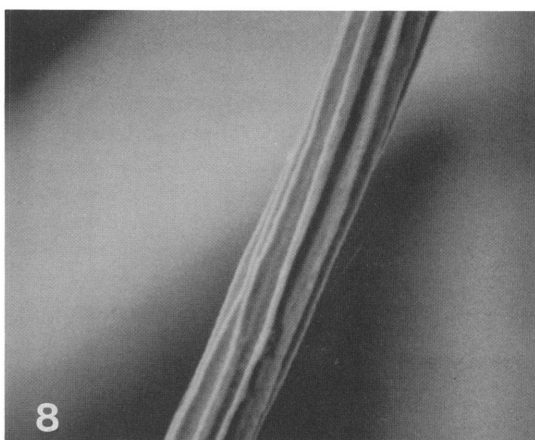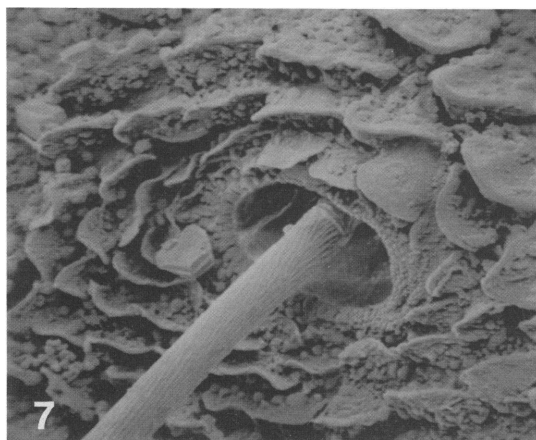
FIGS. 7-12. Metatarsal trichobothrial bases (left) and hairs (right). 7, 8. *Paraphrynus* sp. (Ambly-pygi), 2000×, 6400×. 9, 10. *Liphistius* sp. (Liphistiidae), 2000×, 5000×. 11, 12. *Heptathela* sp. (Liphistiidae), 2800×, 6800×.
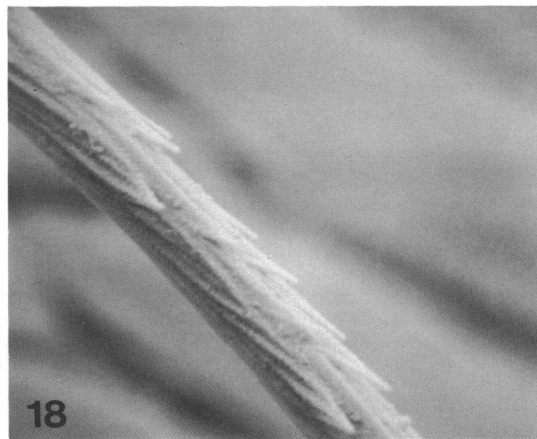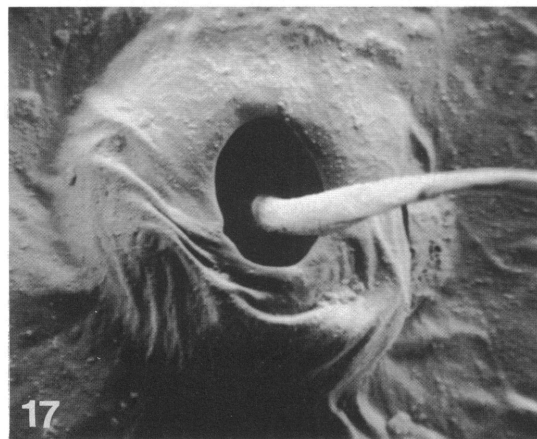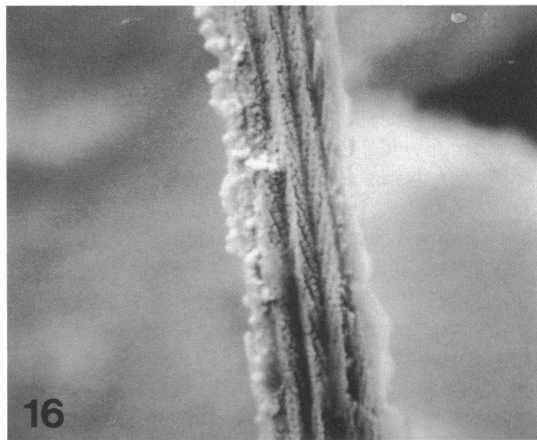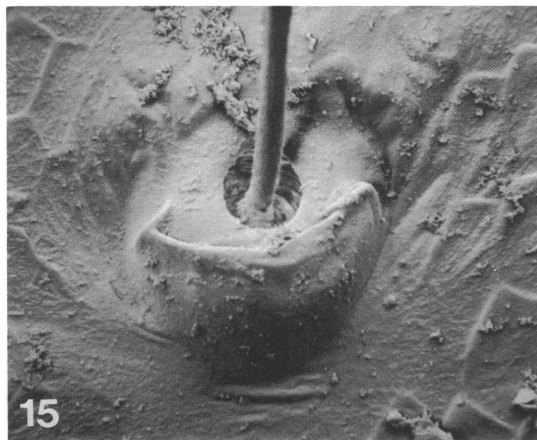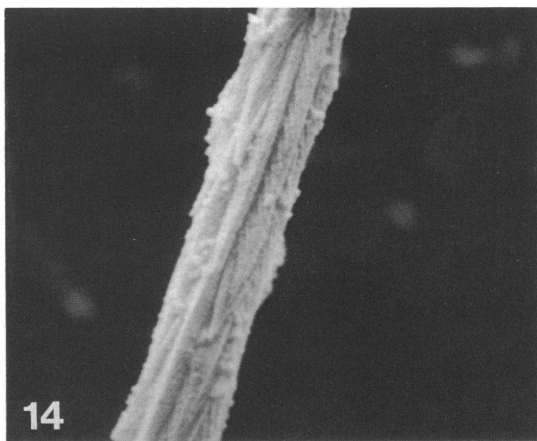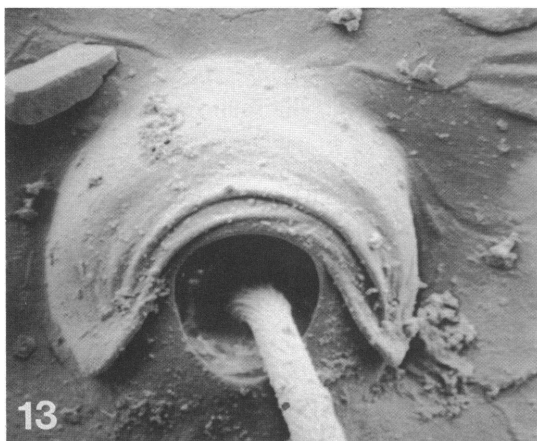
FIGS. 13-18. Metatarsal trichobothrial bases (left) and hairs (right). 13, 14. *Hexura* sp. (Mecicobothriidae), 2800×, 6800×. 15, 16. *Atypoides* sp. (Antrodiaetidae), 1400×, 6900×. 17, 18. *Atypus* sp. (Atypidae), 2800×, 6900×.

cosmia, *Galeosoma*, and *Bothriocyrtum* (Ctenizidae); *Atrax*, *Hexathele*, *Tryssothele*, *Evagrus*, and *Microhexura* (Dipluridae); and *Psalistops* (Barychelidae). Other genera have a dome only (although it may bear numerous parallel wrinkles or ridges): *Myrmekiaphila*, *Nemesia*, *Aganippe*, and *Arbanitis* (Ctenizidae); *Actinopus* and *Missulena* (Actinopodidae); *Micromesomma* and *Migas* (Migidae); *Barychelus* (Barychelidae); *Avicularia* (Theraphosidae); an undetermined genus of Pycnothelidae; and *Paratropis* (Paratropididae). The Araneomorphae have not yet been surveyed in as great detail but preliminary results as well as the micrographs published by Lehtinen (1975) show the dome and single plate structure to be widespread in that group. Both *Liphistius* and *Heptathela*, however, show a different structure, involving a dome and two flattened plates (figs. 9 and 11); in the latter genus the dome is recessed considerably below the plates. Investigation of an amblypygid trichobothrium (*Paraphrynus*, figs. 7, 8) shows no dome or plate surrounding the socket; we therefore regard both the two plate (3a) and single plate or simple dome (3b) conditions as being derived.

4. The structure of the lateral spinnerets differs widely among the three main groups of spiders. In the Liphistiidae they are multisegmented (fig. 5), with up to 12 articles being discernible. The posterior lateral spinnerets of mygalomorphs have three (rarely four in some Atypidae and Mecicobothriidae) articles, whereas the homologous (Machado, 1945; Marples, 1967) posterior spinnerets of araneomorphs have one or two articles. As amblypygids have no spinnerets, out-group comparison is inoperative at this level. Ontogenetic evidence also fails us, as the lateral spinnerets are unisegmented at eclosion and only later develop their annulations (Yoshikura, 1955, fig. 14; Vachon, 1959, fig. 16). Thus, the distribution of these character states supports the monophyly of either the Mesothelae (multisegmented) or Opisthothelae (four or fewer articles), but because we cannot determine the polarity of the transformation series at this level we do not know which.

5. The liphistiids differ from other spiders in having eight (*Liphistius*) or seven (*Heptathela*) spinnerets rather than six or fewer. Since the cribellum and colulus of araneomorphs are known to result from the fusion during ontogeny

of the two "missing" anterior median spinnerets (Montgomery, 1909), the loss of these spinnerets is considered apomorphic.

6. In liphistiids the spinnerets are situated far forward on the abdomen, just behind the second lung plate and far from the anus. In other spiders, the caudal segments are fused during ontogeny (Montgomery, 1909) and the spinnerets and anus become approximate at the end of the abdomen. The latter condition is therefore considered apomorphic.

7. Liphistiids differ from all other spiders in retaining the sternite of the first abdominal segment as a small, round sclerite on the pedicel, near the posteriod pair of coxae (fig. 5). Amblypygids also retain this sternite as a more or less sclerotized structure on the pedicel (Kaestner, 1941, fig. 8) and the loss of the sternite is considered apomorphic.

8. The third abdominal segment of liphistiids, bearing the second pair of lungs, is a distinct sclerite ventrally (fig. 5). This sternite is ventrally distinct in amblypygids but not in spiders other than the liphistiids, and the loss of this external indication of segmentation is considered apomorphic.

9. According to Millot (1933) the subesophageal ganglia of the four species of Liphistiidae that he examined differ from those of mygalomorphs and araneomorphs in consisting of 17 rather than 12 neuromeres. Millot (1949, p. 295) also reported 17 neuromeres in amblypygids, so the lower number is considered apomorphic.

The following characters refer to the status of Mygalomorphae and Araneomorphae within the Opisthothelae. Note that at this level the immediate out-group is no longer the Amblypygi but the Mesothelae, and that the polarity of previously uncertain transformation series can be determined at this level.

10. In mygalomorph spiders, the anterior median spinnerets disappear completely, even embryologically (Holm, 1954; Yoshikura, 1958, 1972). In araneomorphs, however, they appear embryologically and are fused to form a cribellum or colulus; the latter structure has several degenerative states in which it is reduced to a relatively weakly sclerotized area or to a clump of modified setae, or it may even disappear entirely during ontogeny. Both states, the immediate loss of the anterior median spinnerets (10a)

or their conversion to a cribellum or colulus with occasional subsequent loss (10b) are considered independently derived as compared with the retention of the spinnerets throughout ontogeny in the Mesothelae.

11. As noted above (character 4) mygalomorphs have three or four articles in their posterior lateral spinnerets (11a) and araneomorphs one or two (11b). Both states differ from the multisegmented condition of liphistiids and are presumed to be independently derived.

12. The paraxial chelicerae of mygalomorphs are shared with liphistiids and the diaxial chelicerae of araneomorphs are considered apomorphic.

13. Liphistiids and mygalomorphs have two pairs of coxal glands, araneomorphs a single pair (Millot, 1949); the loss is considered apomorphic.

14. According to Petrunkevitch (1933), the maxillary glands of mygalomorphs open in a single row but are clumped together on a sieve in araneomorphs. The mygalomorph state is shared with the liphistiids and the araneomorph state considered derived.

FOSSILS

Four families of spiders are known from the Paleozoic, all from Europe and North America. All show traces of abdominal segmentation, but Petrunkevitch (1955) placed two families, the Arthromygalidae and Arthrolycosidae, in the Liphistiomorphae "on account of their clearly segmented abdomen and general appearance. Their spinnerets are not preserved . . ." (p. 132), whereas two others, the Archaeometidae and Pyritaraneidae, were placed in the Araneomorphae. Examination of photographs and illustrations of the specimens involved reveals to us no characters that would allow the definitive placement of any in a suborder, although the specimens might be reexamined to see if they show traces of the invaginations of the fourth coxae found in liphistiids. We agree with Lehtinen (1967, p. 397) that "The structure of the Paleozoic spiders is not sufficiently well known for a reasonable placing of them in the present classification . . .". This is not entirely a disadvantage; so long as our cladograms are restricted to Recent organisms, they can be used directly in studies of historical biogeography, but when

fossil taxa are included this utility disappears because of the inability of the cladogram (or any other methodology) to distinguish between an ancestor and a plesiomorphic sister group.

CLASSIFICATION

Given the cladogram shown in figure 6, how should we classify these groups? Two methods are available: strict subordination (Hennig, 1966) and phyletic sequencing (Nelson, 1972). Both methods produce classifications that are cladistic in that all named taxa are strictly monophyletic; they differ in the recognition of inclusive taxa. A sequenced classification implies that any taxon of a given rank represents the sister group of all subsequently listed taxa of coordinate rank. Thus from figure 6 we could derive the two following sequenced classifications:

1) Order Araneae
    Suborder 1. Liphistiomorphae
    Suborder 2. Mygalomorphae
    Suborder 3. Araneomorphae, or
2) Order Araneae
    Suborder 1. Liphistiomorphae
    Suborder 2. Araneomorphae
    Suborder 3. Mygalomorphae.

Both classifications indicate that the Liphistiomorphae constitute the sister group of Mygalomorphae plus Araneomorphae, and that the last two taxa are sister groups. The position of the last two groups can be switched at will (as could the two sides of the basal dichotomy). This classification has two drawbacks: it eliminates an inclusive taxon for Mygalomorphae plus Araneomorphae that will certainly function as a prediction of general synapomorphy at a very high level, and it is open-ended. For example, if it should appear that the basic dichotomy within the Araneomorphae is between the Hypochiloidea and the other true spiders, it would be possible to raise the Hypochiloidea to subordinal status:

3) Order Araneae
    Suborder 1. Liphistiomorphae
    Suborder 2. Mygalomorphae
    Suborder 3. Hypochilomorphae
    Suborder 4. [all remaining true spiders] .

The system proposed by Petrunkevitch (1933) is essentially one of this type; the process could

be continued down to the species level, so long as alternate sister groups are similarly raised to subordinal rank. Each additional pair of sequenced taxa results in the loss of an inclusive taxon and its associated predictive value. This loss of predictive value is probably of little practical importance at low taxonomic levels, and is compensated for by the convenience of allowing taxa at those levels to contain more than two coordinate subtaxa. At the family level and above, however, the loss of predictive value seems inefficient.

We therefore prefer instead a strictly subordinated higher classification, particularly as in this case names for the taxa have already been provided:

4) Order Araneae
 Suborder Mesothelae Pocock (1892)
 Suborder Opisthothelae Pocock (1892)
  Infraorder Mygalomorphae Pocock (1892)
  Infraorder Araneomorphae Smith (1902).

We also advocate abandonment of the names Orthognatha and Labidognatha, on the grounds that the former taxon is paraphyletic.

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