The Monophyletic Origin of the Orb Web

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TWO VENERABLE groups of spiders spin orb webs: the cribellate Ulobori-
dae, weavers of calamistrated sticky silk, and the ecribellate Araneidae,
weavers of true viscid silk (Figs. 12.2, 12.1). "Cribellate" spiders possess a
cribellum and a calamistrum. The cribellum is a flat, complex spinning plate
from which the cribellate silk issues; the calamistrum is a comb of bristles on
the fourth metatarsi used to comb the cribellate silk from the cribellum.
"Ecribellate" spiders lack these structures. Other aspects of the morphology
of the two families of spiders also differ considerably, yet both groups spin
very similar orb webs. When juxtaposed to the morphological disparity be-
tween the spiders themselves, the similarity in the form of their webs and in
the manner in which they are constructed has inspired a classic evolutionary
controversy—the single versus the dual origin of the orb web. Behavioral
evidence has defined one group, "orb weavers," including some but not all
cribellate spiders, but morphological evidence has defined another, "Cri-
bellatae," including some but not all orb weavers.

The problem can be viewed as two contingent dilemmas. First, are all orb
webs homologous as orb webs, and/or all cribella homologous as cribella?
Second, if the answer to both of these questions is yes, then which homo-
logue is primitive and which derived, or do they both define the same group?
There are several possible answers to these two dilemmas, and all have been
suggested at one time or another in the history of the controversy. An addi-
tional problem contributing to the controversy over the orb web is second-
ary loss or complete modification of features in only some species of a
monophyletic group. Occasionally, the species retaining the features are
split off as a separate taxon defined by the retained primitive features. That
taxon is not then synonymous with any real evolutionary lineage, and is

termed "paraphyletic" because it includes only some of the species legiti-
mately belonging to the lineage.

History of the Controversy over the Orb Web

The controversy over the orb web dates from the response of Thorell (1886)
to some innovations in spider classification proposed by Bertkau (1878,
1882). Thorell pointed out that nearly all arachnologists before Bertkau had
grouped spiders "not on differences in their *organization*, but on certain pe-
culiarities in their *habits*, especially on their mode of locomotion and the
form of their webs" (p. 301). In fact, those arachnologists recognized some
version of the taxon "orb weavers" and placed all orb-weaving spiders in it.
The taxon had various names: Orbiculariae (Walckenaer 1802), Orbitelae
(Latreille 1825), Orbitèles (Walckenaer 1837–47, Vol. 1), Epeiriformes (Si-
mon 1864), Radspinnen (Menge 1866), and Orbitelariae (Thorell 1869,
Dahl 1883). Lister (1678), Clerck (1757), Sundevall (1833), Westring (1861),
and Keyserling (1882) also grouped all orb weavers known to them together
(information from Bonnet 1959: 5017–34). (Although the taxon "orb
weaver" therefore dates conceptually from 1678, cribellate orb weavers were
routinely included in it only after 1789, when Olivier first described a cri-
bellate orb weaver, *Zosis geniculatus*, placing it in Linnaeus's genus *Aranea*.)
    Bertkau had studied the anatomy of spiders extensively, and he used ana-
tomical details rather than "habits" to define spider taxa. Bertkau thought
the practice more scientific, an opinion with which Thorell agreed, at least
in principle (1886: 301). Bertkau's Cribellatae was widely accepted at the
time and afterward, possibly in part because of the general shift from the
study of natural history in the early part of the nineteenth century to com-
parative anatomy in the latter half. Actually, Bertkau was not the first to pro-
pose a taxon defined by the possession of a functional cribellum. Blackwall,
who had discovered the cribellum in 1833, grouped all cribellate spiders in
the "family" Ciniflonidae (Blackwall 1841). Blackwall's suggestion had not
convinced his colleagues, but Bertkau's did, perhaps because of his reputa-
tion as an anatomist and because he offered a comprehensive classification of
spiders based on anatomical details.
    In effect, Bertkau chose one of the solutions to the two dilemmas outlined
above. He said that all cribella were homologous as such, but that all orbs
were not. He said that the orb was convergent in cribellates and ecribellates,
and that the cribellum had never been lost. Hence the Cribellatae were a
monophyletic group. (Bertkau included Zoropsidae, Miagrammopidae, Fil-
istatidae, Oecobiidae, Dinopidae, Uloboridae, Dictynidae, Eresidae, and
Amaurobiidae.) The homology of all cribella as such, and of the colulus

with the cribellum, was soon demonstrated embryologically by Dahl (1901) and Montgomery (1909).

Most araneologists have since agreed with Bertkau's innovations, e.g., Simon (1892), Pocock (1900), Dahl (1904), Comstock (1948), Berland (1932), Caporiacco (1938), Bristowe (1938), Gerhardt and Kaestner (1938), Millot (1949), Bonnet (1959), Kaston (1972a), and Gertsch (1979). The geometric regularity of orb webs makes appealing the idea that orb webs represent the most derived stage in a transformation series of web architectures. Many authors have commented that the orb web is a superb solution to the problems that a sessile, myopic insectivore must face in catching prey (Thorell 1886; Pocock 1895; Comstock 1912; Hingston 1920; Tilquin 1942; Savory 1952; Kaston 1964; Witt 1965, 1975; Langer 1969; Eberhard 1972a, 1981a; Chacón and Eberhard 1980; Kullmann 1972a; Denny 1976; Robinson 1977b; Gertsch 1979). For example, in a book aimed at a lay audience Gertsch (1979: 164) described the orb web as follows:

The two-dimensional snare known as the orb web is a crowning achievement of the aerial spiders. . . . To the evolutionist it is only the last step of a series that has resulted in a circular design—an inevitable shape; and the spider has no more to do with spinning such a symmetrical web than a "crystal has to do with being regular." The web, among all objects produced by lesser creatures an unrivaled masterpiece, is above everything else a superb snare. . . . That a similar trap, produced by a like series of instinctive actions, should have evolved among a separate line of spiders might well seem an impossibility. Nevertheless, the cribellate uloborids have fashioned a web that, except for the substitution of the hackled band for the beaded spiral lines, is a faithful reproduction of the snare of the [araneoid] orb weavers. . . . This most highly evolved of all aerial webs is the result of the random activities of aerial prototypes, which finally established order among the irregular lines in the horizontal platform.

Implicit in that viewpoint may be a disinclination to believe that orb webs, once evolved, would have been lost except in isolated cases by further adaptation to even more specialized life-styles. If orbs are adaptively superior to other web architectures, the notion of convergent evolution on the orb-web style of architecture is more plausible. Not surprisingly, authors who favor arguments for the superiority of the orb as an architectural design are usually sympathetic to the dual-origin theory of the evolution of the orb web.

There are of course other answers to the dilemmas outlined above. For example, Pickard-Cambridge (1897–1905: 45) argued that not all cribella were homologous as cribella:

With regard to the cribellate forms there appears to be no reason why the cribellum and correlated calamistrum should not have become independently specialized in several groups, each of these groups falling under different surrounding influences as they developed.

Lehtinen (1978) expressed a similar opinion regarding the Filistatidae.

Almost immediately after Bertkau published (1882), the obvious alternative occurred to Thorell (1886). He suggested that all cribella and all orb webs were homologous as such, but that the cribellum was a primitive feature for a large group of spiders, perhaps even for all true spiders:

And this again [that most adult male cribellate spiders lack the cribellum] appears to me to prove that the cribellum and calamistrum are organs that have originally belonged to the order of spiders in general, and have in the course of time been reduced and lost in a part of them, those namely that no longer wanted them, and this independently of their greater or less affinity. (p. 322)

Thorell also argued that the orb web was uniquely derived:

Even if we do not assign, in general, any great weight in the phylogeny and classification of the spiders to the form of their webs, it must be admitted that it is at least probable that spiders that fabricate regular or so-called geometrical webs have a common origin and belong to one and the same higher group, or, in other terms, that this industry cannot have arisen spontaneously and independently in two or more different and natural groups. (p. 324)

Finally, Thorell pointed out what to him seemed a conceivable but absurd possibility:

Only on the supposition that all spiders have originally constructed such [geometric] webs, but that most of them have in the course of time lost this talent, could it be admitted that spiders belonging to radically different groups can give the webs such an artificially finished and almost identical form. But for such a supposition there is no reasonable ground. (p. 324)

To anticipate my own argument, Thorell's supposition may not have been as unreasonable as he thought, at least for an unexpectedly large fraction of "all" spiders.

Of course, Petrunkevitch (1928, 1933) thought that the cribellum was a primitive feature of all true spiders, and he agreed with Thorell (1886) and Wiehle (1927, 1928, 1931) that the uloborid and araneid orb webs were homologous as orb webs (Petrunkevitch 1926: 428). They therefore disagreed with most of their colleagues on those issues, but araneologists were apparently unanimous that, wherever orb webs occurred, they indicated monophyletic, and not paraphyletic, taxa. Specifically, neither the taxonomists cited above nor Petrunkevitch nor Wiehle nor Thorell believed that the non-orb-weaving araneoid families might have evolved from orb-weaving ancestors. For the taxonomists who followed Bertkau, the refusal to accept that linyphiids or theridiids had lost the orb-web was logically consistent. However, for Petrunkevitch, Wiehle, and Thorell it was illogical, since they held that Araneoidea were monophyletic, yet that both the orb web and the cribellum were homologous as such.

Lehtinen was the first modern araneologist to argue that Cribellatae as defined were paraphyletic. At first he also held that orb weavers were a mono-

phyletic group (1967: 393–94). He later decided that the orb was convergent in uloborids and araneoids (1978; pers. comm.). Finally, Platnick (1977), in a review foretelling the "final nail in the coffin of the Cribellatae," summarized the available morphological evidence and argued that the distribution of characters among Mesothelae, Mygalomorphae, hypochiloids, and the remainder of the old Araneomorphae is such that the cribellum must be a primitive feature for all true spiders. Specifically, he showed that Crome's (1955) contention that the occurrence of four dorsoventral pairs of abdominal muscles in cribellates was synapomorphic was in fact a misinterpretation of a symplesiomorphic character. The paraphyly of the Cribellatae has become widely accepted (Brignoli 1979; Kaestner 1980; Kullmann and Zimmerman 1976; Forster 1970; Levi 1980a, 1982; Foelix 1982). The morphological argument surrounding the cribellum and the categorical level at which it defines a monophyletic group seems to have been settled. But what is the effect of the reinterpretation of the cribellum on the presumed relationship between uloborids and araneoids?

The collapse of the old Cribellatae has removed the single best reason for not regarding the orb web as a synapomorphy of a group that includes at least uloborids and araneoid orb weavers. No compelling reason has been suggested to ally uloborids with any other group, whereas the orb web itself may be a substantial reason to ally them with other orb-weaving spiders. However, the reinterpretation of the cribellum is irrelevant to the question of the homology of orb webs as such and the group that they properly define—all that has been accomplished is the removal of arguments that for a century have effectively prevented consideration of what is, after all, an independent issue. The same two interpretative dilemmas still persist: are all orb webs homologues, and, if so, what does the monophyletic group defined by orb webs include?

Both Kovoor (1977a) and Opell (1979) suggested that Uloboridae and Araneidae might be closely related, Kovoor on evidence of similar silk glands, Opell on evidence of similar web form and the femoral trichobothria shared by uloborids and tetragnathines. Lehtinen (1978), Brignoli (1979), and Levi (1980a) wondered whether orb webs might not be the primitive web architecture for the entire superfamily Araneoidea, and possibly homologous to the similar web spun by the Uloboridae. Although the impetus behind many of these speculations has been the similarity in web form, none of these authors actually discussed web form or construction behavior in any detail. Kullmann (1972a) considered web form, but he assumed that the Cribellatae were a monophyletic group. He supported what may be called the classical point of view—that the uloborid and araneid orbs were convergently evolved. Eberhard (1972b, 1981a, 1982) presents a summary of over 10 years of research on the building behavior of orb-weaving spiders. He gives data

on most major groups of orb weavers (uloborids, araneids, metines, tetragnathines, nephilines, anapids, symphytognathids, theridiosomatids, and mysmenids). Although emphasizing the paucity of information to support generalizations, he suggests that, thus far, the evidence favors the convergent evolution of uloborid and araneoid orbs. Eberhard (1982) also suggests that the absence of an orb web in theridiids is probably original and does not represent the loss or modification of an orb web, thus agreeing with Thorell (1886), Kullmann (1972a), and most araneologists in between.

In my view, the evidence points the other way. The orb webs of uloborids and araneids appear to be homologous. If Araneoidea are monophyletic, then the primitive web architecture of the superfamily is indeed the orb web. Therefore araneoids that do not spin obvious orbs, such as linyphiids, theridiids, nesticids, and mimetids, have either lost the ability or modified the form of the orb beyond recognition.

An assessment of the positive evidence for the single origin of the orb web, and consequently for the monophyly of orb weavers, seems overdue. First the monophyly of the relevant taxa must be considered to ensure that the groups under discussion are real; then evidence pertaining to silks, silk glands, construction behavior, and web form can be used to test the idea that orb webs, and orb weavers, evolved only once.

Monophyly of Uloboridae, Dinopidae, Araneoidea, and Araneoid Families

Table 12.1 lists the taxa relevant to this discussion and their presumed synapomorphies.

Uloboridae

Opell (1979: 465) identified three synapomorphies for the Uloboridae: loss of poison glands, a ventral row of distinctive macrosetae on the fourth metatarsi, and two apical cymbial setae on the male palp. However, Opell (1982a) also found similar macrosetae on the fourth tarsi of Dinopidae, though he did not mention in which species. Kovoor (1977a) suggested other synapomorphies. The minor ampullate glands of uloborids are in a unique inverted position, compared with their position in all other spiders. Uloborids have a unique pair of glands serving the posterior lateral spinnerets, which Kovoor named the "pseudoflagelliform" glands (examined only in *Uloborus*, *Zosis*, and *Hyptiotes*). Also, the second-instar spiderlings build a distinctive orb web (Szlep 1961). Finally, uloborid web-building behavior is unique in at least four ways (discussed below, along with the justi-

TABLE 12.1
Synapomorphies of Uloborids, Dinopids, Araneoids, and Araneoid Families

Taxon	Character(s)
Uloborids	inverted minor ampullate glands, pseudoflagelliform glands, apical cymbial setae, loss of poison glands, behavioral traits
Dinopids	web structure, eyes in three rows
Araneoids	aggregate glands, flagelliform glands, serrate hairs, $1L_4$ push during sticky-silk attachment, paracymbium (?)
Theridiids	lobed aggregate glands
Nesticids	distinctive basal plate of trichobothria
Linyphiids	palp conformation, route of ejaculatory duct
Nephilines	radii doubly attached to frame, oL_4 downward slide to locate inner sticky-silk loop, temporary spiral not removed
Araneids	rotation of palpal bulb, spin-wrap attack, reduced tapeta in posterior median eyes
Metine-tetragnathines	modified paracymbium, elongate chelicerae
Theridiosomatids	sternal pit organs, palp conformation, route of ejaculatory duct, temporary spiral as circles
Symphytognathids	fused chelicerae
Mysmenids	male metatarsal clasping spurs, femoral tubercle
Anapids	labral spur between chelicerae

NOTE: For references and more detailed discussion, see text.

fication for viewing the behaviors as derived). Uloboridae appear to be monophyletic by these nine characters.

Dinopidae

Dinopidae are also a family important to the consideration of the evolution of the orb web, but little is known of their morphology or behavior. Their monophyly is supported by their unique web form (Fig. 12.13) and their eye arrangement in three rows. A careful reading of Theuer's thesis (1954) on the biology of Dinopis spinosus makes quite reasonable the inference that the species spins a modified orb. The sequences in its construction behavior, for example, are similar to frame, radius, temporary spiral, and sticky spiral construction in orb weavers. But Theuer was not specifically evaluating the dinopid web as an orb web when he described the behavior, and, in the light of Eberhard's (1982) identification of salient characters in orb-web construction, many critical observations are missing. If indeed the web of Dinopis (and Menneus: Akerman 1926) is a modified orb,

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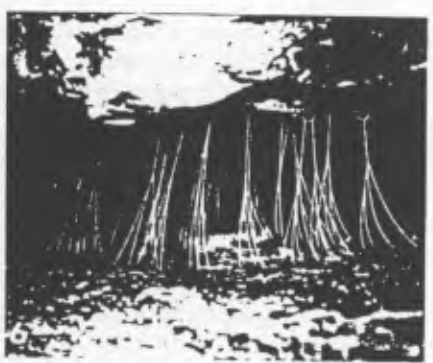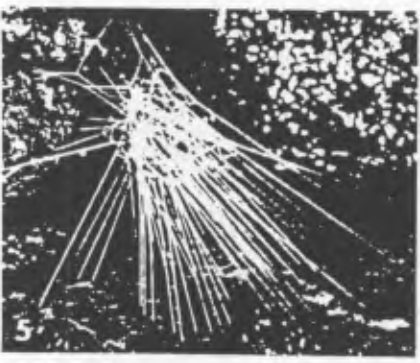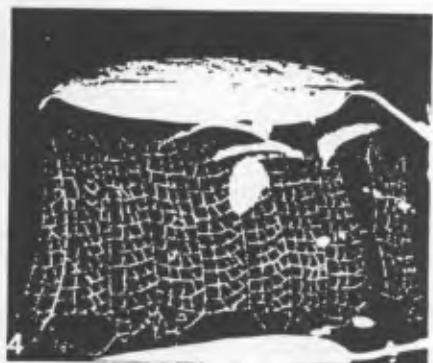
and all orb webs are homologous, the family would have to be the sister group of Uloboridae, Araneoidea, or their inclusive taxon. Both uloborids and dinopids possess pseudoserrate plumose hairs, which are lacking in araneoids (Green 1970: 8). But loxoscelids and thomisids have similar hairs, and Green noted that in general many intermediate hair types exist. Pseudoserrate plumose hairs, however, are weak evidence that dinopids may be the sister group of uloborids rather than araneoids. Shear (this volume), citing Kullmann 1975 and Opell 1979, points out that the cribellate silk of dinopids and uloborids is "puffed" along its length (see the photographs in Kovoor 1977a, and Kullmann 1972a), and states that the cribellate silk of other cribellates, e.g., *Hypochilus* (Hypochilidae), *Callobius* (Amaurobiidae), *Filistata* (Filistatidae), *Dictyna* (Dictynidae), *Stegodyphus* (Eresidae), lacks this feature. At present the feature appears to be a synapomorphy for uloborids and dinopids. Because araneoids are ecribellate, it can never be known whether or not their cribellate ancestor spun "puffed" cribellate silk. In other words, the feature could also be a synapomorphy for all orb weavers. Similarly, the pseudoserrate plumose hairs may also be an orb-weaver synapomorphy.

Uloborids and dinopids also use a wrap attack to subdue prey, and face away from the prey when wrapping (Eberhard 1967; Robinson and Robinson 1971). However, a wrap attack occurs in various other spider taxa, e.g., metine-tetragnathines (Eberhard 1982), Oecobiidae and Hersiliidae (Eberhard 1967), Pholcidae (pers. obs.), Nesticidae, Theridiidae, and Araneidae. Although more comparative work is needed on wrap attacks to separate convergent from homologous similarity, the literature suggests that the orientation of dinopids and uloborids towards prey is distinctive. This feature may be a synapomorphy of the two groups. Dinopids possess ventral macrosetae on their fourth tarsi.

Because both uloborids and araneoids possess a pair of specialized glands

Figs. 12.1–12.6: Webs of araneoid spiders. 12.1. Web of a typical araneid (*Micrathena gracilis*). Note the open hub (bitten out after sticky spiral construction) and the adjacent nonsticky spiral. 0.2×. (Voucher No. VII.3.1981:nph18). 12.2. Web of a typical uloborid (*Uloborus penicillatus*). The reticulate pattern of the hub indicates that the radii are laid early in nonsticky spiral construction and that hub modification is absent. 0.5×. (Voucher No. VIII.6.1980:6ph32.) 12.3. Representative linyphiid sheet web (unknown tropical genus). The spider is just visible beneath the sheet at the center of the web. 0.4× (Voucher No. VII 12.1980:12ph30.) 12.4. Web of *Synotaxus* sp (Theridiidae). The continuous vertical lines delimit the modules of the web. The numerous short vertical line segments are sticky silk. The spider can vary the number of modules spun from night to night. Approximately 0.2×. Courtesy of M. K. Stowe. 12.5. Web of *Achaearanea* sp (Theridiidae). The distal ends of the straight lines are sticky. The central network is the retreat. 0.5× (Voucher No. VIII.30 1980 16ph7.) 12.6. Web of *Eidmanella pallida* (Nesticidae). The distal ends of the branched vertical lines are sticky. The spider hangs upside down in the upper part of the web. 0.4× (Voucher No. VIII.4.1981.7ph16.)
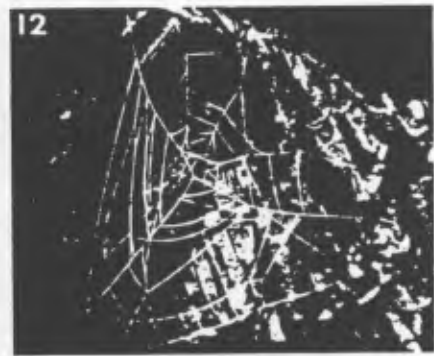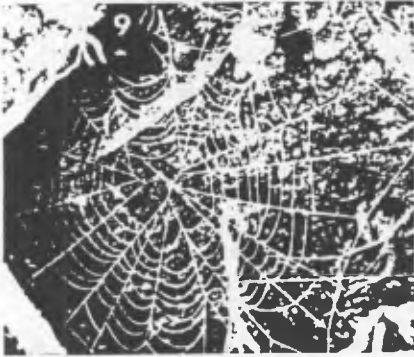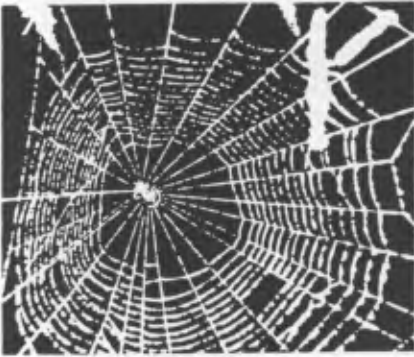
exiting on the posterior lateral spinnerets (either pseudoflagelliform or flagelliform; see below), it may be predicted that dinopids also have a similar pair of glands. If the dinopid glands are recognizably distinct from pseudoflagelliform glands and flagelliform glands, one must infer that the common ancestor of the three taxa merely had "specialized" glands. On the other hand, the predicted dinopid glands may share features with either taxon. Because the condition in dinopids is unknown, the former position is taken here. On the whole, little is known about dinopids, and consistent inclusion of the group in the following discussion is impractical.

Araneoidea

Araneoidea have been called one of the most distinctive and easily defined groups of spiders (Lehtinen 1967, 1975). Defining features that have been proposed are (1) a body covering of serrate hairs, (2) a fairly consistent trichobothrial pattern, especially the lack of tarsal trichobothria, (3) a web-spinning habit, (4) a globose abdomen, (5) complicated palps, and (6) spinneret arrangement (features 1–4: Lehtinen 1967; features 5 and 6: Kaestner 1980). Is any of these characters a convincing synapomorphy for the superfamily Araneoidea? Green (1970) pointed out that serrate hairs do occur in other families, and Lehtinen (1975) confirmed it. Only if the immediate outgroup of araneoids, and preferably several immediate outgroups, lacked serrate hairs could the araneoid serrate hair be considered a synapomorphy for the superfamily. No recent detailed arguments identifying a sister group to the Araneoidea other than the Uloboridae or Dinopidae exist, and both of these taxa reportedly lack true serrate hairs. Thus, the araneoid hair type could be a true synapomorphy, given favorable cladistic structure in the outgroup relationships.

Figs. 12.7–12.12. Webs of theridiosomatid spiders.   12.7. Web of *Epeirotypus* sp. (Theridiosomatidae). Note the similarity to a conventional orb: two-dimensional frame, radii, sticky spiral, and hub loops 0.3×. (Voucher No. IV.13.1981:15ph31.)   12.8. Partially constructed web of *Epeirotypus* sp. (Theridiosomatidae). Note the nonsticky "circles" instead of a spiral and the incomplete sticky spiral. 0.4× (Voucher No. VII.30.1981:nvph31.)   12.9. Web of *Theridiosoma gemmosum* (Theridiosomatidae). Note the radial anastomosis. 0.5× (Voucher No. VI.30.1981 2ph12.)   12.10. Incomplete web of *Theridiosoma gemmosum* (Theridiosomatidae). The single nonsticky circle is characteristic of the genus. Compare this hub (before radial anastomosis) with that in Fig. 12.9 0.3× (Voucher No. VII.2.1981:gen.ph15.)   12.11. Web of *Wendilgarda* sp. (Theridiosomatidae). The lower vertical lines are sticky and are normally attached to the surface film of moving tropical streams. Note the lack of a frame and the dissimilarity to a conventional orb web. 0.5× (Voucher No. VIII.11.1980.nvph1.)   12.12. Web of *Ogulnius* sp. (Theridiosomatidae). A frame is lacking and the radii are attached directly to the substrate. Note the irregular course of the sticky-silk line. 0.3× (Voucher No. VII.6.1979.1ph1.)

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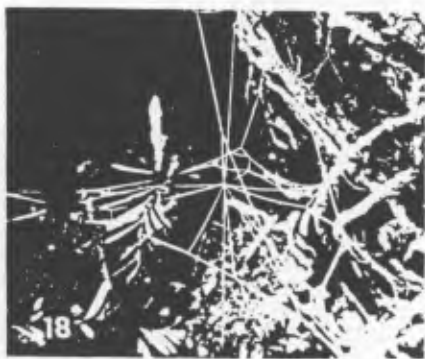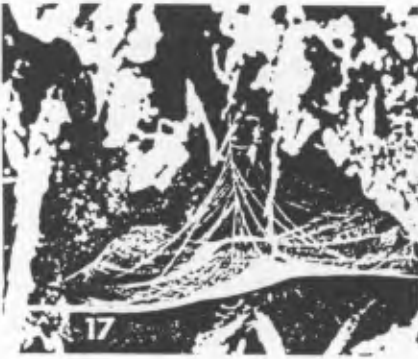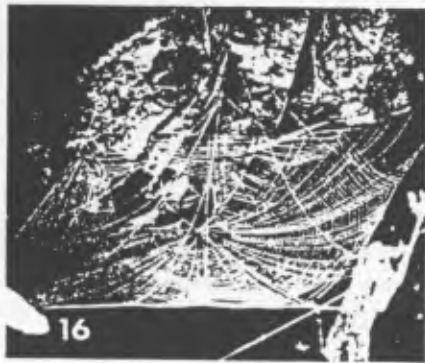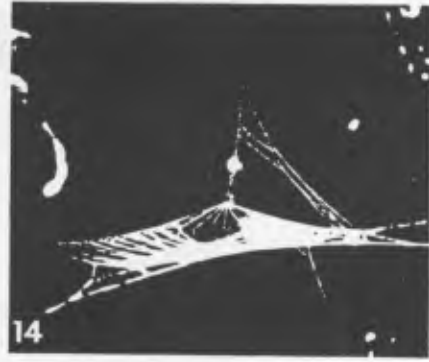
With regard to the second feature, Lehtinen (1980) showed that the trichobothrial pattern as such is not unique to Araneoidea. The third character is a "web-spinning habit," but what sort of web? If the orb is taken as the primitive web architecture of araneoids, the uloborids are a likely sister group. Although the orb might define the inclusive taxon, it could not then be synapomorphic for the Araneoidea. If the primitive araneoid web form is not the orb, but something like the web spun by theridiids (Fig. 12.5), or linyphiids (Fig. 12.3), as suggested by Pocock (1895), Comstock (1912), Kaston (1964), and Kullmann (1972a), then many other taxa spin similar webs, e.g., amaurobiids, pholcids, ochyroceratids, agelenids, psechrids, and tengellids. Without a more precise description of the "web-spinning habit," the character is not unique to Araneoidea.

The fourth character, a globose abdomen, occurs in many araneoid families, but, like the "web-spinning habit," the character is indistinctly defined and characterizes other spider families as well. Likewise, the complicated palps and spinneret arrangement have yet to be shown to be unique to Araneoidea.

One discrete character, not widely cited in the taxonomic literature, can be emphasized as a synapomorphy of the superfamily: aggregate silk glands. Kovoor (1977c) summarized the conclusions of Apstein (1889), Hopfmann (1935), and Anatasiu-Dumitrescu (1941, 1942) and suggested that aggregate glands were unique to Araneoidea. These glands provide the viscid coating of the sticky-silk lines, and have been found in Theridiidae (*Steatoda*, *Theridion*, *Teutana*, and *Latrodectus*), Linyphiidae (*Linyphia*), Araneidae (*Araneus*, *Argiope*, *Cyclosa*, and *Nemoscolus*), metine-tetragnathines (*Pachygnatha*, *Tetragnatha*, *Meta*, and *Zygiella*), and nephilines (*Nephila*) (Kovoor 1977c; Kovoor and Lopez 1980). Aggregate glands have been found in all araneoids

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Figs. 12.13–12.18. Webs of dinopid and anapid spiders. 12.13. Web of *Dinopis spinosus* (Dinopidae). Approximately 3×. Courtesy of M. K. Stowe. 12.14. Web of *Anapis* sp. (Anapidae) The egg sac is positioned above the hub. The straight vertical line is constructed simultaneously with the radii. The diagonal lines at right are part of the sticky spiral. 0.9×. (Voucher No. VII.11.1980:16ph23.) 12.15. Web of *Anapisona simoni* (Anapidae). Infrequent accessory radii are visible. The catenary lines attached to the central vertical line are part of the sticky spiral. Note the egg sac just above the hub 0.8×. (Voucher No. VII.11.1980:10ph38.) 12.16. Web of *Anapis heredia* (Anapidae). Note the numerous accessory radii, radial anastomosis, out-of-plane radii, and infrequent sticky-silk lines attached to the central vertical line. 1×. (Voucher No VIII.10.1980:7ph20.) 12.17. Web of *Chasmocephalon shantzi* (Anapidae). Note the accessory radii, radial anastomosis, out-of-plane radii, and out-of-plane sticky-silk lines. 1×. (Voucher No. IV.4.1980:11ph2.) 12.18. Web of *Chasmocephalon shantzi* (Anapidae) before sticky spiral construction. The out-of-plane radii are constructed simultaneously with the planar radii. 0.5×. (Voucher No. IV.5.1980:nyph28.)

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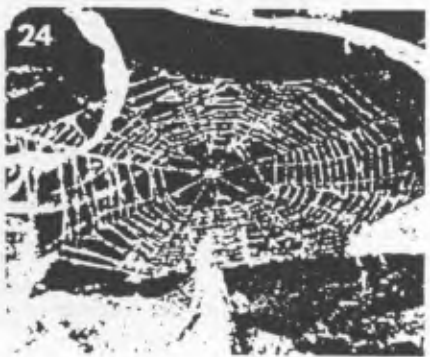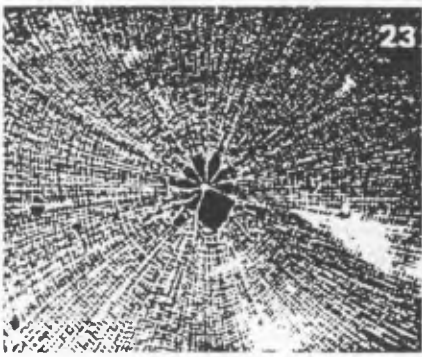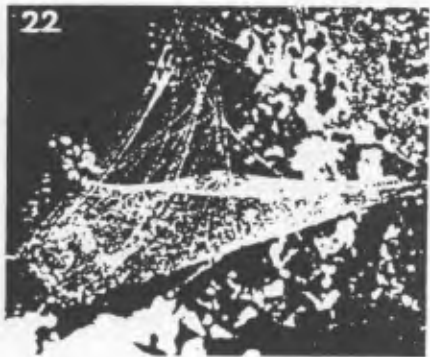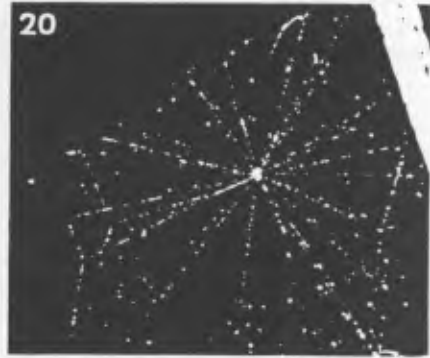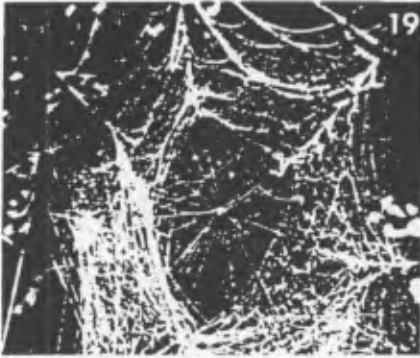
investigated thus far, and never in nonaraneoid species (45 nonaraneoid genera are cited in Kovoor 1977c). Although few araneoid taxa have been studied histologically, the webs of theridiosomatids, anapids, symphytognathids, mysmenids, and nesticids possess sticky silk lines more or less identical to those characteristic of the five lineages mentioned above. Because of the excellent correlation between the complex gland type and the appearance of viscid-silk lines in the web, it seems safe to presume that species having that kind of sticky silk also have aggregate glands. On the basis of that provisional inference, aggregate silk glands may stand as a synapomorphy of the superfamily.

Kovoor (1977c) found that flagelliform glands occurred in all araneoids studied (Table 12.2 below). She found similar glands in uloborids, the pseudoflagelliform glands. Although the glands are indeed similar, they can be distinguished by histological characters (Kovoor 1977a, 1978; Kovoor and Zylberberg 1979), so that true flagelliform glands become an additional synapomorphy for araneoids.

Shear (this volume) argues that the paracymbium of the male palp in Araneoidea is unique to the group, a possible fourth araneoid synapomorphy. Neither uloborids nor dinopids possess a paracymbium (Archer 1948). Heimer (1982) investigated the function of the paracymbium and stated that together with the median apophysis it served to arrest the rotation of the palpal bulb during expansion. He stated that the cymbial setae and median apophysis of uloborids acted in the same way, implying homology of the uloborid cymbial setae and araneoid paracymbium. But he also stated that the details of palpal rotation in uloborids and araneoids differed considerably, although he did not make the nature of the difference clear. However,

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Figs. 12.19–12.24. Webs of mysmenid and symphytognathid spiders. 12.19. Web of *Mysmena* sp. (Mysmenidae). The outer envelope of sticky silk has been torn away to reveal the three-dimensional pattern of radii inside the web. Entire webs are roughly spherical or egg-shaped. The spider is at the center of the web. 0.8×. (Voucher No. VII.29.1980:11ph8.) 12.20. Web of *Mysmena* sp. (Mysmenidae) with radii completed, but early in sticky spiral construction. Note the few sticky-silk lines connecting the radii, and the frame lines supporting the radii. 1×. (Voucher No. VII.4.1980:nvph19.) 12.21. Section of a web of *Mysmena guttata* (Mysmenidae). The spider is barely visible beneath the egg sac positioned just above the hub. Radial anastomosis is present. 2.0×. (Voucher No. VIII 8.1980:8ph11.) 12.22. Web of *Maymena ambita* (Mysmenidae): The architecture is similar in all respects to that of anapid webs (compare Figs. 12.14–12.18). 1.8×. (Voucher No VII.4.1981 3ph5.) 12.23. Web of an unidentified symphytognathid genus from Puerto Rico. The web displays numerous accessory radii and radial anastomosis, and is strictly two-dimensional and bounded by a frame (not shown). 1.2×. (Voucher No. VIII.27.1980:5ph23.) 12.24. Web of a *Patu* sp. immature (Symphytognathidae) Nearly all the radii visible are structural, although a few accessory radii are present. 0.7×. (Voucher No. VII.12.1980:5ph7.)

Opell (1979) hypothesized that the cymbial setae were part of a stridulation mechanism in the cladistically primitive uloborid genera *Waitkera, Tangaroa,* and *Polenecia,* so that the function of the cymbial setae is unclear. The different hypothesized functions do not necessarily conflict, because the stridulatory function may be original and the function in arresting the palpal bulb derived. The evidence therefore suggests homology, but also needs much more study.

Eberhard (1982) has found two behavioral features correlated with the attachment of viscid-silk lines to nonsticky-silk (NS) lines. All araneoids that he observed use the outside third and fourth legs to grip the NS line as the sticky-silk (SS) line is attached (Eberhard 1982, character B1). However, uloborids use the same grip in frame, radius, and temporary spiral construction, and an elaboration of it in SS construction (pers. obs.; see below). The second character also involves SS construction. During SS attachment, the inside fourth leg of the animal holds the SS line and extends in a characteristic fashion (Eberhard 1982, character C1). The latter character is absent in uloborids and dinopids (pers. obs.), but is present in all araneoid taxa examined thus far and appears to be a fifth synapomorphy. Eberhard (1982, character E1) also states that all araneoid orb weavers attach the sticky spiral to all radii encountered, whereas uloborids skip some attachments. But to judge from photographs and drawings of dinopid webs (*Dinopis subrufus:* Baum 1938; Roberts 1955; Clyne 1967; *Dinopis longipes:* Robinson and Robinson 1971; *Dinopis spinosus:* Theuer 1954; *Menneus camelus:* Akerman 1926) dinopids also attach SS lines to all radii, so that uloborids are probably autapomorphic in this respect. However, as far as is known, the five characters discussed above are unique to the superfamily Araneoidea.

Araneoid Families

Platnick and Shadab redefined the families Anapidae (1978a) and Mysmenidae (1978b), and Forster and Platnick (1977) redefined the family Symphytognathidae. Their synapomorphies for each taxon are listed in Table 12.1. Millidge (1977, 1980) argued that Linyphiidae (including the erigonine genera) are monophyletic on the basis of a conglomerate of characters of the male palp. Although the linyphiid palp is relatively well known as the result of the work of Millidge, Merrett (1963), van Helsdingen (1969), and others, those characters now believed to be unique to Linyphiidae may also appear in other araneoid families as their palp morphology becomes better known. At present, however, Linyphiidae as defined by Millidge seem to be monophyletic.

The Theridiidae are usually considered a poorly defined group, diagnosed mainly by the comb setae of the fourth tarsi (Levi and Levi 1962). Two characters correlated with the comb setae deserve more emphasis in any diag-

nosis of the theridiids: the possession of "lobed" aggregate glands and the use of sticky silk in the wrap attack to subdue prey. Kovoor (1977b) showed that these distinctive lobed glands are modified aggregate glands. As noted, the silk glands of few araneoid families have been investigated, but thus far these modified glands are unique to the theridiids. Eberhard (1967), Robinson (1969b, 1975), Robinson and Robinson (1971), and Robinson, Mirick, and Turner (1969) have documented the diversity of wrap attacks in spiders. The wrap attack of theridiids, however, is distinctive because the silk early in the attack is wet viscid silk, not dry silk. The spider throws viscid silk at the prey from some distance, and uses the comb setae of the fourth legs to handle the silk. I have seen viscid-silk wrap attacks in *Latrodectus, Achaearanea, Enoplognatha, Theridion, Steatoda, Argyrodes, Synotaxus*, and *Chrysso*. Apparently it also occurs in *Coleosoma* (Cutler 1972a), *Euryopis* (Carico 1978), *Anelosimus* (T. E. Christenson, pers. comm.; Eberhard 1979a), and other theridiid genera (Bristowe 1958). The lobing of the gland and its distinctive short duct (Kovoor 1977b) probably enable the spider to deliver large volumes of viscid silk at the beginning of the wrap attack. Araneids, uloborids, and dinopids, of course, use a wrap attack, but their swathing silk is said to be dry rather than viscid, and reportedly issues from a different gland (Kovoor 1977c).

In the past, Nesticidae have been defined by the form of the paracymbium in the male palp, but Lehtinen and Saaristo (1980) stated that the nesticid paracymbium is not diagnosable apart from that of linyphiids (Millidge 1977), tetragnathines (Levi 1981), mimetids (Shear 1981), or the other araneoids that possess a paracymbium. However, Lehtinen and Saaristo did state that the form of the basal plate of nesticid trichobothria is unique to the family (p. 58). The comb setae on nesticid fourth tarsi are similar to those of theridiids, but the form of their aggregate glands is unknown. Bristowe (1958) mentioned that *Nesticus cellulanus* uses a wrap attack "similar to Theridiidae," and Kirchner and Kullmann (1972) confirmed that this species does use viscid-silk to wrap prey. The viscid-silk wrap attack and comb setae suggest that nesticids are the sister group of theridiids. If nesticids also have lobed aggregate glands, they may yet be a monophyletic lineage (by the basal plate of the trichobothrium) within theridiids. Should that synapomorphy fail, no differential diagnosis of nesticids apart from theridiids is available. In any case, references below to "theridiids" are to the lineage including both groups.

Wunderlich (1980) proposed that the sternal pit organs, first described by Archer (1953), are a synapomorphy for Theridiosomatidae if that taxon is relimited to include only *Epeirotypus, Ogulnius, Theridiosoma*, and *Wendilgarda*. In all theridiosomatid palps the conformation and topology are consistent (a relatively huge tegulum, a hood-shaped conductor, and a bladelike

median apophysis occur in similar orientations), and the route followed by the ejaculatory duct from the reservoir to the embolus is nearly identical in all genera. In *Epeirotypus* and *Theridiosoma* the temporary spiral appears as one or two circles (Eberhard 1982, character H2; pers. obs.). *Wendilgarda* and *Ogulnius* lack temporary spirals (pers. obs.).

Araneidae are a large and diverse family. This group may need to be re-limited before it is truly monophyletic. Its overall limits have certainly been constrained by the presence or absence of an orb web in otherwise doubtful taxa. For example, when theridiosomatids (as defined above) were considered a subfamily of the Araneidae, every type species of a new genus was first considered a theridiid. The morphology of these species obviously suggested theridiids to taxonomists such as Pickard-Cambridge and Keyserling. When these workers discovered the orblike webs of the species, they were transferred to Araneidae. In a like manner, the web form seems to be the only rationale for retaining nephilines, tetragnathines, and araneids in the same taxon. However, the existence of orb webs in other families means that this feature cannot be synapomorphic for Araneidae unless the form of the web or the construction behavior is unique.

Levi (1983) states that, in contrast to other araneoids, all araneids except the tetragnathines, metines, and nephilines have the bulb of the palp twisted in the cymbium so that the sclerites face medially; he also states that the same group has reduced tapeta in the posterior median eyes. Eberhard (1982) points out that during their wrap attack these araneids spin the prey and wind silk on it as on a bobbin ("spin-wrap attack"). When referring to "Araneidae" or "araneids," therefore, I mean the lineage comprising Araneinae (including gasteracanthines), Mastophorinae, Argiopinae, and Cyrtophorinae, as those groups are defined by Levi (1983). The group appears to be monophyletic by the above three characters. Eberhard (1982, character J2), relying mainly on the work of Robinson and Robinson (1980), indicated that araneid males perform a distinctive behavior termed "tarsal rubbing" during courtship. But tarsal rubbing occurs in metine-tetragnathines (*Leucauge papuana*: M. H. Robinson, pers. comm.), and a similar behavior occurs in theridiosomatids (*Wendilgarda* and *Epeirotypus* spp.: pers. obs.). Araneids also use a lateral tap of the outside first leg to locate the inner loop of sticky spiral during SS construction (Eberhard 1982, character A2), but that feature occurs in uloborids.

Nephilines use a downward slide of the fourth tarsus to locate the inner loop of sticky spiral (Eberhard 1982, character A3), but *Nephila clavipes* also taps laterally with the outside second leg (Eberhard 1982; pers. obs.). Nephiline radius construction is unique in one detail (Eberhard 1982, character F2), and nephilines also do not remove the temporary spiral during SS construction. The last-named character also occurs in *Cyrtophora* and *Mecy-*

nogea, but those genera are araneids, thus implying parallel losses. Nephilines, including *Nephila*, *Herennia*, and *Nephilengys*, appear to be monophyletic by these three characters.

Levi (1983) states that tetragnathines and metines tend to have a modified paracymbium and distinctive, elongate endites and chelicerae. How the metine-tetragnathine paracymbium is to be distinguished from that of nesticids or linyphiids is not clear—the character may be a symplesiomorphy (see Shear, this volume). The occurrence of elongate endites or chelicerae is also not an especially well defined character. The monophyly or paraphyly of the metine-tetragnathine lineage is especially critical because in many ways it exemplifies the "primitive araneoid" (Levi 1981a). To facilitate discussion the metines and tetragnathines will be treated here as if they were a monophyletic lineage, but that monophyly is tenuous.

Families such as Archaeidae, Hadrotarsidae, Mimetidae, Micropholcommatidae, Textricellidae, and Nicodamidae have often been included in the Araneoidea because of their general appearance (Levi 1982). The inclusion of Nicodamidae is especially problematic if the cribellate *Megadictyna* are retained in that family. But so little is known about the behavior and webs (if any) of these families that they cannot be discussed in this context.

Comparison of Uloborid and Araneoid Orb Weavers

I shall now examine in detail the similarities and differences between uloborid and araneoid orb weavers. First I compare silks and silk glands (and other morphological traits), then web-building behavior, and finally the web form itself.

Silk Glands and Morphology

Again, because nothing is known of their silk glands, dinopids cannot be included in the comparison of silks and silk glands, even though it is likely that they are orb weavers (J. Coddington, in prep.). However, the excellent recent work of Kovoor (1972, 1977a, 1977b, 1977c, 1978), Kovoor and Zylberberg (1979), and Kovoor and Lopez (1980) allows a general comparison of the silk glands of uloborids and araneoids (Table 12.2). Some of the similarities are clearly symplesiomorphies. For example, Apstein (1889) believed that ampullate, piriform, and aciniform glands were present in the ancestor of all true spiders. Kovoor (1977c) thought, however, that the category "aciniform" was so indistinct that only the first two gland types could be confidently assigned to the common ancestor of all true spiders. On the other hand, Millot (1949: 661) believed that the aciniform gland was probably the plesiomorphic gland type in spiders. Cylindrical glands also occur

TABLE 12.2
Occurrence of Silk Glands and Spinnerets in Uloboridae and Araneoidea

Gland	Anterior median*	Anterior lateral	Posterior median	Posterior lateral
		Spinnerets		
Uloboridae (*Uloborus* sp., *Zosis geniculatus*, *Hyptiotes paradoxus*)				
Major ampullate*	—	2	—	—
Minor ampullate*	—	—	2	—
Pseudoflagelliform	—	—	—	2
Cylindrical*	—	—	6 or more	8 or more
Aciniform*	—	—	many	many
Piriform*	—	many	—	—
Cribellate	many	—	—	—
Araneoidea (14 genera in six lineages; see text)				
Major ampullate*	—	2	—	—
Minor ampullate*	—	—	2	—
Flagelliform	—	—	—	2
Cylindrical*	—	—	2	4
Aciniform*	—	—	many	many
Piriform*	—	many	—	—
Aggregate	—	—	—	4

NOTE For references and more detailed discussion, see text
*Functional anterior median spinnerets are absent in araneoids
*This type of gland occurs in nearly all araneomorph spiders

in almost all true spiders (they are absent in some groups: Kovoor 1977c). Hence the commonality of ampullate, piriform, aciniform, and cylindrical glands in uloborids and araneoids is probably symplesiomorphic. Araneoids therefore differ from uloborids in three gland types: cribellate, flagelliform, and aggregate.

The first difference is easily explained. If the thesis that all true spiders are descended from a cribellate ancestor is correct (Platnick 1977), the presence of cribellate glands in uloborids is symplesiomorphic and their absence in araneoids derived, so that the absence could be considered an additional synapomorphy of the superfamily (although a "loss" character). The difference is consonant with the hypothesis that uloborids are an immediate outgroup to the araneoids.

The flagelliform glands of araneoids are presumed to be the source of the core fibers of the SS line (Sekiguchi 1952; Peters 1955b; Anderson 1970; Work 1981). As Kavanaugh and Tillinghast (1979) point out, Sekiguchi, who discovered the gland and claimed to have demonstrated its function, did not actually prove that the silk from the flagelliform gland formed the core fibers of the araneoid viscid-silk line. Nevertheless, the circumstantial evidence accumulated since Sekiguchi's work is compelling (Witt, Reed, and Peakall 1968; S. O. Anderson 1970), and most workers have taken the asso-

ciation for granted. In her study of uloborid silk glands (in *Uloborus* sp., *Zosis geniculatus*, and *Hyptiotes paradoxus*), Kovoor (1977a, 1978) named a pair of glands similar to the araneoid flagelliform glands the "pseudoflagelliform" glands. She showed that the two types of glands were similar in placement, shape, and staining reactions and in their absence in adult males. On the basis of this evidence for homology she suggested that the pseudoflagelliform glands served a similar function in uloborids, i.e., provided the core fibers of the SS line. To my knowledge, no one to date has confirmed her suggestion, but the morphological evidence for homology seems compelling, and an analogous function may be predicted.

The SS core fibers in uloborid and araneid orbs do differ substantially in their physical properties. Araneid SS core fibers are highly elastic, non-birefringent elastomers (Work 1981); they can stretch up to six times their resting length. Ampullate-gland silk will stretch only about one and one third its resting length (Denny 1976; Work 1981). In *Steatoda triangulosa* (Theridiidae) the SS lines are not as elastic as the SS lines of araneids (pers. obs.). Uloborid SS lines are also not as elastic as araneid SS lines (Eberhard 1976), although the SS lines of uloborids are nevertheless more elastic than their own NS scaffolding lines (Eberhard 1972b: 437). Eberhard's observations are apparently the first comparison of araneid and uloborid silk properties, and more extensive quantitative comparisons would be valuable. For example, it is unknown whether the differences in orb-weaver SS lines are differences in degree, perhaps due to varying proportions of amino acids, or whether the differences preclude homology of the glands. However, comments by Lucas, Shaw, and Robinson (1960), S. O. Anderson (1970), and especially Denny (1976) suggest that simple quantitative changes in the amino-acid composition of silks can affect their physical properties considerably. On the whole, Kovoor's hypothesis that the uloborid pseudoflagelliform glands and the araneoid flagelliform glands are homologous seems reasonable.

The hypothesis is also corroborated by outgroup comparison. If orb weavers are monophyletic, the sister group of the orb weavers must have been cribellate because uloborids are both orb weavers and cribellate, and the cribellum is a primitive trait of all true spiders. Of course, most non-orb-weaving cribellate spiders use cribellate silk. Kovoor (1977c: 151) states that the core fibers of the SS lines in the Filistatidae, Eresidae, and Amaurobiidae are certainly ampullate silk. Morphologically, uloborids and araneoids are unique in having specialized glands serving the posterior lateral spinnerets.

At least some araneoids are specialized in one other respect. Both Work (1981) and Kavanaugh and Tillinghast (1979) report the presence in araneoid webs of a distinctive nonbirefringent cement at all SS-line and radius junc-

tions ("SS-R" cement). This type of cement, which is found only at these junctions, is universal in both araneoid lineages studied thus far (*Araneus, Neoscona, Eriophora, Argiope,* and *Micrathena; Nephila* and *Nephilengys*). Work (1981) comments that the source of the cement is unknown, and that the mechanism by which it operates is wholly mysterious. Its occurrence in the above two lineages suggests that it may be an additional synapomorphy for araneoids, or a subset of araneoids. It appears to be absent in both uloborids (*Uloborus penicillatus*) and dinopids (*Dinopis* sp.) (Opell 1979; Kullmann 1975). If its occurrence is restricted to SS-R junctions, the cement would be a useful diagnostic for establishing homologies between elements in araneoid webs that do not resemble orbs.

The final difference in the silk glands of uloborids and araneoids is the unique presence of aggregate glands in araneoids. In all araneoid species studied thus far there are two pairs of aggregate glands opening on the posterior lateral spinnerets (Kovoor 1977c: 147–48). The hypothesis that uloborids are an immediate outgroup of araneoids would therefore imply that the araneoid aggregate glands are the homologues of some gland type in uloborids, unless that homologue has been lost or transformed in uloborids. Outgroup comparison makes this event unlikely, because araneomorph spiders in general have only cylindrical and aciniform glands serving the posterior lateral spinnerets. Both of these gland types are still present in uloborids. The cylindrical glands are exclusively concerned with cocoon silk; they are usually rudimentary in juveniles and absent in males. Because juvenile araneoids of both sexes use aggregate-gland silk, ontogenetic comparison indicates that cylindrical glands are not the homologues of aggregate glands. Either aggregate glands arose de novo or they are homologues of the aciniform glands.

Orb-weaving spiders usually have dozens or hundreds of aciniform glands per spinneret (Kovoor 1972, 1977a), meaning that with respect to one another the glands can only be homonoms, not homologues (Riedl 1979). (Homonoms, as contrasted with homologues, are standardized morphological substructures that occur in large numbers in an individual, e.g., setae or nephrocytes in spiders.) Homonoms cannot be distinguished individually and thus hypotheses about strict homology (always about morphological singulars) do not apply. However, homology between homonoms as unique sets can be hypothesized. The relative number of aciniform glands in uloborids is thus uninformative. No reason exists to suppose that araneoid aggregate glands arose de novo, and therefore it is simplest to presume that aggregate glands, as a group, are homologous to aciniform glands, as a group. Kovoor (1977a) considered the homology of uloborid aciniform and araneid aggregate glands quite plausible. She suggested that a number of aciniform glands might have coalesced to form the enormous aggregate glands unique to Araneoidea (p. 100).

As Levi (1980b) pointed out, there are few morphological similarities between uloborids and araneoids, and many differences. Most of the differences (Lehtinen 1967, 1975, 1978) are probably araneoid autapomorphies. However, the work of Wilson (1962a, 1962b, 1969) documents another potential synapomorphy for uloborids and araneoids. These two groups possess a particular kind of valve in the anterior lateral spinnerets that controls the spinning of the ampullate-gland dragline and the scaffolding of orb webs. In addition, they have a unique muscle, the duct-levator muscle. Wilson (1969) stated that, among 12 families and 18 genera studied, these two characters occurred only in *Uloborus*, *Steatoda*, *Theridion*, *Meta*, *Zygiella*, *Tetragnatha*, *Pachygnatha*, and *Araneus* (representing four orb-weaver lineages). Wilson (1969) also examined *Linyphia* and found neither the valve nor the muscle, but he offered no details concerning the spinneret morphology of linyphiids. Despite this negative evidence, it can still be predicted that the features will characterize all araneoid higher taxa. Wilson (1969: 107) stated that the control valves and muscles showed "differences of detail which prevent one from assuming that they are strictly homologous," but he did not explain his concept of homology, and he was interpreting the morphology under the explicit assumption that, regardless of his evidence, the two groups were convergent. Significantly, the control valve and muscle were absent in *Amaurobius ferox* and *Amaurobius terrestris*, cribellate species in a family (Amaurobiidae) that is a potential sister taxon to the orb weavers. *Amaurobius* also lack specialized glands on the posterior lateral spinnerets (Kovoor 1977c). Comparison with one potential outgroup to the orb weavers therefore supports this feature as a synapomorphy of orb weavers.

In summary, the evidence of the specialized glands on the posterior lateral spinnerets (either pseudoflagelliform or flagelliform), the ampullate-gland control valve, and the duct-levator muscle supports the monophyly of the orb weavers and none of the differences between uloborids and araneoids refutes it. Of course few taxa have been studied. The monophyletic hypothesis would indeed be refuted if, for example, synapomorphies that precluded the relationship with araneoids were found linking uloborids with other non-orb-weaving taxa. However, no such evidence has been found, and in fact the monophyly of orb weavers seems to be the only hypothesis supported by any substantial evidence at all.

Web-Building Behavior

Even though the comparison of orb-weaver silk glands and spinneret morphology suggests that orb weavers are monophyletic, the monophyly could be refuted if a detailed comparison of web-building behavior in uloborid and araneoid orb weavers showed incompatible differences between them. The assertion that the orb webs of the two groups are convergently evolved usually has rested on arguments about the adaptive value of web

form. One would not necessarily expect details of web construction to be similar. In fact, if many possible ways to construct and attach silk lines exist, the probability of identical or closely similar behaviors should be small in any one instance, and minute for several independent instances combined. Of course, one could also claim that the details of behaviors are themselves adaptive, and that any similarity in them is also due to convergence under selective pressures. But is there any similarity for which this claim cannot be made? Clearly the only imaginable limit to that argument is imagination itself. There is no way to defeat the position. The best that one can do is to show that similarities are improbable by chance alone, and that no or very little evidence contradicts the simpler hypothesis of similarity due to common ancestry. Common ancestry, it must be admitted, is a simpler explanation than convergent evolution in otherwise equivalent cases. How then do uloborids and araneoids construct orb webs?

Web construction can be represented conveniently by a flowchart. The use of flowcharts to represent stereotyped sequences of behavior follows Robinson and Olazarri (1971). The overall sequences of web construction in uloborids and araneoids are compared in Fig. 12.25. The uloborid sequence is summarized from Eberhard's (1972b) study of *Uloborus diversus* and the araneoid sequence from Peters (1937), Tilquin (1942), and Savory (1952). Each sequence has been verified by personal observations. The overall sequences are obviously similar, but some of the similarity is probably due to what Seilacher (1973) has called "fabricational constraints," i.e., constraints imposed by the properties of the materials used, or by physical laws (such as geometry, gravity, mechanics, or temporal sequence). Fabricational constraints produce structural similarities due neither to heredity nor to natural selection—they are artifacts of limited possibilities. For example, because silk lines can support no bending or compressive force, constructions made of them must be in tension, and that limits the possible geometries of simple structures with few peripheral anchor points (to, e.g., planes, catenaries, or hyperbolic paraboloids, composed of straight-line segments). It also means that if all lines are to be taut in webs, only certain combinations of angles at the nodes of the web are possible. The basic sequence primary radius construction—NS construction—SS spiral construction is also inevitable. These similarities might still be due to common ancestry, but the possibility of independent origin is hard to exclude because no reasonable alternatives exist. Just as common ancestry is a simpler explanation than selection, fabricational constraint is a simpler explanation than common ancestry.

A more detailed look at construction behaviors, however, shows that they are more often similar than different, and that the differences do not refute the hypothesis that araneoids are derived from a cribellate orb-weaving ancestor. Primary radius construction (including exploration behavior) has not
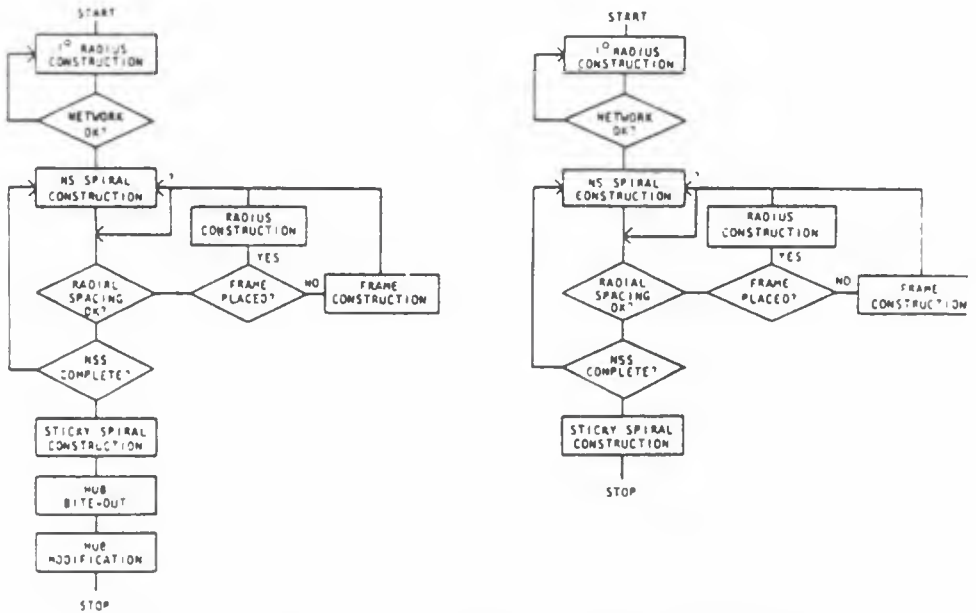
Fig. 12.25 General sequences of web construction of araneoids except nephilines (*left*) and of uloborids and nephilines (*right*). The araneoid sequence is summarized from Peters 1937, Tilquin 1942, and Savory 1952, the uloborid sequence from Eberhard 1972b. The inclusion of nephilines with uloborids is based on my own observations of *Nephila clavipes* and data from Eberhard 1982. NSS = nonsticky spiral.

been studied in detail in any group, but the process of frame construction in both groups is strikingly similar. *Uloborus diversus* and *Araneus diadematus* both construct a radius each time they construct a frame line. Tilquin (1942) has termed these "secondary" radii. By the time all frame lines are complete, a more or less equal number of secondary radii are in place, thus defining a "protohub," and construction of the "tertiary" radii continues. (Often "secondary" frames are added in the corners of the web by both uloborids and araneoids.) Uloborids use all the movement patterns seen in araneoids, but they also intercalate an additional movement pattern not seen in araneoids (Eberhard 1972b: 425): they cut the second half of the frame loose and move out farther on the first half before reattaching the second half and making the final secondary radius. Araneoids do not move the second half of the frame line, but make the secondary radius directly (Peters 1937; pers. obs.). In effect, uloborids add a behavior not seen in araneoids. Because all movement patterns in araneoid frame behavior occur in uloborid frame behavior, the additional movements of uloborids are probably autapomorphies for the group (Nelson 1978).

But are there other conceivable ways to make frame lines? Yes, because several perfectly feasible alternatives are given in descriptions of the process that are in fact incorrect although perfectly plausible (e.g., McCook 1889; Comstock 1912; Hingston 1920; Levi and Levi 1968; Dugdale 1969). I have watched frame construction in *Philoponella*, *Nephila*, *Chrysometa*, *Leucauge*, *Tetragnatha*, *Azilia*, *Argiope*, *Eriophora*, *Micrathena*, *Gasteracantha*, *Neoscona*, *Cyclosa*, *Salassina*, *Theridiosoma*, *Epeirotypus*, *Anapis*, *Anapisona*, and *Maymena*. The Uloborid genus *Philoponella* behaved essentially as described for *Uloborus* by Eberhard (1972b), and the araneoid genera as described by Peters (1937), Savory (1952), and Foelix (1982). With the difference noted above, frame lines and secondary radii are made the same way by both uloborids and araneoids.

Both araneoids and uloborids construct frames and radii as a subroutine within hub construction (Fig. 12.25) (Hingston 1920; Peters 1937; Tilquin 1942; Eberhard 1972b). *Uloborus diversus* completes the primary radii (and therefore the protohub), and then begins laying hub loops. Hub construction is interrupted almost immediately to make frame lines (and therefore secondary radii) and/or tertiary radii, then resumed, and the cycle repeated. This "nested" behavioral sequence continues until all radii are constructed, whereupon hub loop construction passes smoothly into temporary spiral construction. Eberhard (1972b: 429) stated that

There was no abrupt transition between radius and hub construction and temporary spiral construction. The spider continued making hub attachments after laying the last radius, and after circling the hub one or more times, it began to move away from the hub as it continued its progress in a circular direction attaching its line to each radius it crossed.

Some araneoids, such as *Neoscona*, *Eriophora*, *Tetragnatha*, *Azilia*, *Theridiosoma*, *Chrysometa*, and *Epeirotypus*, space the loops of the temporary spiral abruptly wider than those of the hub loops (pers. obs.), but the patterns of leg movements appear indistinguishable from those of uloborids. Other araneoids, such as *Nephilengys*, *Herennia*, *Nephila*, *Salassina*, *Micrathena*, *Gasteracantha*, *Cyclosa*, *Zygiella*, and *Metepeira* make the transition between hub loops and temporary spiral gradually, but again using the same leg movements. In both groups, therefore, there is no qualitative distinction between hub loops and the temporary spiral, and the movement patterns involved appear identical. The hub loops and temporary spiral together can thus simply be called the nonsticky spiral. A similar point was made by Tilquin (1942). In most araneoids, frame and radius construction is completed earlier in nonsticky spiral construction than it is in uloborids, so that it often appears to occur before the latter behavior.

Another obvious, but unnecessary, similarity between uloborids and araneoids concerns the direction in which the temporary and sticky spirals are

laid. In both groups the temporary spiral, being part of the nonsticky spiral, is laid from the hub outward, and the sticky spiral from the periphery inward. As Eberhard (1972b), Levi (1980a), and other authors have noted, this particular sequence seems to be arbitrary. However, only two possibilities exist (another example of fabricational constraints), and therefore the odds are even that two groups would coincide in sequence by chance alone.

Uloborids also differ from araneoids in making "doubled" radii and in biting out the protohub formed by the primary radii before commencing hub construction (Eberhard 1982, character F4; 1972b: 426–27). To make a doubled radius, the uloborid attaches its line to the hub, exits along a pre-existing radius, attaches the trailing line to a point on the frame, and returns to the hub, thus forming a doubled radius. (Because of the bilateral symmetry of the spinnerets, all single lines in a web consist of two strands, but these strands can be seen only with a microscope, and when ethologists speak of a "doubled" line they generally mean that the animal has spun two lines, each made of two strands.) Araneoids follow the same sequence, but when returning to the hub they cut and reel in with the first legs the line laid on the way out, while laying a new single line behind them with the fourth legs. This line becomes the definitive radius (Eberhard 1982, character F1). Because uloborids "cut and reel" during primary and secondary radius construction, the absence of cutting and reeling during tertiary radius construction is probably another autapomorphy for the group. (In all araneoids except nephilines, radii are always cut and reeled.)

Other, apparently derived features of most araneoids are biting out the center of the hub after completion of the sticky spiral ("hub bite-out" in Fig. 12.25) and either adding lines to the hub or leaving it open ("hub modification"). (For a description of these behaviors see Eberhard 1981a: 195.) Neither uloborids nor nephilines modify their hubs after they spin the SS line (Eberhard 1982, character G1).

If uloborids are an immediate outgroup of araneoids, one might expect these behavioral traits (i.e., hub loops as part of NS spiral construction, frame and radius construction persisting throughout NS spiral construction, and lack of hub bite-out and hub modification) to persist in some araneoid group. In fact, all these traits occur in nephilines, a group also considered primitive with respect to other araneoids on morphological grounds (Levi 1983). Eberhard (1982, character F2) states that, like uloborids, *Nephila*, *Nephilengys*, and *Herennia* do not cut and reel radii. *Nephila clavipes* does not cut and reel any lines at all in its web (pers. obs.), but this difference is probably an autapomorphy of the nephilines (if it also occurs in other nephiline taxa). There is also no clear distinction between hub loop construction and temporary spiral construction in these genera. Nephilines are unique in attaching the second line of the doubled radius to a point slightly

displaced from the attachment of the first line on the frame. As Eberhard (1982) points out, this peculiarity is apparently another autapomorphy of the group. The basic pattern of frame construction and radius construction, and their occurrence during NS spiral construction, can be taken as synapomorphies of all orb weavers, and as primitive behavioral traits for the araneoids. Certainly such similarities cannot be ascribed to fabricational constraints.

Another similarity between uloborids and araneids is the use of a lateral tap of outside leg 1 to locate the innermost loop of the SS line (Eberhard 1982, character A2). Nephilines also use a lateral tap, but of the second leg rather than the first. Thus all three taxa use a lateral tap of an outside leg, in contrast to other araneoid orb weavers, so the trait is presumably primitive (although the use of oL, in *Nephila* may be autapomorphic). Nephilines also use a downward slide of the fourth leg holding on to the radius to detect the innermost SS loop as the SS line is attached (Eberhard 1982, character A3). This trait also appears to be an autapomorphy of the nephiline genera.

All araneoids use the outside third and fourth legs to brace the radius when the SS line is attached; they also use the inside fourth leg to pull or push the SS line from the spinnerets as SS attachment occurs (Eberhard 1982, characters B_1 and C_1, respectively). Uloborids also use the oL,L, grip to brace the radius (*Philoponella*: pers. obs.), but they use the inside fourth leg as well to brace the radius; they do not manipulate the SS line at all (Eberhard 1982, characters B_2 and C_2, respectively). However, *Uloborus diversus* uses an oL,L, grip on radii to attach the NS spiral while the iL, holds the NS spiral line (Eberhard 1972b: 429; pers. obs. of *Philoponella*). The identical behavior by araneoids in a different context (the handling of SS lines) is quite plausible if araneoids and uloborids are sister groups. The use of the L,L, NS-line grip appears to be a synapomorphy for orb weavers, and the iL, push of the SS line during SS construction a synapomorphy for Araneoidea. The addition of the iL, leg to the oL,L, grip during SS construction in uloborids is apparently another autapomorphy.

Finally, uloborids and araneoids differ markedly in how they produce SS lines. In araneoids they are formed almost as a by-product of movement. The juxtaposition of aggregate and flagelliform spigots on the mesal surface of the posterior lateral spinnerets apparently allows the formation of viscid-silk lines without the intervention of legs. All cribellates have to brace both fourth legs against each other to comb cribellate silk from the cribellum onto the core fibers. But this difference in behavior is clearly due to anatomy, a fabricational constraint imposed by the nature of cribellate silk. The lack of SS-combing behavior might be claimed as a further synapomorphy of the araneoids, but the character is so obviously correlated with anatomy

that it is not independent evidence apart from aggregate glands of the monophyly of Araneoidea. Araneoids often do perform "L, pulls" (Eberhard 1981a) when combing sticky silk that are reminiscent of the combing of uloborids, but the resemblance seems too superficial to claim homology.

One real difficulty is the nearly total lack of information on spider groups that might be sister groups of the orb weavers, such as dictynids, tengellids, amaurobiids, eresids, or filistatids. Should such a behavior as a L,L, NS-line grip be found in those groups, the character would become a symplesiomorphy for the orb weavers. (However, Eberhard (1982) did not find it in cribellate-silk production in *Filistata*, *Tengella*, or *Mallos*.) It may be invalid in a specific case, and it certainly is invalid in general, to assume that because a web does not look like an orb it is not derived from one or is not a primitive precursor of one. Orb-weaver monophyly is not finally corroborated, however, until those behaviors basic to orb weavers (e.g., L,L, NS-line grip, frame behavior, radius behavior, oL, lateral tap to locate lines, NS spiral construction, and frame and radius behavior as a subroutine in NS spiral construction) are known to be absent in the potential outgroups.

In summary, comparison of the construction behavior of uloborids and araneoids indicates that many similarities could be synapomorphies insofar as most of the similarities are not due to fabricational constraints. The simplest interpretation of the differences between the two groups is usually as autapomorphies of uloborids or as derivations of behaviors present in uloborids, and therefore as synapomorphies for the Araneoidea. The available behavioral evidence supports the monophyly of all orb weavers and the sister relationship of the uloborids (and/or the dinopids) to the superfamily Araneoidea. Eberhard's work (1972b, 1981a, 1982) has shown that construction behavior provides many diverse behavioral details that corroborate the monophyletic hypothesis.

Web Form

The final comparison is of web form, perhaps the feature of orb webs that has most convinced workers that the orb-web architecture is highly evolved and highly adaptive, and therefore likely to be the result of convergent evolution. It was the similarity of uloborid and araneoid orb-web architecture that probably provoked the hypothesis of convergent evolution of the orb web (Figs 12.1, 12.2). After all, if the webs did not look similar the whole controversy would not have arisen. For Thorell (1886), and those who agreed with him, that similarity was the troubling flaw in Bertkau's argument for the monophyly of the cribellates (see above). Orb webs have always inspired admiration for their design. In view of Bertkau's evidence that they were convergently evolved, that admiration led to an easy rationale for the con-

vergence—the great adaptive value of the orb architecture explained the troubling similarity. But is that reputed adaptive value even relevant to the issue of convergence?

Seilacher (1973) suggests that similarity of form has three basic causes: fabricational constraint (discussed below), common ancestry (advocated here), or function. "Function" includes convergence, because to invoke convergent evolution as an explanation of form one has to postulate that a particular solution to a problem in natural design has such adaptive value that natural selection renders convergence on that solution likely. But that solution need not be the best by independent design criteria to claim convergence. It only need be good enough so that within the smaller set of "good enough" designs it is likely that two similarly endowed groups might happen on the same solution. If the hypothesis of convergence does not claim optimality, then the only way it can be conclusively disproved is by demonstrating that orb webs have no adaptive value at all—the negation of optimality. That position is contradicted by the existence of spiders relying on orb webs to catch prey. Even though many authors have speculated that orbs are superbly designed to do what they do (see, e.g., Witt 1965, 1975, Burgess and Witt 1976, Eberhard 1981a, and works cited therein) few have claimed that orb webs are the best imaginable design. Indeed, Witt (1965) argued that although they work well, they are not optimal in any one sense, but rather are a compromise between many conflicting requirements. It seems clear that all that can be demonstrated experimentally is that orb webs are functional ways to do whatever it is the observer imagines they do.

Could convergence still be used as an explanation if orbs could be shown to be better than any existing web architecture for specific purposes, such as the entrapment of flying insects in their flyways, or the rapid transmission and localization of vibrations, or the efficient use of materials in relation to area covered? One could still not claim to have proved convergence, because any number of equally good and equally likely web architectures might exist if only the observer could imagine them, build models, and demonstrate their adaptive equivalence to orb webs. For example, the web of *Synotaxus* (Fig. 12.4) is also a nearly invisible vertical snare suspended from a few points, and it is effective at trapping flying insects (pers. obs.). Yet it is built on a modular, rectilinear plan (Eberhard 1977b). The webs of *Scoloderus* spp. (Eberhard 1975; Stowe 1978) and the metine genus in New Guinea (Robinson and Robinson 1972) are architecturally (but not in mode of construction) more similar to the web of *Synotaxus* than to the webs of other orb weavers. Numerous other orb weavers have also modified the basic architectural style of an orb web; alternative designs can and do exist (Stowe, this volume). It may also seem likely that signal transmission would be less efficient in a sheet web than in an orb web (Witt 1965). However, the meta-

tarsal lyriform organs of web spiders are extremely sensitive vibration re-
ceptors (Walcott and Van der Kloot 1959; Liesenfeld 1961; Barth 1972). The
critical variable is the total travel time of the spider to the capture site; the
ease of moving on a dry sheet may compensate for the presumed attenuation
of the signal. Thus, in the absence of the extreme claim of optimality (or its
opposite), a claim of convergence based on adaptive value again depends on
unspecifiable probabilities and unmeasurable approaches to adaptive perfec-
tion. To claim convergence, therefore, it is not enough to show that orb
webs are good at what they do, because one cannot show that they are per-
fect, nor can one show that they are perfectly not perfect, and the middle
ground is the purview of fruitless contention. Indeed, their comparison to
perfection is itself limited by the observer's ability to imagine perfection.
Therefore orb webs cannot be demonstrated to be convergent (or homolo-
gous) by arguments involving their adaptive value alone.

A claim of convergence can be justified only by evidence showing that one
group of orb weavers is more closely related to non-orb weavers than to
other orb weavers. It is never great adaptive value that substantiates con-
vergence (although it may make it more plausible); it is always and only evi-
dence that shows that two taxa similar in some feature cannot be so closely
related that the similarity is due to the simpler explanations of fabricational
constraint or common ancestry. Such evidence is what Bertkau (1882) and
the workers who agreed with him thought they had in the fact of the cri-
bellum. With the demonstration that Bertkau's Cribellatae are paraphyletic
(Lehtinen 1967, Platnick 1977), the reason for believing that orb webs are
convergent evaporates, because there is no other evidence based on shared
derived characters that uloborids are more closely related to any other group
except araneoids. Evidence of relatedness that refutes the interpretation of
similarity as homology is a prerequisite for a claim of convergence, simply
because convergence presupposes some genealogical hypothesis. Thus ul-
oborid and araneoid orb webs were not thought to be convergent because
they were adaptive; if anything they were thought to be adaptive because
they were convergent. Convergence therefore is an a posteriori explanation
of taxonomic discordance. If there is no discordance the hypothesis of com-
mon ancestry is always simpler.

But what of fabricational constraints? If, in the absence of discordance,
homology is a preferable alternative to convergence, then fabricational con-
straint is preferable to homology for the reasons outlined earlier. Uloborid
and araneoid orbs share the following distinctive architectural features: (1) a
two-dimensional frame connected to the substrate at relatively few points,
(2) a pattern of nonsticky radial lines converging on a point, (3) a NS spiral,
later mostly removed, and (4) a permanent spiral of sticky silk. By "sticky
silk" I simply mean silk to which things stick, without specifying the

mechanism of adhesion (i.e., true viscid silk or cribellate silk). All of these features are potential synapomorphies of the taxa. None appears to be the consequence of fabricational constraints. For example, coincidence of a hub in the web and a two-dimensional frame bounding the lines exiting from the central point is only one architectural style, as demonstrated by the existence of diverse other designs; compare, e.g., the webs of *Eidmanella* (Fig. 12.6), *Synotaxus* (Fig. 12.4), *Ogulnius* (Fig. 12.12), *Mysmena* (Fig. 12.19), *Achaearanea* (Fig. 12.5), and *Wendilgarda* (Fig. 12.11). Point symmetry bounded by a two-dimensional frame clearly is not the only architecture possible. (That all these webs are probably derived from orb webs does not affect the argument that the "orb" architecture is not inevitable—on the contrary, the webs of *Ogulnius*, *Mysmena*, and *Wendilgarda* are certainly derived from orbs, thus showing that the orb is not an inescapable adaptive optimum.)

As mentioned previously, hub-reinforcing loops are nearly indistinguishable behaviorally from the temporary spiral. In orb weavers that spin an extensive temporary spiral such as araneids, nephilines, and uloborids, it is obviously of some use, but many orb weavers spin quite regular sticky lines (not necessarily spirals) without the help of a temporary spiral, e.g., *Epeirotypus* (Figs. 12.7, 12.8), *Theridiosoma* (Figs. 12.9, 12.10), *Anapis* sp. (Fig. 12.14), *Anapis heredia* (Fig. 12.16), *Poecilopachys* (Clyne 1973), *Cyrtarachne* (Stowe, this volume), and *Pasilobus* (Robinson and Robinson 1975). Thus a temporary spiral is not necessary for sticky spiral construction. The simplest interpretation seems to be that its occurrence in both uloborids and araneoids is a synapomorphy rather than a feature either so adaptive that its identical form in the two taxa is convergent or so necessary that its existence is inevitable.

The occurrence of a sticky spiral in both groups also does not seem to be an inevitable consequence of the design of the NS network. The webs of both *Synotaxus* and *Achaearanea* combine sticky and nonsticky silk without anything like a spiral. The recent discovery of an orblike web in the psechrid genus *Fecenia* (Robinson and Lubin 1979b) and Szlep's (1966) earlier work on *Titanoeca* show that when vaguely spirallike designs are present in other taxa, they are still quite different in form and mode of construction from those of true orb weavers. It seems simplest to accept the spirals spun by uloborids and araneoids as homologues.

The similarities in web form thus do not seem to pose any real difficulties for the monophyletic hypothesis for the origin of the orb web. The real difficulties, at least as they were articulated by Kullmann (1972a), have been the nature of the transition between a cribellate and an ecribellate orb. Kullmann listed four serious problems (p. 401):

(1) It is highly improbable that, while preserving the same method of capture, the highly developed and extremely efficient dry cribellate snare is merely exchanged for the ecribellate viscid capture-thread. Simultaneously, the behavior of weaving cribel-

late threads plus the typical cribellate organs must have been reduced while being replaced by new spinning-organs plus any necessary motor pattern.

(2) Since orb-webs without any capture threads are totally useless, in the time of transition either spiders which simultaneously produced cribellate and ecribellate capture-threads must have existed, or the change from one system to the other happened suddenly. Both ideas are fantastic.

(3) One absurdity more—the Uloboridae are the only spiders without poison glands. Since they are not primitive, they must have descended from other spiders, these organs obviously have been reduced. After becoming ecribellate, they must have regained them, as all Araneidae are poisonous.

(4) The typically structured hairs covering the body differ in both families. The Uloboridae have hairs like all cribellates—they are plumose. Those of Araneids are smooth or more or less serrated only; they are identical with those of other ecribellate families, especially theridiids and linyphiids. There is no doubt that these families are related, but it is difficult to imagine that cob-webs of theridiids and sheet-webs of linyphiids developed via orb-webs of Araneids from those of Uloborids.

Kullmann's first two points dwell on the fantastic nature of the necessary transition. I can at least suggest why the transition is less than fantastic, although the reasons are as hypothetical as Kullmann's objections. From the point of view of selection or adaptive value, the length of time required to build the scaffolding for either an uloborid or an araneid orb is about the same for similar-sized webs—about 20 minutes on the average. However, an uloborid requires far longer to construct a cribellate sticky spiral (1–2 hours?) than an araneid requires to construct an equivalent viscid spiral (as little as 10–20 minutes). The extra time is consumed in the tedious process of combing out the cribellate silk; in araneids, viscid silk is produced as a by-product of the spider's movement. Thus araneids (and araneoids) spend less time exposed to predators and parasites, while performing an activity that probably renders the spider less alert than when it is at the hub or in a retreat. The convergent occurrence of barrier webs, signal lines, and retreats among many orb weavers attests to the selection pressure exerted by predators and parasites.

Second, although both uloborid and araneoid orb weavers move from one radius to the next, uloborids go quite slowly, all the while frenetically combing out cribellate silk. The araneid moves quickly, with no such frenzied movements, presumably a metabolic economy.

Third, Tillinghast, Kavanaugh, and Kolbjornsen (1981) have shown that the viscid silk of *Argiope trifasciata* (Araneidae) contains substantial quantities of carbohydrates—much more than is contained in ampullate silk. Kovoor (1977b) showed that the aggregate silk of *Latrodectus* (Theridiidae) also contains mucosubstances. If it is presumed that the carbohydrate content of all types of uloborid silk is comparable to that of araneid nonsticky silk because they are all fibrous, the dramatic increase in the carbohydrate content of viscid silk (by length the largest component of any orb web) may represent a considerable economy in the total protein investment in the web.

Peakall and Witt (1976) argued that because *Araneus diadematus* recycles its web there is little or no "protein" cost associated with an orb web, but that argument may be invalid. Webs in nature are often damaged to the extent that the spider loses some or all of the silk. Therefore, while the silk is in a web, the spider is at risk for the material. On the other hand, spiders eat a high-protein diet (Foelix 1982); perhaps carbohydrates are for them more "costly" than proteins. Without data on that variable and on the amounts of protein in webs, we can neither deny nor confirm that web loss may be a substantial risk for orb weavers.

Fourth, authors have remarked on the persistent, almost paradoxical stickiness of cribellate silk (Foelix and Jung 1978), and also implied that cribellate silk might be more effective in retaining prey than viscid silk (Opell 1982a), but its superiority has not been shown in field studies. Eberhard (1980b) noted that the stickiness of cribellate silk in nature was often substantially reduced within a few days or less owing to rain or dust accumulation. Finally, the idea of an ancestral cribellate spider producing slightly sticky viscid silk from aciniform glands exiting on the posterior lateral spinnerets while still producing cribellate silk is not unimaginable.

The transition from a cribellate- to a viscid-silk orb is also not as improbable as Kullmann imagines. Second-instar uloborid spiderlings lack functional cribella and spin dry-silk orbs (Szlep 1961). The spiderlings catch some prey, and this fact confounds Kullmann's second point; it also suggests that any second-instar spiderling that could produce sticky silk might profit. Szlep (1961) states that the supernumerary radii characteristic of juvenile uloborid webs are made from a different silk, finer and softer than radial silk. Although she did not identify it, the logical guess is that it is aciniform silk. As noted, Kovoor (1977c) believed that aciniform silk may have been the precursor of aggregate silk, so that, if required, a plausible scenario exists for the origin of the viscid-silk orb web.

We know rather little about silk and its functions, and what we know is confined to only a few groups—there is virtually no evidence to settle these questions one way or the other. The points that I have made are merely speculations to render less objectionable implications that Kullmann felt to be fantastic. Certainly the monophyly of orb weavers, based on some evidence, should not be rejected because of preconceptions about hypothetical adaptive situations.

Kullmann's third and fourth points do not really concern the implausibility of the homology between uloborid and araneoid orb webs. The third point stems from the presumption that modern uloborids would have to have been ancestors of araneoids; all that the monophyletic hypothesis requires is that they share a common orb-weaving ancestor with poison glands. The fourth point merely states that serrate hairs are a derived feature

of Araneoidea, an interpretation that does not conflict with the relationship between uloborids and araneoids suggested here. The idea of theridiids and linyphiids as orb weavers is unsettling, but when the orbs of other araneoid families are considered, the idea may become less objectionable.

In sum, the four similarities in web form given earlier are unique to orb weavers. There is no compelling evidence against them as synapomorphies. The evidence from behavior and silk glands is consonant with that form, and together they imply (1) that the orb web arose only once, (2) that orb weavers are a monophyletic group, (3) that uloborids (and/or dinopids) are the sister taxon of araneoids, and (4) that the orb web is primitive for all araneoids.

The total number of species descended from orb-weaving ancestors therefore approaches one-third of all described spider species (as estimated from Levi 1982). Far from confirming that the orb web is the adaptive pinnacle of spider-web architecture, achieved once or twice during the evolution of the order, the evidence suggests that the orb web is an ancient feature, discarded by many derived groups such as Linyphiidae, Nesticidae, and Theridiidae. The araneoid orb did not emerge from the chaos of the theridiid cobweb, as most previous authors have claimed (Pocock 1895; Comstock 1912; Kaston 1964; Kullmann 1972a)—it was the other way around.

Web Architecture Within the Araneoidea

I shall now briefly discuss the web architecture of the araneoids that still spin orb webs. For taxa such as linyphiids and theridiids no comparable information exists. The preceding discussion orients the transformation series in web architecture within the Araneoidea. The primitive web architecture, and how it was constructed, can be deduced. This information permits a reasonable first hypothesis for phylogeny within the araneoid superfamily.

In the preceding discussion it was argued that the primitive web form of the Araneoidea was a two-dimensional orb web, i.e., a point-symmetrical array of radial lines bearing a viscid-silk spiral, the whole bounded by a two-dimensional frame attached to the substrate at relatively few points. The construction of each frame line involved the simultaneous construction of a radial line, and those secondary radii met at a protohub that was reinforced by the construction of a nonsticky spiral outward from the protohub. Nonsticky spiral construction was interrupted frequently to construct more frame and radial lines. Radius construction ceased early in the spinning of the nonsticky spiral and, after completion of the nonsticky spiral, construction of the sticky spiral began. This was an uninterrupted sequence consisting of stereotyped movements, probably involving a sideways tap of the

outer first leg to locate the innermost loop of sticky spiral. In addition, the outside third and fourth legs were used to grip the radius during SS attachment, and the inside fourth leg pulled more sticky silk from the spinnerets, just before the spinnerets attached the SS line to the radius. Completion of the sticky spiral was the last step in web construction, and the center of the hub was neither removed nor modified.

This description of the plesiomorphic web architecture and the method used to construct it is a generalization based on the distribution of architectural and behavioral characters among the orb weavers. Nearly all the available information on behavior concerns the uloborids, nephilines, and araneids. As the information presented below indicates, rather little is known about how the rest of the araneoid orb weavers construct their webs.

Metine-Tetragnathines

As Eberhard's (1982) data show, the building behavior of metines and tetragnathines is nearly identical to that of araneids. They differ primarily in using an iL, forward tap to locate the inner SS loop, as in theridiosomatids, symphytognathids, anapids, and mysmenids (Eberhard 1982, character A1).

Theridiosomatidae

Despite the small size of the family, theridiosomatid webs are astonishingly diverse. Only the webs of *Epeirotypus* (Fig. 12.7) and *Theridiosoma* (Fig. 12.9) resemble orbs; the webs of *Wendilgarda* (Fig. 12.11; see also Coddington and Valerio 1980) and *Ogulnius* (Fig. 12.12) are very different. Like all araneoids except the nephilines, *Epeirotypus* and *Theridiosoma* bite out the center of the hub after sticky spiral construction, but hub modification in these genera is much more extensive and results in a completely rebuilt hub (Eberhard 1981a; pers. obs.). Both *Epeirotypus* and *Theridiosoma* appear to have "nonsticky circles" instead of a nonsticky spiral (Figs. 12.8, 12.10). The building behavior of *Wendilgarda* and *Ogulnius* differs substantially from the araneoid sequence in Fig. 12.25 but is consonant with it (pers. obs).

Eberhard (1981a, 1982) has shown that theridiosomatids are similar to anapids in a number of features. During sticky spiral construction, *Epeirotypus* and *Theridiosoma* locate the innermost loop of the SS line with an iL, forward tap, their body axis parallel to the radius (Eberhard 1982, character A1). Eberhard (1981a) also observed that *Epeirotypus*, *Theridiosoma*, *Ogulnius*, and two anapid species hold the SS line away from the radius with their fourth legs as they move between SS attachments, presumably to prevent it from adhering to the radius. He did not mention if symphytognathids or mysmenids did the same.

A third similarity is the apparent anastomosis of radii before they reach the hub (Eberhard 1981a). In theridiosomatids, true radial anastomosis (i.e.,

of structural radii after sticky spiral construction) occurs only in the genus *Theridiosoma*. (As presently defined, the genus *Theridiosoma* is paraphyletic, and will have to be relimited.) Radial anastomosis in symphytognathids, anapids, and mysmenids has not been shown to involve other than the accessory radii added after sticky spiral construction. No *Epeirotypus* species joins its radii either before sticky spiral construction or after. The presence of the plesiomorphic condition in *Epeirotypus* (lack of radial anastomosis), combined with the incontestable monophyly of theridiosomatids, suggests that radial anastomosis in *Theridiosoma* must have arisen independently in that group.

One similarity unites theridiosomatids exclusively with symphytognathids, anapids, and mysmenids. All of these taxa add hub loops after the hub bite-out as part of hub modification (Fig. 12.25). Other araneoids may add lines to fill in the open center of the hub, but they do not add them to the periphery of the hub, nor do they add them in a stereotyped sequence reminiscent of nonsticky spiral construction.

Symphytognathidae

Symphytognathids spin strictly two-dimensional orbs. Few people have seen them build, but as Eberhard (1981a) points out, some details of construction behavior can be inferred from the appearance of the web. Symphytognathid webs are peculiar in two respects. First, after sticky spiral construction, the spider returns to the hub and constructs many accessory radial lines that are not specifically attached to the SS line (Fig. 12.23; see also Forster and Platnick 1977, Fig. 1). Figure 12.24 is a photograph of the web of a *Patu* sp. immature and shows the smaller number of structural radii. Accessory radii are also characteristic of second-instar uloborid webs (Szlep 1961), but Szlep stated that the accessory radii of uloborid webs were not made of the same silk as the structural radii. A similar comparison of the accessory and structural radii of symphytognathids has not been made. The use of a silk type other than ampullate-gland silk in a radial position in orb webs would be unique, but until Szlep's assertion is corroborated and the situation in symphytognathid webs evaluated, any suggestion that symphytognathids might be allied to uloborids by this character would be premature.

Second, like the webs of anapids and *Maymena* (Mysmenidae), symphytognathid webs exhibit "radial anastomosis." Eberhard (1982) states that in anapids this extensive modification of the hub and radii occurs after the SS line is complete, but he did not specifically say whether the structural radii were joined to each other (as in *Theridiosoma*; see above) or whether only the accessory radii were joined to the structural radii. My own observations of anapids and *Maymena* support the latter alternative, so that the char-

acter is more appropriately termed "accessory radius anastomosis." As a result of this process, fewer radial lines meet at the hub, and the tension in all radial lines is reduced (Eberhard 1981a: 194–95). Radial anastomosis of either type is unknown as a general feature in araneids, tetragnathines, nephilines, and uloborids. Eberhard (1981a) has seen radial lengthening in a few species in these groups (in two tetragnathine species and one *Gasteracantha* species), but this occurrence is by no means general and does not result in radial anastomosis.

Anapidae

All known webs of anapid species resemble one another quite closely, e.g., the webs of *Anapis heredia* (Fig. 12.16), *Anapis* sp. (Fig. 12.14), *Anapisona felida* (Platnick and Shadab 1978a, Fig. 1—printed upside down), *Anapisona simoni* (Fig. 12.15), and *Chasmocephalon shantzi* (Fig. 12.17). The webs share the usual two-dimensional frame and point symmetry, but during radius construction some lines are laid out of the plane of the orb and attached directly to the substrate above the plane of the web. (Note the straight, roughly vertical lines in Figs. 12.14–12.17, and see also Fig. 12.18, which shows a *C. shantzi* web before sticky spiral construction.) When the spider subsequently encounters one of these out-of-plane radii during sticky spiral construction, it may either skip it or treat it like a planar radius. The result is sporadic catenary SS lines connecting the out-of-plane radii with the rest of the web (Figs. 12.14–12.18).

Eberhard (1981a: 194) states that the anapid species that he has observed lengthen their radii in the same way as symphytognathids do. Anapids also lack extensive nonsticky spirals (Eberhard 1982, character H3) and place their egg sacs just above the hub (Figs. 12.14, 12.15). In addition, at least *C. shantzi* (pers. obs.) uses an iL, forward tap to locate the inner loop of the SS line during SS construction (Eberhard 1982, character A1). Like symphytognathids, anapids construct accessory radii after SS construction (Figs. 12.15–12.17).

Mysmenidae

At present the mysmenids include two genera that are known to have very dissimilar web architectures, *Maymena* and *Mysmena*. Thus far, known *Mysmenopsis* species do not spin webs (Platnick and Shadab 1978b), and the webs of other genera are unknown. Figure 12.22 is a photograph of the web of *Maymena ambita*, and Figs. 12.19–12.21, are a series of photographs of webs of various *Mysmena* species.

Maymena webs include the out-of-plane radii characteristic of anapid webs (see above), accessory radius construction, accessory radius anastomosis like that of symphytognathid webs but not like that of *Theridiosoma* webs (pers.

obs.), and radial lengthening (Eberhard 1981a). Like anapids, *Maymena* place their egg sacs just above the hub (pers. obs.). To my knowledge the webs of *Maymena* and those of anapids do not differ substantially, although detailed study of the building behavior of these spiders may disclose some contrasts.

Mysmena, on the other hand, spin an orb web that is among the most derived architectures known. Yet, as Figs. 12.19 and 12.20 show, this three-dimensional orb is produced mainly as a result of a proliferation of out-of-plane radii. The spiders do not spin a nonsticky spiral (pers. obs.); the sticky spiral is laid in a typical fashion, using the iL, forward tap to locate the innermost loop of sticky silk (Eberhard 1982, character A1). Apparently the spiders do not always move out on the exit radius far enough to contact the inner loop; i.e., some SS attachments are made without inner-loop contact (pers. obs.). As in *Maymena*, anapids, and the theridiosomatid *Ogulnius* (Fig. 12.12), the trajectory of the SS line is simply a fabricational consequence of radial lines in three dimensions. Close inspection of the hubs of completed webs reveals the presence of radial anastomosis, but it is not known whether radial lengthening occurs. Also like *Maymena* and anapids, *Mysmena* hang their egg sacs just above the hub (Fig. 12.21).

The Phylogeny of Orb Weavers

The implications of the preceding discussion are summarized in Fig. 12.26. The cladogram was produced using component analysis (Nelson and Platnick 1981). Often the occurrence of a feature in a few members of a taxon has been assumed to be enough to propose it as a general feature of the taxon. Some of these assumptions are critical, such as the presence of aggregate and flagelliform glands in all araneoid higher taxa, the use of a viscid-silk wrap attack by nesticids and theridiids, or the generalizations about anapids from the few species described in the literature or that I have observed.

Some characters mentioned in the text, but omitted in the cladogram, may turn out to be informative when better studied. These include SS-R cement (Kavanaugh and Tillinghast 1979; Work 1981), data on wrap attacks, and the various forms of araneoid paracymbia. Other characters not even considered here, such as the kind and number of spigots on spinnerets, may also turn out to be informative. The lack of a functional cribellum in araneoids is probably synapomorphic, but until homologies between coluli are better understood (Lehtinen 1967), the derived nature of the araneoid colulus cannot be defined.

The interpretation of some characters is problematic. For example, uloborids do not cut and reel radii, but they do cut and reel frames. Nephilines
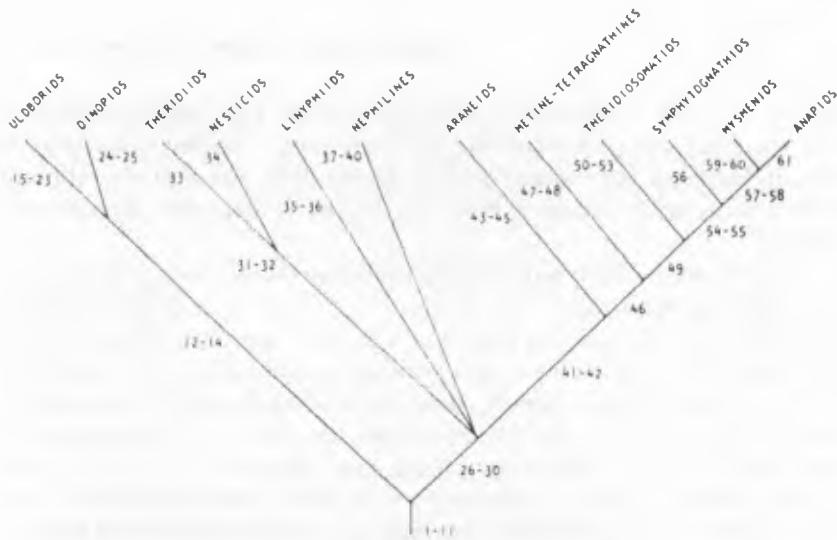
Fig. 12.26. Cladogram for orb-weaving spiders. Characters defining the branch points are listed below and explained in the text.

1–11. 1, specialized glands on posterior lateral spinnerets; 2, duct-levator muscle and control valve in anterior lateral spinnerets; 3, two-dimensional frame; 4, hub; 5, nonsticky spiral; 6, sticky spiral; 7, frame behavior (cut and reeled); 8, radius behavior (cut and reeled); 9, frame and radius behavior during nonsticky spiral construction; 10, oL, lateral tap to locate inner sticky-silk loop; 11, oL,L, nonsticky-line grip.

12–14: 12, puffed cribellate silk; 13, pseudoserrate plumose hairs; 14, fourth-tarsal macrosetae.

15–23. 15, cymbial setae; 16, inverted minor ampullate glands; 17, pseudoflagelliform glands; 18, loss of poison glands; 19, second-instar web with accessory radii; 20, uloborid frame behavior; 21, protohub bite-out; 22, iL, radius grip during sticky spiral construction; 23, radii not cut and reeled.

24–25. 24, eyes in three rows; 25, web structure (Fig. 12.13).

26–30. 26, aggregate glands; 27, flagelliform glands; 28, serrate hairs; 29, paracymbium on male palp; 30, iL, push during sticky-silk attachment.

31–32: 31, sticky-silk wrap attack; 32, fourth-tarsal comb setae.

33: lobed aggregate glands.

34: basal plate of trichobothria.

35–36: 35, conformation of male palp; 36, route of ejaculatory duct.

37–40: 37, temporary spiral not removed; 38, radii doubly attached to frame; 39, oL, downward slide to locate inner sticky-silk loop; 40, frames and radii not cut and reeled.

41–42: 41, final hub bite-out; 42, hub modification.

43–45. 43, rotation of palpal bulb; 44, spin-wrap attack; 45, reduced tapeta in posterior median eyes.

46: iL, forward tap to locate inner sticky-silk loop.

47–48. 47, modified paracymbium?; 48, elongate chelicerae.

49: hub loops after sticky spiral construction.

50–53. 50, sternal pit organs; 51, palp conformation; 52, route of ejaculatory duct; 53, temporary spiral as circles, when present.

54–55: 54, accessory radii; 55, radii lengthened.

56: fused chelicerae.

57–58: 57, out-of-plane radii; 58, egg sac suspended above hub.

59–60: 59, male metatarsal spurs; 60, femoral tubercle.

61: labral spur between chelicerae

cut and reel neither, and the remaining araneoids cut and reel both. The interpretation taken here is that absence of cutting and reeling is secondary, wherever it occurs within orb weavers. One might, for example, consider cut and reeled frames as a synapomorphy for orb weavers, nephilines autapomorphic in lacking them, and cut and reeled radii as a synapomorphy for the remaining araneoids. But the mere presence of cutting and reeling during movement via draglines in many spider groups suggests that most taxa are capable of it. Thus, its absence in nephilines is probably derived.

The method used by orb weavers to locate the inner loop of sticky silk during sticky spiral construction is a similar character. Uloborids and araneids use an oL, lateral tap, nephilines use an infrequent oL, lateral tap and a frequent oL, downward slide, and the remaining araneoids use an iL, forward tap. Depending on the situation in dinopids, the plesiomorphic technique is probably an oL, lateral tap, but other possibilities could be argued. A third case is the use by uloborids of an iL, grip to brace the current radius during SS attachment in addition to the oL,L, grip. Eberhard (1982) calls this an oiL, grip because these legs are in fact closest to the site of attachment. In view of the prevalence of the oL,L, grip elsewhere in uloborid building behavior and in orb-weaver building behavior generally, it seems simpler to interpret the iL, grip as an addition to the plesiomorphic orb-weaver behavior. A similar argument justifies uloborid frame behavior and the bite-out of the protohub as additional uloborid autapomorphies. Regardless of the alternative favored, the cladistic structure of Fig. 12.26 remains unaffected because of the numerous other characters supporting the monophyly of orb weavers on the one hand and of Araneoidea on the other.

The cladogram makes several implicit predictions, besides the validity of the generalizations just mentioned. For example, it predicts that Dinopidae will possess a pair of specialized glands serving the posterior lateral spinnerets (homologues of the pseudoflagelliform and flagelliform glands), a duct-levator muscle in the anterior lateral spinnerets, and an ampullate-duct control valve of the type characterizing uloborids and araneoids (Wilson 1969). In addition, the four architectural features and five behaviors listed as synapomorphies of all orb weavers are predicted to occur in Dinopidae.

The main point of this review has been to demonstrate the monophyly of all orb weavers, and, in the absence of any contrary evidence, the 11 characters documenting that monophyly seem adequate. Some of the branch points in Fig. 12.26, however, are not well established. For example, the monophyly of the uloborid-dinopid lineage is based on only three characters, primarily because so little is known about dinopids. Because araneoids are so autapomorphic, the characters unique to uloborids and dinopids may be retained plesiomorphies; thus "puffed" cribellate silk and pseudoserrate plumose hairs may actually be additional orb-weaver synapomorphies. In that case the lineage of orb weavers would exhibit a basal trichotomy. How-

ever, rather than postulating gain of those characters in the stem taxon of orb weavers and their subsequent loss or modification in araneoids, it is simpler to view them as single gains uniting uloborids and dinopids.

Several nodes of the cladogram are especially weak, e.g., that uniting the araneids with the rest of the araneoids, which is based solely on the occurrence of hub bite-out and hub modification. Although the generality of those features in all araneoids except nephilines is fairly well established (Eberhard 1982; pers. obs.), their absence in nephilines could be secondary. Nephilines appear to have lost or modified many features, e.g., cut and reeled frames and radii, an oL, lateral tap to locate the inner SS loop, and temporary spiral removal.

Similarly, the only character uniting the metine-tetragnathine lineage (if indeed that lineage is monophyletic) with the remaining araneoids is the iL, forward tap to locate the inner SS loop. This feature is, however, universal in the terminal taxa of the tree; i.e., all of the species observed in these taxa use an identical behavior. An oL, lateral tap does occur jointly with an iL, forward tap in at least one *Tetragnatha* species and in some *Chrysometa* species (Eberhard 1982).

The only really derived localization behavior among all orb weavers may be that of nephilines, which use the iL, in a downward slide. As Eberhard (1982) points out, that behavior is practical only in species that are large compared with the size of their webs, and all the nephilines are large spiders building closely meshed webs. It is significant that *Nephila clavipes* uses an infrequent oL, lateral tap to touch the SS line several radii in advance of the current SS-R attachment. Both uloborids and araneoids do a "leg over leg" behavior, using the first two outer legs to pull the current inner SS-R junction towards them (pers. obs.). This behavior supports the hypothesis both that the iL, forward tap is derived and that nephilines belong outside that group.

Multiple loss of the cribellum among orb weavers is a possibility. In that case the femoral trichobothria common to uloborids and tetragnathines might be synapomorphic, as might the accessory radii common to symphytognathids and juvenile uloborids. The similarity between uloborids and tetragnathines in posture at the hub may also be significant. (The first and second legs are appressed and extend straight out.) But these suggestions require a convergent development of all five characters supporting the monophyly of the Araneoidea, especially of the aggregate glands. On the other hand, the aggregate glands as a synapomorphy is based mainly on the morphological similarity of SS lines in araneoids, and not on any knowledge that aggregate glands are present in all araneoids.

The theridiid-nesticid and linyphiid lineages can be placed only at the basal node of the Araneoidea, on the basis of behavioral data. That placement implies that both groups certainly are araneoids, but may also turn out

to be sister taxa of any of the araneoid lineages more precisely placed in Fig. 12.26. Since the data reviewed here are insufficient to allow either of the lineages to be placed with its sister taxon, they are placed at the most restrictive node possible, i.e., the basal node of the araneoids. The cladogram of Fig. 12.26 logically includes all the more fully resolved possibilities (Nelson and Platnick 1981).

Linyphiids and theridiids are among the most derived araneoid taxa behaviorally, and it may not be possible to discern any action patterns typical of orb weavers in their building behavior beyond a L,L, NS-line grip and a L, pull. Few detailed studies exist of the building behavior of theridiids (but see Cutler 1972a; Freisling 1961; Szlep 1965). It is my impression that both *Latrodectus* and *Achaearanea* spiders touch the substrate with a L forward tap just before SS attachment, but in doing so the spiders are hanging head down on a vertical line, and in this position few alternatives exist to touching the substrate with the first legs. Some theridiids do have sticky silk doubly connected in their webs, e.g., *Theridion impressum* (Wiehle 1933) and *Synotaxus* (Fig. 12.4), and it would be important to know which legs are used in attachment behavior. Szlep (1965) did speculate that the building behavior involved in the construction of the lower sheet of a *Latrodectus* web was vaguely similar to that of orb weavers, but her observations are too general to allow any conclusions.

It is unlikely that behavioral synapomorphies will be found uniting theridiids or linyphiids with any single taxon within the Araneoidea, since those two groups are very specialized. The webs of theridiids and linyphiids are probably not the result of elaboration of the orb-web algorithm, but rather of simplification—i.e., of prolongation and elaboration of the initial stages of web construction, so that the action patterns uniquely characteristic of orb weaving never appear. Exact placement of these taxa will probably be based on morphological evidence. In linyphiids more attention might be paid to the erigonine genera because sticky silk is said to be more abundant in their webs (Bristowe 1958). The signature, as it were, of theridiid webs is the use of segmental sticky silk, usually attached at one end to the substrate, rather than a continuous SS line attached only to silk, as in most orb weavers.

Ironically, this review has not really addressed the question of how the orb web first evolved. Its main point has been the demonstration that the orb webs of uloborids and araneoids are homologues. One effect of that argument is to remove the question of the origin of the orb web from the domain of people who work on araneoid spiders. As noted previously, the existence of a cribellate orb weaver within a monophyletic taxon of orb weavers makes it advisable to presume that the sister taxon of orb weavers was cribellate, and probably still is (excepting the possibility that the sister lineage independently lost the cribellum). Interestingly, nearly all the "proto-orbs" pro-

posed by previous authors are spun by cribellate spiders, e.g., *Titanoeca* (Amaurobiidae) and *Stegodyphus* (Eresidae) (Szlep 1966), *Dictyna* (Dictynidae) (Kaston 1964), *Filistata* (Filistatidae) (Norgaard 1951), *Zoropsis* (Zoropsidae) and *Acanthoctenus* (Acanthoctenidae) (Wiehle 1931), *Fecenia* (Psechridae) (Robinson and Lubin 1979b). If indeed any of these webs is homologous to orbs, the definition of an orb web becomes a matter of taste depending on what degree of "orbness" merits the name. Eberhard (1972b) has shown that, in uloborids, frame, hub, and radius construction are difficult to distinguish. This basic similarity in behavioral pattern suggests that the NS network of an orb arose through a process of simplification and stereotypy of the most basic knot an orb weaver ties: the addition of one NS line to another to make a three-way junction, or trivalent node. This act might well be called "3-NS" behavior; one wonders how general a behavior it is in web-building spiders. As Denny (1976) has pointed out, orb webs actually consist of a network of nodes of which only one, the "hub," has a valence higher than 3. (In topology the valence of a node is the number of lines meeting at that node: Loeb 1976.) In fact, even the hub of an orb web consists of trivalent nodes, as hub construction in uloborids and nephilines clearly demonstrates. The hub of an orb web appears to have a high valence only because its trivalent nodes are closely spaced. The NS network qualitatively consists simply of the iteration of 3-NS behavior; quantitatively it consists of the distortion of sequential trivalent nodes so that short series of nodes are closely spaced (forming the hub), and the nodes alternate to those series are dispersed (forming the frames and radii). This pattern of 3-NS attachments in conjunction with a centripetal-motion pattern accounts for the point symmetry of orbs, and reveals how simple the algorithm resulting in an orb web may actually be. Of course, in some araneoid orbs the series of closely spaced trivalent hub nodes are often truly coalesced, at least during radius construction, into a single node of exceptional valence. We can therefore describe the architecture of an orb web as consisting of a number of trivalent nodes combined with one interior node that has a valence of approximately two-thirds the total number of nodes. Any network fitting this topological description will appear vaguely orblike in the architectural sense.

On the other hand, the diversity of orb webs within Araneoidea demonstrates that a purely architectural notion of an orb web is insufficient. For example, if our concept of an orb web is based only on the coincidence of point symmetry and a two-dimensional frame, we shall recognize orbs only when they look like orbs. The recognition of highly derived orb webs such as those of *Wendilgarda* (Fig. 12.11), *Miagrammopes* (Lubin, Eberhard, and Montgomery 1978), or *Mastophora* (Eberhard 1980a) would therefore be nearly impossible if the taxonomic affinities of the builder in question did

not strongly suggest that the web must be a derived orb. Obviously a more heuristic way to view orb webs is as a behavioral process involving the use of silks from particular glands in a particular behavioral sequence. But is there any silk or action pattern so peculiar to orb webs that we can confidently identify an orb when we recognize that feature? At present we know very little about the fundamental behaviors and silks of webs, or even the basic features of web architecture, that might have led to the evolution of the orb web. It is therefore entirely fitting to end this review with a question: what, if anything, is an orb web?

Acknowledgments

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