EVOLUTIONARY SHIFTS IN THE SPECTRAL PROPERTIES OF SPIDER SILKS

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Abstract.—We measured the reflectance properties of unpigmented silks spun by a systematic array of primitive (Deinopoidea) and derived (Araneoidea) aerial, web-spinning spiders, as well as silks spun by Araneomorphae and Mygalomorphae spiders that do not spin aerial webs. Our data show that all of the primitive aerial web spinners produce catching silks with a spectral peak in the ultraviolet (UV), and cladistic analysis suggests that high UV reflection is the primitive character state for silk spectral properties. In contrast, all of the derived aerial web spinners produce silks that are spectrally flat or characterized by reduced reflectance in the UV. Correlated with the evolution of these catching silks is a 37-fold increase in species number and apparent habitat expansion. This suggests that the unique silk proteins spun by the araneoids have been important to their ecological and evolutionary diversity.

Key words.—Spectral properties, spiders, spider silks.

One basis of evolutionary change is the achievement of an adaptation or complex of adaptations that allows species to make better use of resources than their ancestors (Wright 1978). Numerous examples in the literature illustrate how molecular variations in proteins, shaped by natural selection, have allowed organisms to adapt to diverse habitats or microenvironments (reviewed in Gillespie 1991). Silks, a diverse group of crystalline proteins spun by all spiders, may be an example of a molecule that has been fundamental to the evolution of a predator's foraging ecology.

Although it has been suggested that the chemical composition of silks spun by spiders is much less variable than that of silks produced by larval insects (Rudall and Kenchington 1971), almost all research on the molecular, structural, and mechanical properties of spider silk has been completed on the support and viscid threads spun by fewer than 15 species of orb spinners (Lucas et al. 1955; Zemlin 1968; Denny 1976; Wainwright et al. 1976; Work 1977, 1981, 1985; Gosline et al. 1984; Craig 1987; Vollrath and Edmonds 1989; Xu and Lewis 1990; Dong et al. 1991; Beckwith 1991; Hinman and Lewis 1992). However, the orb-spinning spiders and their close relatives (the Araneoidea) include only about one-third of all described spiders. Thus, there exists a broad diversity in the types of silks spun by

aerial web-spinning spiders, in addition to silks spun by all other spider species, yet to be explored.

We propose that if the physical properties of silk proteins have been important to spider speciation and the evolution of spider prey-capture methods, then silks spun by phylogenetically primitive and phylogenetically derived, aerial, web-spinning spiders will differ systematically. We tested this hypothesis by comparing the spectral properties of unpigmented silks spun by 16 species of spiders in the superfamilies Deinopoidea and Araneoidea. For outgroup comparison, we also examined the spectral properties of silks spun by five spiders that spin sheet webs and the retreat silks of three nonweb-spinning spiders.

MATERIALS AND METHODS

Spiders from Which Silks Were Sampled

Silks were collected from spiders in the infraorders Mygalomorphae and Araneomorphae. Silks sampled from Mygalomorphae include those spun by *Aphonopelma* sp. (Theraphosidae), *Ishnothele* sp. (Dipluridae), and *Hexurella* sp. (Mecicobothriidae). Among the Araneomorphae, the true spiders, we sampled silks spun by the most primitive spider in the group, *Hypochilus* sp. (Hypochilidae; Platnick 1977), and silks spun by a variety of more derived spiders in-

cluding those in the families Eresidae (*Stegody-phus* sp.), Diguetidae (*Diguetia*), Salticidae (*Phiddipus otiosus*), Lycosidae (*Sossipus* sp.), and Filistatidae (*Kukulcania* sp.).

The spectral properties of silks spun by spiders in the phylogenetically primitive, aerial web-spinning spiders, the Deinopoidea, and its sister taxon, the phylogenetically derived aerial web-spinning spiders, the Araneoidea (Coddington 1986), were examined in more detail. Among the Deinopoidea, silks were collected from webs spun by *Deinopis* sp. (Deinopidae), *Uloborus glomosus* (Walckenaer), *Hyptiotes cavatus* (Hentz), *Philoponella tingena* (Chamberlin and Ivie), and *Miagrammopes animotus* (Chickering) (Uloboridae). Among the Araneoidea, we measured the spectral properties of viscid silks produced by 11 species in 10 genera of spiders and four families (Araneidae, Tetragnathidae, Theridiosomatidae, and Theridiidae). They include *Argiope argentata* (Fabricius), *Micrathena schreibersi* (Perty), *Mangora pia* (Chamberlin and Ivie), *Eustala anastera* (Walckenaer), *Eustala* sp., and *Neoscona domiciliorum* (Hentz) (Araneidae), *Nephila clavipes* Linnaeus, *Leucauge* sp., *Tetragnatha* sp. (Tetragnathidae), *Epilineutes globosus* (O. Pickard-Cambridge) (Theridiosomatidae), and *Latrodectus mactans* (Fabricius) (Theridiidae).

Definition of Light Environments

We classified the light environments in which the sampled spiders were foraging into three general groups. Diurnal, nonforest habitats were classified as "bright." Diurnal, forest habitats were classified as "dim," and nocturnal habitats were classified as "dark."

Silk Measurement Techniques

Most spiders spin silks that are unpigmented and most silks appear flat white, translucent, or iridescent. These differences in the reflectance properties of silks are apparent at casual observation and suggest that silk proteins differ in their physical structure. To capture this range of variation, we focused our analysis on quantifying silk spectral variations spun by an array of phylogenetically primitive and derived spiders. Nevertheless, to make sure that any variation in spectral properties of silks spun by individuals of the same species was minor relative to variations in spectral properties of silks spun by different species, we collected and compared samples of sticky silks spun by five adult *Argiope argentata* (Araneidae).

Silks were collected on notched cards (Craig 1987) from the catching surface of sheet webs, the catching threads of three-dimensional space webs, the sticky spiral thread of webs spun by aerial web weavers and from the retreat silks spun by nonweb-spinning, hunting spiders. No data are currently available to indicate the degree of homology among these silks.

When silks are stressed their molecular configuration may change (Dong et al. 1991), and hence their spectral properties as well. To standardize our data, we collected silk at the tensions at which the spiders laid them. In most cases, silks were collected and analyzed on the same day they were produced.

Each sample was illuminated with a beam of monochromatic light and the light reflected back was measured in a UV-visible (350 nm–700 nm), incident-light microspectrophotometer. When the spectral properties of sticky silks spun were measured, the light was directed at one viscid droplet (araneoid catching thread) or combed, silk puff (deinopoid catching thread) and the thread on which they adhered. The microspectrophotometer is based on a Leitz Ortholux microscope with MPV Pol-Opak illuminator, Nikon CF Fluor $20 \times /0.75$ or $40 \times /0.85$ objectives, and Zeiss UV-projective coupled to a Hammamatsu R928 photomultiplier (Bernard 1982). The field stop of the Epi-illuminator was reduced to illuminate a single strand. The aperture stop was reduced to make the illumination as unidirectional as possible, and the incident angle was made oblique to minimize instrumental stray light. Light reflected from the strand was collected over the full numerical aperture of the microscope objective. The instrumental baseline was calibrated with a National Bureau of Standards SRM-20003D spectral reflectance standard.

We measured the spectral properties of silks over a range of 350 nm to 700 nm at 10-nm intervals. It is not possible to relate microspectrophotometer absolute spectra to field absolute spectra. Therefore, the normalized spectral reflectance functions were calculated by dividing the reflectance at each wavelength by the maximum reflectance for that sample. This allows us to compare the shape of silk reflectance spectra and the variation in reflectance as wavelength changes.

Phylogenetic Techniques

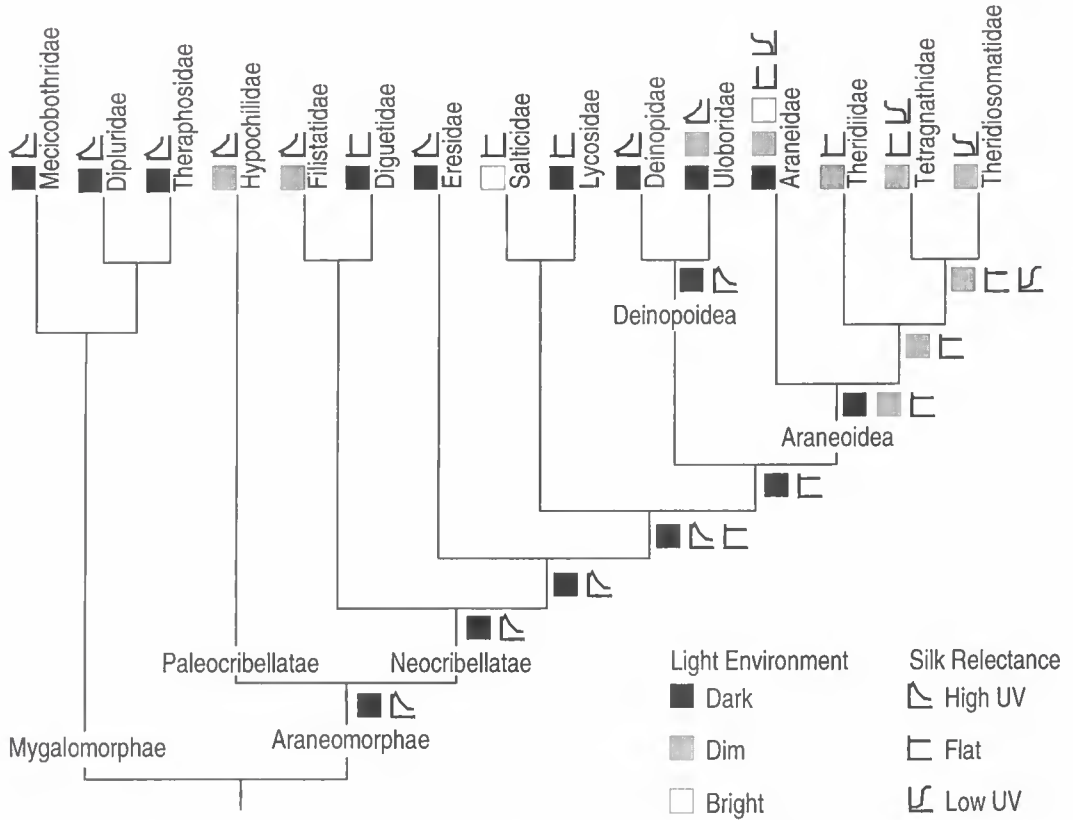To infer the ancestral character states for silk reflectance properties and foraging environ-

FIG. 1. Spectral properties of silks and spider foraging environments mapped onto a cladogram of the order Araneae redrawn from Coddington and Levi (1991). This figure illustrates the phylogenetic distribution of spiders that spin silks characterized by high reflectance in the ultraviolet, silks that are spectrally flat, and silks that are characterized by reduced reflectance in the UV. Light environments, in which the sampled spiders forage, also are illustrated. They include nocturnal, dim, and bright habitats. When the ancestral character state of silk reflectance or light environment is unambiguous, it is illustrated by a single icon at a node. Multiple icons at node illustrate features whose ancestral character state remains unresolved.

ments, we plotted the data on the most recently proposed cladistic structure of the Araneae. The cladogram in figure 1 has been redrawn from Coddington and Levi (1991), and taxa for which we did not have data have been eliminated.

Some of the taxa in figure 1 include spiders that spin silks characterized by more than one spectral property or spiders that forage in more than one light environment. Thus, in effect, they are "polymorphic" for these characters. For the data and terminal taxa examined here, polymorphisms arise in the Uloboridae, Araneidae, and Tetragnathidae. Nixon and Davis (1991) suggest that all character states for polymorphic taxa should be encoded and included in analyses to infer correctly ancestral states. Therefore, all of the combinations of silk spectral patterns and spider foraging environments, illustrated on the

cladogram at terminal taxa, were encoded. Given the character states illustrated at the tips of the branches, ancestral character states were inferred using the DOS EQUIS procedure with all characters treated nonadditively (Farris 1988). Whenever the results of the optimization technique suggested more than one possible character state at an internal node in the cladogram, all possible results are illustrated.

Results

General Patterns

We found three different types of spectra, illustrated in figure 2, that characterize the silks spun by spiders: (1) retreat silks such as those spun by *Latrodectus mactans* (Theridiidae) that are spectrally flat and reflect between 80% to

TABLE 1. Silk spectral properties, light habitat, and foraging mode for a diverse array of primitive and derived spiders. Information on web type and light habitat are from Shear 1986 or observations made at silk collection.

| Phylogenetic group		Light habitat	Spectra	Web type
Family	Genus/species			
Theraphosidae	*Aphonopelma* sp.	Nocturnal	UV peak	None
Dipluridae	*Ishnothele* sp.	Nocturnal	UV peak	None
Mecicobothridae	*Hexurella* sp.	Nocturnal	UV peak	Funnel and sheet
Hypochilidae	*Hypochilus* sp.	Dim	UV peak	Vertical sheet
Eresidae	*Stegodyphus* sp.	Nocturnal	Cut on at 550 nm	Sheet
Lycosidae	*Sossipus* sp.	Nocturnal	Flat	Funnel and sheet
Diguetidae	*Diguetia* sp.	Nocturnal	Flat	Sheet
Filistatidae	*Kukulkania*	Nocturnal	UV broad	Sheet
Salticidae	*Phiddipus otiosus*	Bright	Cut on at 550 nm	None
Deinopidae	*Deinopis*	Nocturnal	UV broad	Modified orb
Uloboridae	*Miagrammopes animotus*	Nocturnal	Peaks in UV, blue, green, orange	Space
Uloboridae	*Hyptiotes cavatus*	Dim	Peaks in UV, violet, green, red	Reduced orb
Uloboridae	*Uloborus glomosus*	Dim	Peaks in UV, blue green	Orb
Uloboridae	*Philoponella tingena*	Dim	Peaks in UV, blue, orange	Orb
Theridiidae	*Latrodectus mactans*	Dim	Flat	Space
Theridiosomatidae	*Epilneutes globosus*	Dim	Cutoff at 390 nm	Orb
Tetragnathidae	*Leucauge* sp.	Bright, dim	Flat	Orb
Tetragnathidae	*Tetragnatha* sp.	Bright, dim	Flat	Orb
Tetragnathidae	*Nephila clavipes*	Bright, dim	Cutoff at 370 nm	Orb
Araneidae	*Eustala* sp.	Nocturnal	Flat	Orb
Araneidae	*Eustala anastera*	Nocturnal	Flat	Orb
Araneidae	*Neoscona domiciliorum*	Nocturnal	Flat	Orb
Araneidae	*Mangora pia*	Dim	Flat	Orb
Araneidae	*Argiope argentata*	Bright	Cutoff at 350 nm	Orb
Araneidae	*Micrathena schreibersi*	Bright	Cutoff at 410 nm	Orb
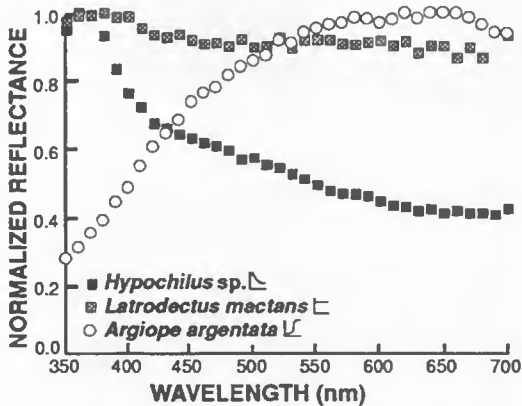
FIG. 2. Types of reflectance spectra observed. Retreat silks spun by *Latrodectus mactans* (Theridiidae) are spectrally flat and reflect 80% to 100% light across all wavelengths; silks spun by *Hypochilus* sp. (Hypochilidae) are characterized by a spectral peak where at least 30% more light is reflected across a region of about 30 nm than adjacent regions; and silks spun by *Argiope argentata* (Araneidae) are characterized by a spectral cutoff where reflectance shifts by more than 40% from low to high reflectance (other species may spin silks that are characterized by a spectral cuton where reflectance shifts from high to low reflectance across an analogous region).

100% across all wavelengths, (2) catching silks such as those spun by *Hypochilus* sp. (Hypochilidae) that are characterized by spectral peak or reflect at least 30% more light across a region of about 30 nm than at adjacent regions of the spectrum, and (3) viscid silks such as those spun by *Argiope argentata* (Araneidae) characterized by a spectral cutoff of at least 40% and reflectance gap at adjacent wavelengths. All of the data are tabulated in table 1. A subset of these that illustrate the reflectance patterns noted in table 1 are depicted graphically in figure 3A–F.

Intraspecific Variation in the Spectral Properties of Silks

Comparison of silks spun by five different *A. argentata* show they are characterized by almost identical spectra (fig. 3F) and indicate that the molecular composition of catching silks spun by spiders of the same species is similar. Therefore, differences in the reflectance patterns of silks spun by different spider species may reveal alternative structures for spider silk proteins. This study focuses on outlining the spectral and hence poten-
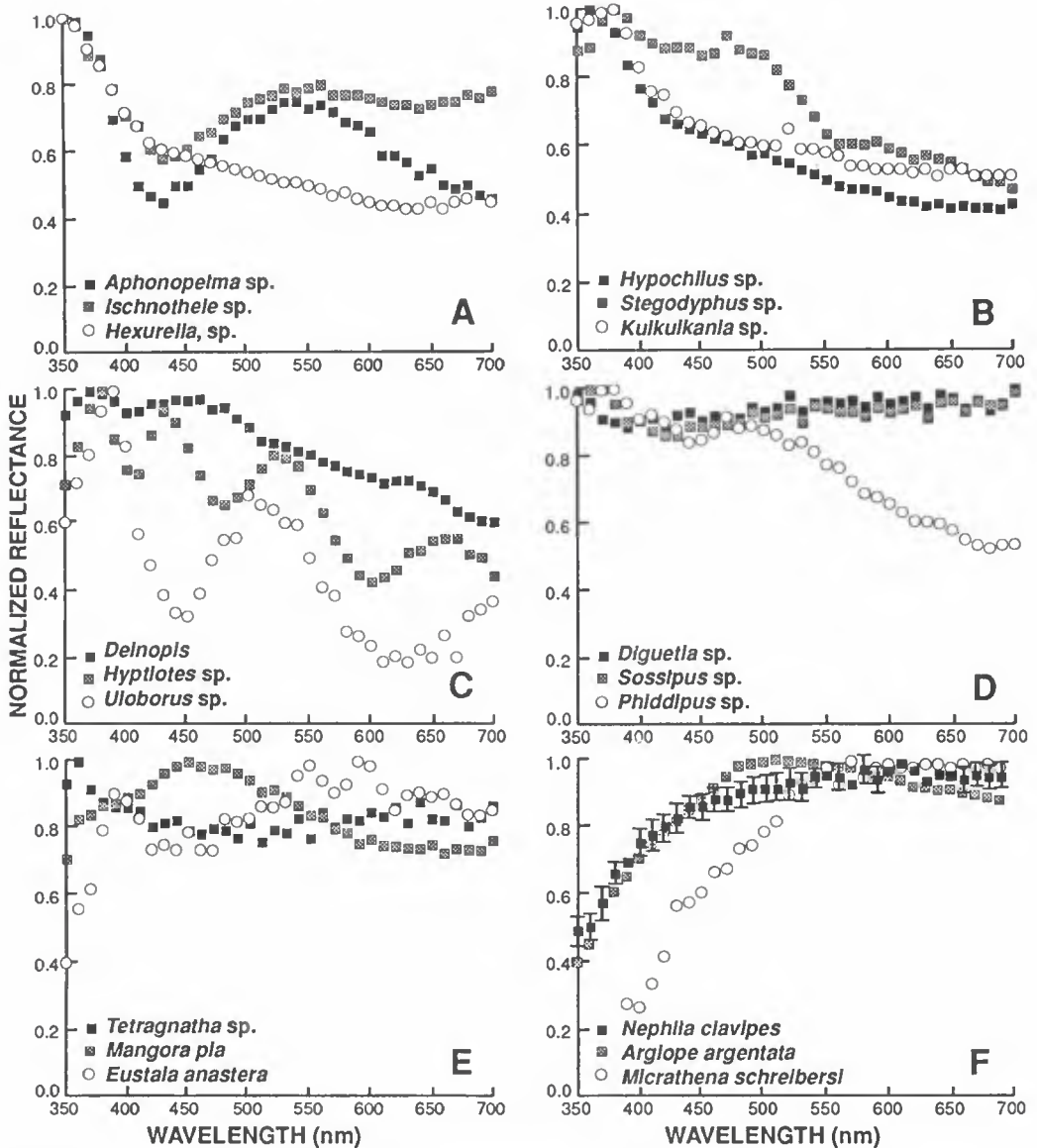
Fig. 3. Silk spectra spun by spiders in the Mygalomorphae (A) and Araneomorphae (B–F), with cribellum (B–C) and ecribellate (D–F) spiders, primitive aerial web weavers (C), and derived (E–F) aerial web weavers. A. Spectral properties of silks spun by the mygalomorph spiders *Aphonopelma* sp., *Ischnothele* sp., and *Hexurella* sp. B. Spectral properties of silks spun by the araneomorph spiders with cribellum *Hypochilus, Kulkulkania, Stegodyphus.* C. Spectral properties of silks spun by primitive aerial web weavers with a cribellum, *Deinopis, Hyptiotes, Uloborus.* D. Silks spun by ecribellate, nonweb-spinning spiders *Sossipus, Phiddipus, Diguetia.* E. Spectral properties of silks spun by ecribellate, derived aerial web weavers *Mangora pia, Eustala anastera, Tetragnatha.* F. Spectral properties of silks spun by ecribellate, derived aerial-web weavers, unmasked silks spun by *Nephila clavipes,* silks spun by *Argiope argentata,* and *Micrathena schreibersi.* Reflectance measures for silks spun by *A. argentata* indicate mean and standard deviation for five different individuals of approximately the same size. These data show that silks spun by mygalomorph spiders (A) and cribellate spiders are characterized by a spectral peak in the ultraviolet region (B–C, silks spun by *Deinopis* are characterized by a broader band reflectance that includes both the ultraviolet (UV) and blue). All of these spiders forage at night or in dim, diurnal sites. The ecribellate spiders including those that do not spin webs (D), as well as web spinners (E–F), produce silks that are spectrally flat or are characterized by reduced reflectance in the ultraviolet region. These spiders forage at night, as well as in a variety of diurnal light environments.

tial molecular variation among silks spun by different species of phylogenetically primitive and derived orb spinners and compares these results to the spectral properties of silks collected from the sheet webs and retreats spun by nonweb-spinning spiders.

Spectral Properties of Silks Spun by the Mygalomorphae

The phylogenetically primitive spiders *Aphonopelma* sp., *Ischnothele* sp., and *Hexurella* sp. (Infraorder Mygalomorphae; Platnick 1977) all produce silks that peak in reflectance at 350 nm (fig. 3A) but that differ at other wavelengths. Silks spun by *Ischnothele* sp. range from 60% to 80% reflectance from 400 nm to 500 nm, whereas the silks spun by *Aphonopelma* sp. drop to only 40% reflectance at 400 nm but have a secondary peak at 500 nm. In contrast, the silks spun by *Hexurella* sp. peak in reflectance at 370 nm and drop to about 45% reflectance at all other wavelengths between 500 nm and 700 nm. None of these spiders spin aerial webs to intercept prey, and all are most active at night (fig. 1; table 1).

ARANEOMORPHAE

Sheet-Web and Nonweb Spinning Spiders

Comparison of the spectra in figure 3B–F shows that the reflectance properties of silks produced by the araneomorph spiders are diverse. Silks spun by *Hypochilus* (sheet web), the most primitive of the araneomorph spiders (Platnick 1977), are characterized by a spectral peak in the UV region at 380 nm that drops to 60%–40% reflectance at wavelengths between 400 nm to 700 nm (fig. 3B), similar to the spectra of silk spun by *Hexurella*. The spider *Stegodyphus* sp. (sheet web) produces silks characterized by broad-band reflectance in the UV and blue with a cut-on point at about 550 nm (fig. 3B), whereas *Kukulcania* sp. (sheet web) produces silks with similar spectral properties to those spun by *Hypochilus*. The sheet-web weaving spiders are active primarily at night or in dim light. The spiders *Diguetia* (sheet web) and *Sossipus* (sheet web) produce silks that are spectrally flat (fig. 3D). *Phiddipus*, a nonweb-spinning spider, produces silks characterized by a cuton point at about 550 nm and is active during the day.

Phylogenetically Primitive, Aerial, Web-Weaving Spiders (Deinopoidea)

The property of ultraviolet reflection is marked among the catching silks spun by the primitive, aerial web-weaving spiders in the superfamily Deinopoidea. *Deinopis* sp. spin catching silks that broadly reflect wavelengths in the UV and blue regions (fig. 3C). The phylogenetically primitive, aerial web weavers *Hyptiotes cavatus, Uloborus glomosus, Miagrammopes animotus,* and *Philoponella tingea* (fig. 3C and/or table 1), spin silks characterized by multiple spectral peaks in the ultraviolet (350 nm–400 nm), green (500 nm–550 nm), and yellow (550 nm–600 nm) regions of the spectrum. Thus, although the spectral properties of silks spun by the deinopoids are diverse in the region of the spectrum above 400 nm, they all retain a reflectance peak in the ultraviolet. All of the deinopoids forage at night or in dim light (table 1).

Phylogenetically Derived, Aerial, Web-Weaving Spiders (Araneoidea)

Unlike the phylogenetically, primitive, aerial web-weaving spiders, none of the derived spiders produce catching silks with a peak in the UV region of the spectrum. Many of the derived, web weavers, such as *Eustala anastera, Eustala* sp., *Mangora pia, Leucauge* sp., *Tetragnatha, Neoscona domiciliorum,* and *L. mactans,* produce silks that are spectrally flat or white. All of the spiders sampled to date that spin white silks forage at night or in dim light (table 1 and/or fig. 3E). Alternatively, the diurnal araneoids that spin silks characterized by reduced reflectance in the UV region forage in either bright or dim light. These include the silks spun by *Nephila clavipes* that forage in the forest understory, silks spun by *A. argentata* (table 1, fig. 3F), and silks spun by *Epilineutes globosus* (table 1). The catching silks spun by these spiders are characterized by a broad-band cut off at about 370 nm. None of the phylogenetically primitive, aerial web weavers, the Deinopoidea, spin silks characterized by reduced reflectance in the UV region or are found foraging in the brightest light environments where araneoids are found.

Phylogenetic Analysis of Silk Reflectance and Light Environments

The phylogenetic analysis shows that the primitive character state for silk spectral properties is high UV reflectance, and the primitive foraging environment for spiders is nocturnal (fig. 1). Furthermore, spiders that do not spin webs or that produce sheet webs, as well as the phylogenetically primitive, orb-spinning spiders, produce silks that are spectrally flat or that are characterized

by a UV peak. Only spiders in the superfamily Araneoidea produce silks characterized by reduced reflectance in the UV. Although these data are preliminary, our current findings show that the araneoid spiders are the only aerial web spinners that forage in bright environments.

Summary

In summary, spiders in the primitive and derived families of aerial web weavers spin at least three different types of silks that are used for prey capture alone: high-UV reflecting silks, low-UV reflecting silks, and spectrally flat silks. Although these data represent only a small subset of silks spun by spiders, the cladistic analysis suggests that the property of UV reflection is a primitive character state for silk proteins. In addition, all of the deinopoid spiders produce catching silks with a UV spectral peak but none of the derived araneoid spiders produce silks with a UV peak. The ability to produce silks that reflect white light is a derived feature of spiders that evolved frequently throughout the Araneae and among both web-spinning and nonweb-spinning species. Our current information, although limited, suggests that only the derived, web-spinning spiders produce silks characterized by reduced UV reflectance.

DISCUSSION

Spider silks contain two kinds of protein subunits: crystalline regions that give the silks strength and noncrystalline regions that give silks extensibility (Gosline et al. 1986). Although differences in the amino-acid sequences in the two regions could account for some of the silks' mechanical properties, it is known that the molecular ordering of the crystalline regions occurs during the flow of liquid silk from the silk glands through the spinnerets (Denny 1980; Kerkam et al. 1991). Therefore, the variations in silk structural properties that have been revealed in this study may have resulted from selection on the protein itself (the amino-acid sequences in the different protein subunits (i.e., Xu and Lewis 1990; Hinman and Lewis 1992) as well as the conditions under which the protein is produced (Kerkam et al. 1991). Rudall and Kenchington (1971) dismissed the importance of variations in silks produced by insects reasoning that because they were used outside the body, silks are not subject to as stringent selection pressures as are proteins used for intracellular purposes. In the case of spiders, we propose instead that the differences in silks result from selection for functional properties specific to the ecological purposes for which they are used.

The simplest silk production system is found in spiders in the genus *Antrodiaetus* (Mygalomorphae: Antrodiaetidae; Kovoor 1987). *Antrodiaetus* has four functional spinnerets and one kind of silk gland that produces the two different types of protein that comprise their silk threads (Palmer et al. 1982). Spiders, like *Antrodiaetus* that line subterranean burrows with silks (i.e., Coyle 1986) or spin silks to encase their eggs, need to produce only fibers that are strong or dense enough to protect the spiders from the walls of its burrow and to protect their egg cases from tearing, parasitism, and desiccation.

The most complex silk producing systems are found among the araneoid spiders. The araneoids have six functional spinnerets and six different kinds of silk glands each producing one to three types of protein (Kovoor 1987; Coddington 1989). Two of these glands, the flagelliform and aggregate glands, are unique to the araneoids and from these the viscid catching threads are drawn. The complete dependence of the araneoids on silks for prey capture and the functional specialization of their silk-producing system suggests that selection pressures affecting the evolution of araneoid silks differ from those affecting the evolution of other silk proteins. Below we compare and discuss the importance of the mechanical properties and spectral properties of prey-capture silks to the foraging ecology of deinopoid and araneoid web-spinning spiders.

Comparison of the Mechanical Properties of Silks Spun by Primitive and Derived Web Spinners

Spiders spin aerial webs to intercept flying insects by absorbing their kinetic energy. The energy-absorbing properties of the silks are a function of silk tensile strength, elasticity, and thread size (Denny 1976; Gosline et al. 1992; Craig 1987). Although there have been no systematic comparisons of the mechanical properties of deinopoid and araneoid silks, preliminary data for catching threads spun by *Uloborus walckenaerius* suggests that they are much less elastic, although equally strong, compared with the catching threads spun by *Araneus diadematus* (Vollrath pers. comm. 1993). Like the silks spun by *Bombyx mori* (Gosline et al. 1992), the inelasticity of *U. walckenaerius* silks may result from a high proportion of crystalline subunits in the protein.

In general, the viscid catching silks spun by araneoid spiders exhibit extreme elasticity. For example, the spiral thread produced by *Mangora pia* extends to 6.2 times its resting length before breaking (Craig 1987). Through high tensile strength and greater elasticity the araneoids can capture larger and/or faster flying prey than the deinopoids.

Spectral Properties of Web Silks and Their Importance to Prey Capture

Web visibility is an important component of insect-spider interactions. Spiders forage in diverse light environments and even at night insects can see webs and avoid them (Craig and Freeman 1990). The webs' catching silks spun by the deinopoids are characterized by reflectance peaks in the UV and blue regions of the spectrum and are drawn from the pseudoflagelliform, paracribellar, and cribellar glands (Kovoor 1987). The capture silks spun by the araneoids are derived from the flagelliform and aggregate glands and may be homologous in origin to deinopoid silks. None of the araneoids spin prey-capture silks with spectral peaks in the UV or blue regions of the spectrum, but some araneoids spin silks that are characterized by reduced UV reflectance.

Correlated with this difference in spectral properties between silks spun by araneoid and deinopoid spiders is a 37-fold increase in species number and an apparent expansion of the derived, aerial web-weaving spiders into new light environments. Whereas the deinopoids forage exclusively in shaded sites, such as the forest understory and at night, the araneoids forage in shaded sites, at night, and in open sites where the web is brightly illuminated throughout the spiders' foraging period. We propose that where increased levels of illumination enhance web visibility, insect visual response to silk colors and brightness are an additional factor affecting the evolution of silk molecular organization.

Craig and Bernard (1990) explored the behavior of *Drosophila* sp. to webs spun by *Uloborus glomosus,* a primitive, orb-weaving spider, that spins catching silks characterized by spectral peaks in both the UV and blue regions of the spectrum (fig. 3C). *Drosophila* were introduced into the enclosed baseleg of a Y-shaped choice number and UV-reflecting webs spun by *U. glomosus* were fixed to either chamber arm. One web was illuminated with white light containing a UV component and the second web was illu-

minated with white light from which the UV component had been filtered. *Drosophila* were then released from the baseleg and flew to either chamber arm. In all of the trials, more flies flew to webs that reflected UV + white light than webs illuminated with white light from which the UV light had been filtered. In a second study, Craig and Lesch (unpubl. data) further explored this result by videotaping *Drosophila* as they flew towards webs spun by *U. glomosus.* When the web was illuminated with white light from which the UV component had been filtered, the flies turned away from it before they were intercepted. When the same web was illuminated with white light containing a UV component, the flies were intercepted. Thus, even though *Drosophila* could see and avoid the web when it did not reflect UV light, they were unable to avoid interception when the web reflected UV. These studies suggest that UV-reflecting silks stimulate wavelength-dependent behavior or insect motor responses to particular wavelengths that cannot be modified by learning. Therefore, if spiders evolved to spin silks that elicit wavelength-dependent behavior, insects could be drawn to webs that they otherwise would recognize and avoid if spun from different colors of silk.

If the spectral properties of araneoid silks have been important to habitat expansion by web-spinning spiders, two alternative scenarios regarding their ecological role could be envisioned: (1) silks may camouflage the web outline, (2) silks may attract prey to the web area. In the first case, spiders could have evolved to spin silks that are characterized by reduced brightness or spectral properties that match background vegetation. Both of these factors would make the web difficult for insects to see. In the second case, spiders could have evolved to spin silks characterized by enhanced brightness or spectral properties that contrast with background vegetation. Thus, webs would be more visible to prey and hence easier for insects to see and avoid. However, because spiders spin webs from more than one type of silk protein, some silk components of the web may contrast with background vegetation and attract insects to them, whereas other components of webs may match background vegetation and camouflage the web outline.

Argiope argentata, a derived, aerial web-spinning spider, seems to have adapted the later foraging behavior. The web's spiral thread is characterized by reduced reflectance in the UV. It would appear white to approaching insects (Men-

zel 1979; see fig. 3F), making webs difficult for insects to see. In contrast, the spider also produces decorative silks characterized by enhanced reflectance in the UV. By manipulating the presence and absence of web decorations in the field, Craig and Bernard (1990) found that more insects were intercepted at decorated webs than at webs from which the decorations had been removed. They proposed that UV-reflecting web decorations attract prey to the web area. This hypothesis was tested by comparing the rates that insects were intercepted at webs spun by spiders foraging in groups, some of whom decorated their webs and others that did not (Craig 1991). Spiders that decorated their webs attracted more prey than spiders that did not (Craig and Bernard 1990); spiders that foraged in groups of two or more (the spider's body also reflects UV light) captured more prey than solitary foragers. Group foraging spiders that spun web decorations drew prey to their webs and away from undecorated webs spun by neighboring individuals (Craig 1991).

In conclusion, the data presented in this paper represent only a first step to quantifying the diversity of spider silk proteins. Nevertheless, cladistic analysis of our findings suggests that (1) the primitive foraging environment of spiders was nocturnal, (2) the primitive character state for silk spectral properties is high UV reflectance, and (3) the evolution of unique silk glands and proteins may have enabled the araneoids to use new habitats and led to a 37-fold increase in the number of aerial web-spinning species.

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