TAXONOMIC VARIATION AMONG SPIDERS IN THE ABILITY TO REPEL WATER: SURFACE ADHESION AND HAIR DENSITY

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ABSTRACT.   A variety of arthropods forage and avoid predators via locomotion on the surfaces of ponds and streams. For these animals, cuticular hydrophobicity functions to keep them dry and well supported by the water's surface tension, and also allows them to move easily between wet and dry habitats. Among spiders, members of the family Pisauridae exemplify this semi-aquatic lifestyle and, not surprisingly, these spiders remain entirely dry even when submerged. In the current study, we sought to quantify the degree to which spiders in a variety of families resist wetting by liquid water. Two properties of a spider's cuticular hairs are predominant in determining this resistance: adhesion energy (a consequence of molecular interactions between the hair surface and water) and hair density. When hair density is low, the adhesion energy of the cuticle itself also plays a role. Among the ten families we studied, pisaurids and pholcids defined the ends of the spectrum of resistance, with the pisaurids nearly 50 times more resistant to wetting than the pholcids. We discuss both the impact of this variation on spiders' potential for aquatic locomotion and the variety of selective forces that may have contributed to this impressive variation in capabilities.

Keywords: Cuticle, adhesive forces, hydrophobicity, evolution

Fishing spiders (Pisauridae) are conspicuously adept at life on the water. They move easily across the water surface (Gorb & Barth 1994; McAlister 1959; Shultz 1987; Suter et al. 1997), males can find females by following the females' pheromone-impregnated draglines on the water surface (Roland & Rovner 1983) and both sexes detect prey by decoding the surface waves created as insects struggle to escape the adhesive energy of the surface tension (Bleckmann 1985). We expect pisaurids to possess a suite of attributes that facilitate their lifestyle, whether these attributes antedated the move to a semi-aquatic habit or, as adaptations, were subsequent modifications. Among the expected attributes is a surface (both of legs and body) that remains dry when in contact with liquid water (Fig. 1). The rationale for this expectation has several parts. First, other arthropods such as water striders (Insecta: Gerridae and Veliidae) under similar circumstances share the trait (e.g., Andersen

1976); second, aquatic locomotion is substantially enhanced when the legs providing the propulsion remain dry (Suter & Wildman 1999); third, access to oxygen when submerged is strongly facilitated by plastron respiration (e.g., Rovner 1986; Hebets & Chapman 2000) which, in turn, requires a surface covered with hydrophobic hairs (Cheng 1973); and fourth, small organisms find it very difficult to extricate themselves from capillary adhesion if their surfaces are wetted (Fig. 1) (Vogel 1988).

The dangers of capillary adhesion (being unable to climb out of a small puddle, or having several legs stuck to each other by a few drops of water) are not restricted to spiders that live on the water surface. Ballooning spiders can descend into ponds and streams or even into drops of water, raindrops can fall on spiderlings and a stiff breeze can dislodge a spider from vegetation or its web and cause it to land in a puddle or pond. Thus in this con-

Figure 1.—The surfaces of spiders vary both in hair density (hairs/mm) and in the chemical composition of the cuticle and its hairs. At one end of the spectrum are spiders in the family Pisauridae (top) with strongly hydrophobic hairs that are also very dense. Near the other end of the spectrum are the spitting spiders (Scytodidae, bottom) with very few, relatively hydrophilic, hairs. Water droplets on hydrophobic surfaces are approximately spherical while those on hydrophilic surfaces spread widely.

text, a strongly hydrophobic covering would apparently serve spiders in all but the most xeric of environments. To the contrary, our recent survey of water surface locomotion in spiders (Suter et al. in press; Stratton et al. in press) suggested that strong hydrophobicity is far less common than would be expected if susceptibility to entrapment by capillary adhesion were the only selective force influencing cuticular surface chemistry. In the study reported here, we have measured the functional hydrophobicity of spiders in ten families to help us understand the relationship between cuticular hydrophobicity and the selective forces that may have contributed to its evolution and maintenance.

METHODS

Spiders.—We tested 41 spiders in 25 species distributed among 10 families (Table 1). Pisaurids and scytodids were drawn from captive populations maintained in the laboratory of R. Suter, and spiders in the other families were captured in the field for use in this and a related study (Stratton et al. in press). Each field-captured spider was held for up to 4 days in a plastic vial under the high humidity provided by a wet paper towel pad attached to the inside surface of the vial.

We tested a single leg from each spider. To remove a leg for testing, we inserted forceps into the holding container and grasped a single leg (II or III) approximately in the middle of the femur. Most of the individuals tested readily and promptly (after < 3 s) autotomized the grasped leg and survived the leg removal with no other detectable detriment. A few spiders did not promptly autotomize the grasped leg. We immediately released these from the grasp of the forceps, cooled and then froze them at -15 °C, and removed the leg with iris scissors. The still-frozen spider was then preserved in alcohol.

Voucher specimens for this study are deposited in the Mississippi Entomological Museum.

Functional hydrophobicity.—The two surface attributes that contribute to functional hydrophobicity are hair density and the molecule-level physical interaction between the hair or cuticle surface and water. To measure hair density, we digitized a lateral view of each test leg (Olympus SZX12 stereo dissecting microscope, Panasonic GP-KR222 video camera, Sony DCR-TRV900 used as a digital recorder) and imported the image into NIH Image (shareware from NIH) on a Macintosh G4 computer (Apple Computer, Inc.). In Image, we drew three transects on the metatarsus, each perpendicular to the long axis of the leg segment, then measured the length of the transect and the number of hairs transected. Our measure of hair density for that test leg was the average of the densities (hairs/mm) of the three transects.

To quantify the molecule-level interaction between water and the exposed surface of the leg (cuticle per se or cuticular hairs), we measured the contact angles formed between very small droplets of distilled water and the relevant surfaces on the legs of spiders. The rationale for this use of the contact angle is as follows. Ignoring gravity, the forces acting on liquid water resting on a solid surface are the forces of cohesion, attributable to the attraction of water molecules to each other, and adhesion, attributable to the mutual attraction of water molecules and the molecules at the surface of the solid. Conceptually, when the cohesive forces are much greater than the adhesive forces, the water takes on a nearly spherical form and one infers that the solid surface is quite hydrophobic. In contrast, when the cohesive forces are much smaller than the adhesive forces, the water spreads out on the solid surface and one infers that the solid surface is hydrophilic. This relationship was first understood and formalized by Laplace and Young in 1805 as

$$W_a = W_c(1 + \cos \theta_c)/2 = \gamma(1 + \cos \theta_c) \ (1)$$

(Denny 1993, Eq. 12.1), in which W_a is the energy of adhesion, W_c is the energy of cohesion, θ_c is the angle of contact between the solid and the liquid, and γ is the surface tension of the liquid. The convenient algebraic dependence of W_a on θ_c (Eq. 1) made it possible for us to estimate the relative hydrophobicity of even a very small and curved surface, that of a cuticular hair, by measuring the static contact angle in digital images.

To measure contact angles, we mounted each test leg at the edge of a microscope slide positioned so that the tarsus and metatarsus extended beyond the edge of the glass. Using an inverted compound microscope (Nikon Diaphot), we digitized images of small sections of the leg (as above, or using a Nikon

Table 1.—Identities and properties of subjects used in this study. Families are listed in phylogenetic order after Platnick (2002). The pressure index is a function of both the adhesion energy and the hair density (Eq. 2). Values in the three final columns are averages over N individuals.

Family	Genus and species	Individuals N	Adhesion energy W_a (joules)	Hair density (h/mm)	Pressure index
Scytodidae	*Scytodes* sp. A Latreille 1804	3	0.482	20.956	7.690
	Scytodes sp. B Latreille 1804	1	0.603	16.273	2.796
Pholcidae	*Crossopriza lyoni* (Blackwall 1867)	2	0.719	37.619	1.324
	Pholcus phalangioides (Fuesslin 1775)	3	0.777	40.913	−1.731
Theridiidae	*Theridion* sp. Walckenaer 1805	2	0.605	30.469	6.728
	Tidarren sisyphoides (Walckenaer 1842)	2	0.320	23.277	13.050
Tetragnathidae	*Leucauge argyra* (Walckenaer 1842)	3	0.442	31.978	12.201
	Tetragnatha versicolor Walckenaer 1842	3	0.211	66.994	47.359
Araneidae	*Araneus trifolium* (Hentz 1847)	1	0.560	36.989	8.531
	Larinia directa (Hentz 1847)	3	0.607	42.791	8.251
	Mangora placida (Hentz 1847)	1	0.923	28.973	−7.760
Lycosidae	*Geolycosa rogersi* Wallace 1942	1	0.204	40.432	29.125
	Rabidosa carrana (Bryant 1934)	1	0.189	53.439	39.601
	Trochosa terricola Thorell 1856	2	0.486	56.299	18.256
Pisauridae	*Dolomedes tenebrosus* Hentz 1844	1	0.136	53.091	43.182
	Dolomedes triton (Walckenaer 1837)	1	0.115	45.115	37.995
	Dolomedes vittatus Walckenaer 1837	1	0.263	80.192	51.248
Agelenidae	*Agelenopsis* sp. Giebel 1869	1	0.256	28.892	18.727
	Agelenopsis naevia (Walckenaer 1842)	1	0.196	32.535	23.769
	Agelenopsis pennsylvanica (Koch 1843)	1	0.325	48.544	26.860
Thomisidae	*Misumena vatia* (Clerck 1757)	2	0.217	22.205	15.533
	Misumenoides formosipes (Walckenaer 1837)	1	0.323	29.940	16.654
Salticidae	*Habronattus hallani* (Richman 1973)	1	0.274	39.872	24.878
	Phidippus audax (Hentz 1845)	1	0.135	39.158	31.907
	Phidippus regius Koch 1846	2	0.253	29.779	19.615

D100 SLR camera), with cuticular hairs in silhouette, immediately after exposing the leg to a stream of microscopic water droplets. The stream of water droplets, generated by an ultrasonic humidifier (Welbilt MW-500T/88 filled with distilled water), flowed first through a 1.5 m long plastic tube, then through a 0.25 m long glass tube (diameter =
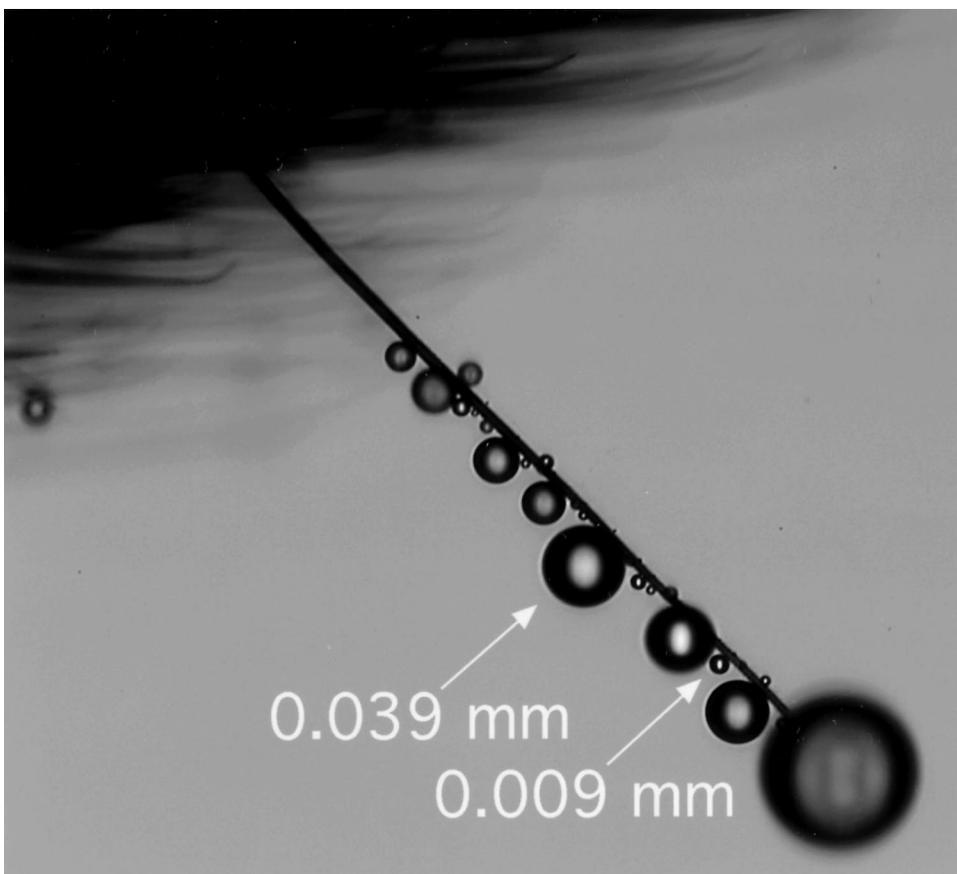
Figure 2.—Micro-droplets deposited on a trichobothrium of *Dolomedes triton*. Droplet size was small enough (3.1×10^{-5} μl and 3.8×10^{-7} μl above) to render the effects of gravity negligible.

5.5 mm), and finally across the 6 cm that separated the tube's opening and the spider's leg. The droplets in the supply stream were so small that they appeared, in aggregate, to be steam, but were at room temperature (21–23 °C).

During the application of the supply stream, water accumulated on the surfaces of cuticular hairs (Fig. 2) or on the cuticle itself. The accumulated water took the form of droplets with shapes that depended upon the ratio of adhesive to cohesive forces acting upon the water. We measured droplets that had diameters < 0.3 mm to avoid any influence of gravity on our measurements (Denny 1993).

We analyzed the digitized images using the angle measurement tool (Fig. 3) in NIH Image (see specifications above). We included in our analysis any droplet for which (a) the intersection between it and the supporting surface

was in focus, (b) the plane defined by that axis and the geometric center of the droplet was perpendicular to the camera's focal plane and (c) the diameter of the droplet was < 0.3 mm. Under these criteria, for the 41 spiders tested, we measured 187 contact angles for droplets on cuticular hairs and 25 contact angles for droplets on the cuticles themselves. For one spider we had only a single measurement of leg-hair contact angle. For all of the others, measurements per spider ranged from 2–13.

Functional hydrophobicity in the current context, that is, the ability of a hair-covered leg to resist the intrusion of liquid water into the space between the leg and the hairs, depends both on hair density and on the energy of adhesion of the hair surfaces. Hairs with a low energy of adhesion (and thus a high contact angle) can be spaced relatively far apart and still resist the water's intrusion, whereas
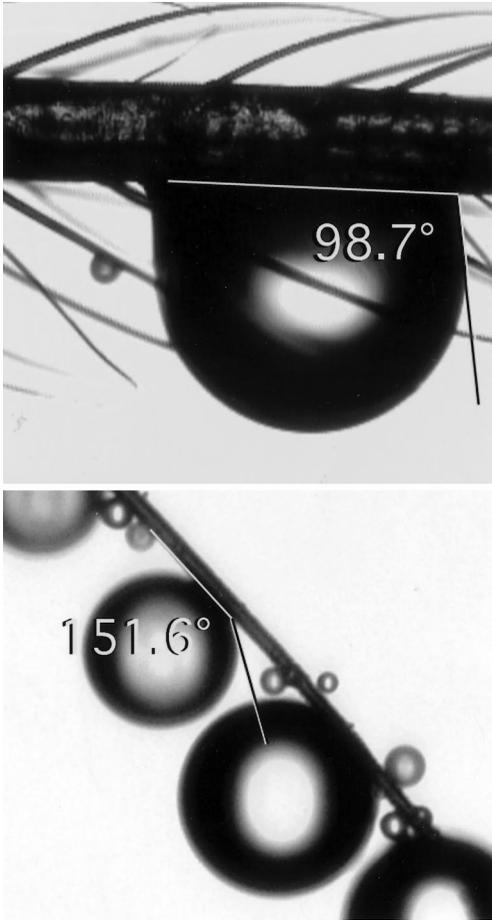
Figure 3.—Contact angles of droplets on the leg cuticle of *Scytodes* sp. (top) and on a trichobothrium of *D. triton* (bottom). Angles > 90° indicate that the energy of cohesion among the water molecules exceeds the energy of adhesion between the spider surface and the water molecules.

hairs with a high W_a must be spaced closer together to achieve the same resistance to intrusion. Denny (1993, p. 265) provides a clear explication, derived from the work of Crisp & Thorpe (1948), of this relationship:

$$\Delta p = \frac{\gamma \cos(\theta_c + \phi)}{\frac{l}{2} - r \cos \phi} \qquad (2)$$

where the sustainable pressure difference is Δp, l is the center-to-center distance between hairs, and ϕ is the angle between the center-to-center line and the location, on a hair, where the air-water interface makes contact. Because of the very small scale at which we

were working, we could not measure ϕ, so we adopted the following as our pressure index:

$$I_p = \frac{\cos \theta_c}{l} \qquad (3)$$

which shares with Eq. 2 the property that it is directly proportional to $\cos \theta_c$ and inversely proportional to l (the inverse of hair density).

RESULTS

Spiders in this study showed conspicuous differences in the ways liquid water interacted with their surfaces (Table 1). These differences were visible at a macroscopic level, for example, in the spherical beads of distilled water that accumulated on the hairy surfaces of pisaurids and in the more flattened drops of water that accumulated on the nearly hairless surfaces of scytodids (Fig. 1). The deposition of microscopic droplets of distilled water onto cuticular hairs (Fig. 2) and onto the cuticular surfaces themselves revealed a similar range of differences in contact angles (Fig. 3) and consequently in the underlying property of the surface, the adhesion energy. The adhesion energies of cuticular hairs (Fig. 4, top) varied from the lowest values in the pisaurids to the highest values in the pholcids and araneids, with an 8-fold difference between the extremes when viewed species by species (Table 1). That is, the hairs of the pisaurids were the most resistant to wetting, the most hydrophobic, and the hairs of the pholcids and araneids were the least resistant to wetting, the most hydrophilic. For 14 spiders spread among 5 families (Araneidae, Pholcidae, Scytodidae, Tetragnathidae, Theridiidae), we measured adhesion energy not only on cuticular hairs but also on the cuticle surfaces themselves. In every case, the adhesion energy of the cuticle exceeded that of the cuticular hairs (mean difference, 0.431 j; paired $t = -6.631$; two-tailed $P < 0.0001$).

Hair density, like adhesion energy, also varied over a wide range among spiders in the 10 families tested (Fig. 4, middle). Pisaurids had the highest densities (59.5 $\pm$ 10.6, mean $\pm$ S.E.) and scytodids had the lowest (19.8 $\pm$ 2.4), with a 4.9-fold difference between the extremes when viewed species by species (Table 1).

Our estimate of functional hydrophobicity, the pressure index (Eq. 3), varied as expected given the variations in adhesion energy and
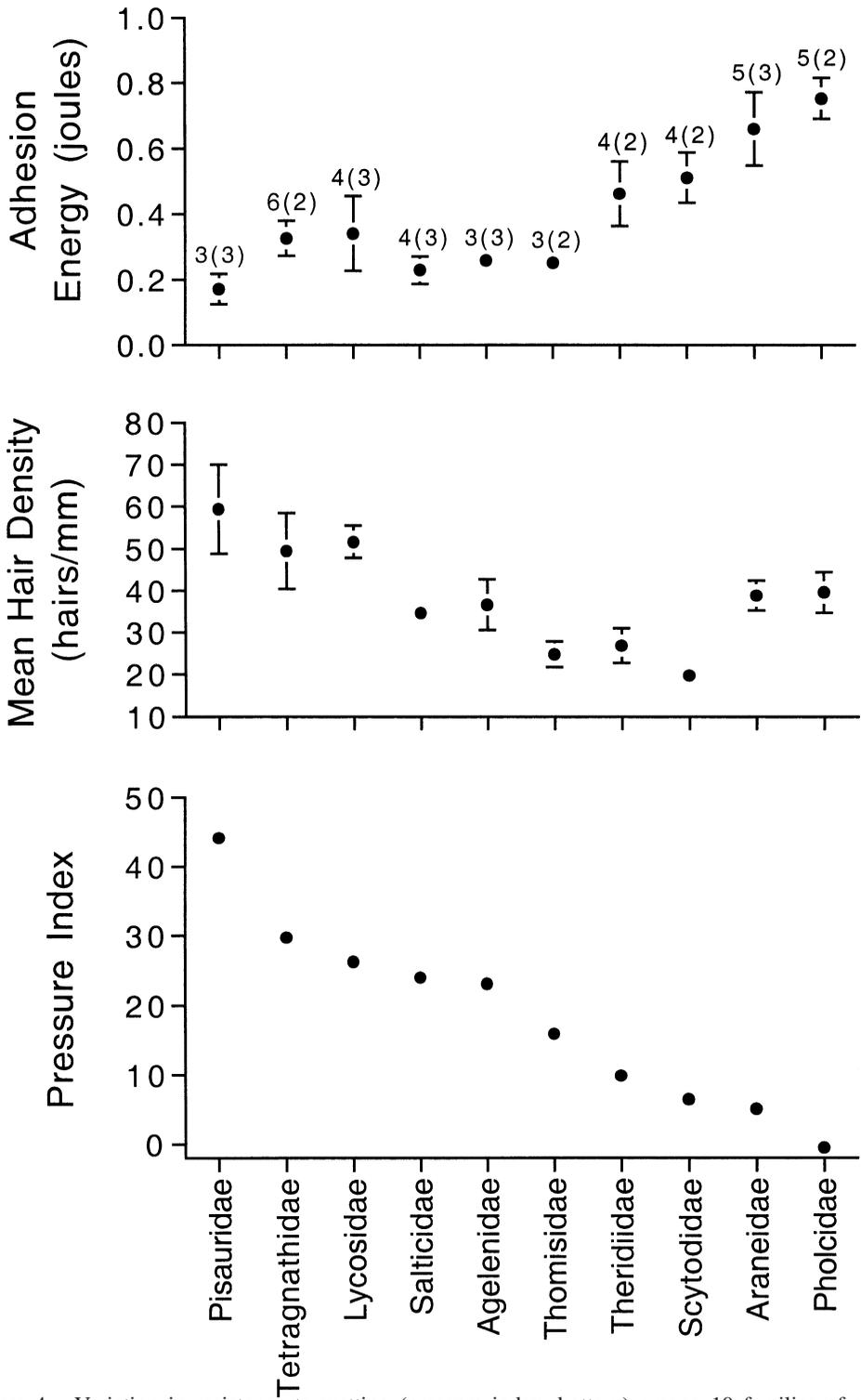
Figure 4.—Variation in resistance to wetting (pressure index, bottom) among 10 families of spiders. The observed variation is a consequence both of the adhesion energy of the hair surfaces (top) and of the spacing of the hairs (middle). Associated with each family in the top graph is a number signifying the number of individuals tested followed by a number in parentheses signifying the number of species tested.
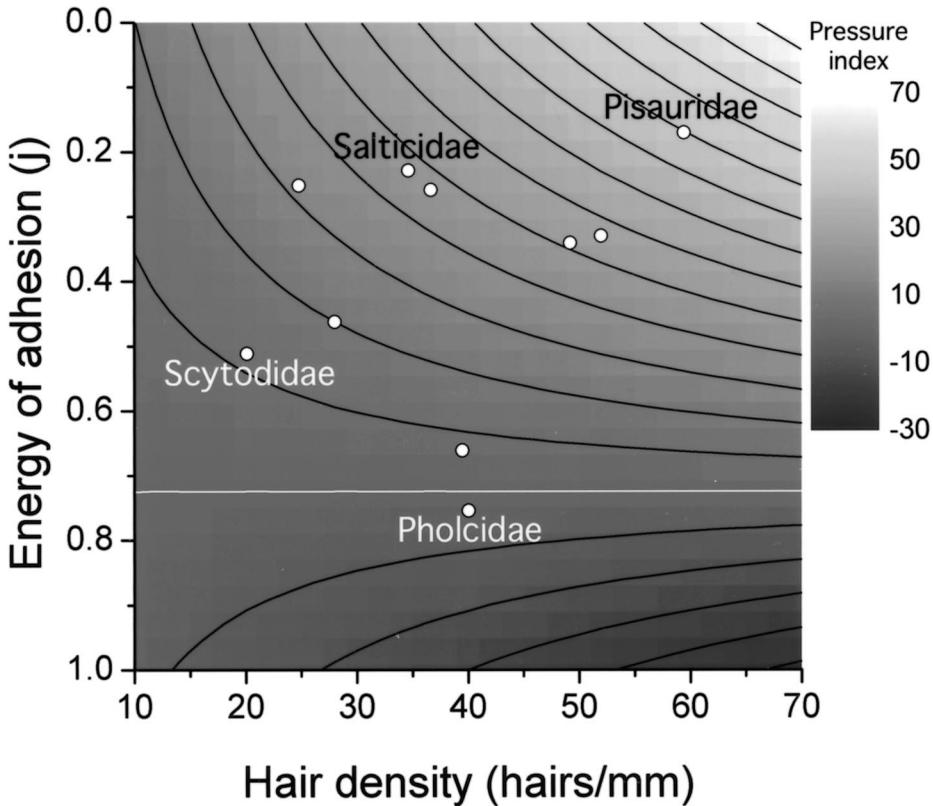
Figure 5.—The influence of hair density and energy of adhesion on the pressure index (z-axis, joules). The data shown here are the same as those in Fig. 4, arranged to emphasize two points. First, hair density and energy of adhesion are not significantly correlated ($r = -0.262$, $P = 0.465$). Second, a variety of combinations of moderately low energies of adhesion (e.g. < 0.4 j) can render a spider well protected from wetting if hair density is sufficiently high (e.g., > 30 hairs/mm). Lines on the graph are pressure index isoclines, with 0 j in white (horizontal line) and those $\neq 0$ shown at intervals of 5 j in black. Data points for all ten families are shown, with labels appended to four for illustrative purposes.

hair density that are its component parts. The surfaces of pisaurids were markedly more functionally hydrophobic than the surfaces of any of the other families of spiders and had a functional hydrophobicity that was nearly 50 times as great as that of the pholcids (Fig. 4, bottom).

The coincidence of very high hair density and very low adhesion energy in the Pisauridae suggests that these two properties may be inversely correlated among species or among families, but that is not the case. A plot of energy of adhesion vs. hair density (Fig. 5) shows that among the families tested there is no significant relationship between the two variables ($r = -0.262$, $P = 0.465$). This absence of a significant correlation is repeated in a comparison of the two variables among species ($r = -0.286$, $P = 0.166$).

DISCUSSION

It would be surprising if fishing spiders (Pisauridae), many of which inhabit riparian environments and actively use the water surface during foraging, searching for mates, and escaping from predators, did not shed water easily from their surfaces (see introduction). Our data indicate, as expected, that their surfaces are strongly hydrophobic, being densely packed with hairs that have very little affinity for liquid water (Figs. 1, 4, 5). Indeed, in the sample of 10 families represented in this study, the functional hydrophobicity of the next highest family, Tetragnathidae, was only two thirds that of the pisaurids (Fig. 4).

The five families at the low end of the scale of functional hydrophobicity include three (Thomisidae, Theridiidae, Pholcidae; Fig. 4) that, in a more comprehensive study of behavior on the water surface, appear to have no capacity to stay afloat when placed on water (Stratton et al. in press). In that same study, the other two families (Scytodidae, Araneidae) had some members with sufficient hydrophobicity to make water surface locomotion possible in theory, and among the araneids it is evident that at least one species is quite adept at aquatic locomotion (Suter et al. in press). Thus the range of functional hydrophobicities that we found in this study includes, at the low end, spiders for which water surface locomotion is morphologically and biochemically insupportable.

We are tempted, and perhaps justified, to view the coincidence of high hair density and low adhesion energy in the pisaurids as an adaptive suite as it is of substantial current benefit to these spiders not only in aquatic locomotion (e.g., Suter 1999; Suter & Wildman 1999) but also in predator evasion (Suter 2003) and in respiration when submerged (Hebets & Chapman 2000; Rovner 1986; Thorpe 1950). The justification for this view is augmented by at least one striking intrafamilial comparison. In the Tetragnathidae, the two species tested (*T. versicolor, L. argyra*) were very far apart in functional hydrophobicity (Table 1), and the one with the much higher functional hydrophobicity is in a genus, *Tetragnatha*, known for its accomplished swimmers (Suter et al. in press).

We find it less easy to explain the substantial variation in functional hydrophobicity in the Tetragnathidae and among the other eight non-pisaurid families tested in this study. Some of that variation is attributable to differences in hair density (Fig. 5; Table 1), and hairs are known to serve sensory, adhesive, and locomotor functions (see text and references in Foelix 1996) as well as visual signaling (e.g., Hebets & Uetz 2000) and defensive (e.g., Marshall & Uetz 1990) functions. But much of the variation is attributable to differences in the energy of adhesion at the interface between the surfaces of the cuticular hairs and liquid water (Fig. 5), and we are uncertain about the functions of hydrophilic hairs. At the core of our quandary is the following question: What benefits accrue to terrestrial arthropods that, like the pholcids in this study, have relatively hydrophilic surfaces?

We offer three general hypotheses for consideration. First, adhesion to substances other than water can play a variety of important roles in the lives of small organisms; because of their relatively high ratio of surface area to volume, small organisms are far more influenced by surface forces than are larger creatures for which inertia is predominant (Vogel 1994). (This is the same scaling effect that causes small organisms to be so vulnerable to being trapped by water's surface tension.) Biological adhesion has attracted substantial attention recently as examples of its importance have come to light. For example, because of the adhesive properties of their tarsi, certain ants can run well on waxy plant surfaces while most cannot (Federle et al. 2000), flies easily walk on inverted smooth surfaces (Gorb 1998) as do many spiders possessing scopulae (Rovner 1978; Foelix 1996, p. 18), and some staphylinid beetles capture springtails with a sticky, protrusible, rod-like labium (Bauer & Pfeiffer 1991). In the current context, the propensity of cuticular hairs to adhere to other substances certainly might drive selection away from hydrophobicity, depending upon the specific circumstances. For example, surface alterations could enhance adhesion to prey surfaces, could reduce susceptibility to surface binding by the spores of pathogens, the eggs of parasitoids, or the silk of other spiders, or could facilitate locomotion on smooth surfaces.

Our second general hypothesis concerns metabolic costs. The hydrophobic properties of the cuticle and hairs of terrestrial arthropods are thought to be attributable to the orderly deposition, either during development or as an ongoing process, of a waxy or oily epicuticular layer (Holdgate 1955). Both the production of this layer and its maintenance through grooming or other mechanisms could be metabolically costly. If that were the case, then selection might favor a decline in hydrophobicity. Testing this hypothesis would be difficult, not because assessing metabolic costs would be daunting but because weighing the cost savings against correlated cost increases would be very complicated. For example, the waxy epicuticle of terrestrial arthropods is credited with a substantial

reduction in transpirational water loss (Crawford 1981), a protection that spiders in xeric environments could ill afford to lose.

Finally, an alternative to both of these hypotheses is the possibility that in some families of spiders grooming is relatively rare. Long periods between grooming bouts would allow the degradation of an otherwise strongly hydrophobic surface due to an accumulation of chemical and particulate debris. Such degradation is known to occur in insects, especially those that inhabit stored grains (Holdgate 1955), but the frequent grooming commonly seen in spiders (personal observation) suggests that this explanation for the variation reported here is unlikely to be correct.

We find none of these hypotheses to be particularly compelling, which leaves us unable to explain why spiders show such a range of capacities to shed water. That same range of capacities, however, does lead to a conclusion about the kinds of preadaptations that are likely to have facilitated the move, by some groups of spiders, into the niche defined by the air-water interface.

Functional hydrophobicity sufficient to allow a spider to move about on the surface of water is far more widespread among spiders than are gaits specialized for aquatic locomotion (Suter et al. in press; Stratton et al. in press). From this we infer that functional hydrophobicity was a preadaptation that facilitated aquatic locomotion (e.g., among the Pisauridae) rather than an adaptation that arose as the ancestors of present-day semi-aquatic spiders began their shift to the more aquatic existence. It follows, therefore, that few theridiids, scytodids, araneids, or pholcids, all of which had indices of hydrophobicity < 10 in this study (Fig. 4), are likely to evolve effective modes of aquatic locomotion in the future. Despite this impediment, we know of one species of araneid, *Larinioides cornutus* (Clerck 1757), that not only is functionally hydrophobic but also adopts a rowing gait much like that of *Dolomedes* when it finds itself on the surface of water (Suter et al. in press).

ACKNOWLEDGMENTS

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