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The mystery of how spiders extract food without masticating prey

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Summary

Standard accounts of how spiders obtain food without masticating their prey are probably largely wrong. Species in the families Uloboridae, Thomisidae, Araneidae and Theridiidae do not inject digestive fluid into the prey's interior, nor do they suck fluids directly from its interior. Rather they regurgitate fluid onto the surface of the prey, and then suck it back up from there. *Philoponella vicina* and other uloborids are extreme in this respect: they wet the entire outer surface of the prey package simultaneously with digestive fluid, and their mouthparts often never touch the prey. Capillarity (along with digestion of prey membranes in *Philoponella*) is apparently responsible both for the dispersion of digestive fluid into the prey, and the exit of liquids from inside the prey.

Introduction

Spiders are well known to feed by regurgitating digestive fluid onto their prey, and then sucking up the resulting nutrient-laden broth (Bertkau, 1885 in Bartels, 1930; Bartels, 1930; Zimmermann, 1934; Comstock, 1948; Kaestner, 1968; Collatz, 1987; Foelix, 1996). The regurgitated fluid, which presumably comes largely from the midgut (Kaestner, 1968) and the maxillary glands (Pickford, 1942), is very rich in proteins (about ten times richer than vertebrate duodenal or pancreatic juice), and is later diluted when it enters the prey (Collatz, 1987). Spiders suck up liquid from the prey by using the muscular sucking stomach, which increases the volume of the foregut. Ingested food is probably nearly completely liquid, as thick brushes of setae in the mouth cavity, and a second filter in the pharynx (the "palate plate") strain out particles as small as about 1 μm (Foelix, 1996).

Some spiders, such as mygalomorphs, many araneids, linyphiids, agelenids and lycosids, use their large chelicerae and the teeth on the distal margin of the basal cheliceral segment to crush and masticate their prey, turning it into "a pulpy mass" (Bertkau, 1885 in Bartels, 1930) as they feed. Thus, the spider's regurgitated digestive juices have ample access to the internal tissues of the prey (Kaestner, 1968; Collatz, 1987), and the spider also has direct access to the nutrient-laden fluid from the interior of the prey. The mechanics of ingestion seem relatively simple in these groups. The most detailed studies of the behaviour and morphology of feeding have been done on groups with large chelicerae which masticate at least some prey (Bartels, 1930; Zimmermann, 1934). Comstock (1948) added that, in general, a spider ". . . sucks the juices pressed from its prey by the mouthparts, . . .".

In other spiders access to the interior of the prey is more complicated and, as we will show below, has been misunderstood. The chelicerae of some groups, such as filistatids, thomisids, scytodids, pholcids, some theridiids, and uloborids (this list is undoubtedly incomplete), are relatively small, and often lack teeth. Although in most of these groups the spider makes small external holes in the prey to inject venom and to feed, the spiders do not masticate their prey, the exoskeleton of which remains more or less intact when the spider has finished feeding (Turnbull, 1962; Kaestner, 1968; Lubin, 1986; Collatz, 1987). These spiders nevertheless gain extensive access to its interior, as the discarded prey is an empty husk; internal tissues of even relatively inaccessible parts such as the distal segments of legs are digested. Some spiders feed in both ways, masticating small, soft prey, but leaving large, rigid prey more or less intact (e.g. the eresid *Stegodyphus* sp. (Y. Lubin, pers. comm.) and the araneid *Allocyclosa bifurca* (McCook), see below).

Descriptions from standard references imply that spiders which leave their prey intact use changes in pressure to feed: ". . . pump digestive juice into the body" of the prey; "the digested soft parts are then sucked out again" (Kaestner, 1968: 179). Collatz (1987) adds that the digestive fluid is injected through small holes that are produced by the chelicerae. Our observations, described below, of *Latrodectus geometricus* C. L. Koch (Theridiidae), *Misumenoides* sp. (Thomisidae), *Allocyclosa bifurca*, and *Philoponella vicina* (O. Pickard-Cambridge) (Uloboridae), contradict these descriptions, and necessitate a rethinking of how spiders feed without masticating prey.

Methods

Mature female spiders collected near San José, Costa Rica were observed feeding at room temperature under a dissecting microscope. Some behaviour of each species was filmed using a digital video camera (30 frames/s) through the microscope. In those species with webs, the wire hoop or jar containing the web was placed under the microscope. The angle of viewing varied as the spider manipulated the prey, and some details were visible in some observations but not in others. It was thus not possible to be sure whether certain details were always the same. In these cases we use the phrase "in at least some cases".

Results

Latrodectus geometricus

Two *Latrodectus geometricus*, which completely lacks cheliceral teeth, were observed feeding on three relatively large prey (approximately 50–100 mg muscoid flies) under the microscope in antero-dorsal views.

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Feeding consisted of many repeated cycles of relatively rapid regurgitation of clear liquid, and then slower uptake of liquid in small rapid pulses. The prey was largely intact when the spider finished, except for holes at sites where she had fed. In one individual feeding at a hole on the dorso-lateral surface of the anterior half of a fly's abdomen, clear liquid periodically accumulated rapidly during regurgitation on the anterior surface of the distal portions of the basal segments of her chelicerae and the space between them, then gradually disappeared during uptake. The liquid pulsed as it disappeared, presumably owing to rhythmic contractions of the spider's sucking stomach. In three video records, the mean frequency of three bouts totalling 76 pulses varied between 4.9 and 7.4 pulses/s. The spider also repeatedly re-grasped the prey with her cheliceral fangs, usually around the time that liquid was appearing on her chelicerae. The rhythmic appearance and disappearance of liquid on the surface of the spider indicated that her mouthparts were not sealed to the surface of the prey; the spider was thus neither forcing liquid into the prey by an increase in pressure, nor drawing it directly out of the prey by sucking.

Further details supported the idea that the "wet–dry" cycles corresponded to repeated regurgitation and ingestion. After the spider had fed on the abdomen of the fly for >10 min, the abdomen of the fly began to collapse slowly during each period of pulsing or ingestion, then expanded rapidly when the spider regurgitated and liquid appeared on her chelicerae. In some of these cases it was clear that the fly's abdomen pulsed while it collapsed at approximately the same frequency as the pulsing liquid. Later, movement of liquid within the prey could be observed directly. Each time liquid appeared between the spider's chelicerae, there was a brief movement of clear liquid within a membrane at the base of the coxa of the fly's leg III which was close to the spider's mouth. Liquid flowed away from the spider each time the spider regurgitated. The fly's coxa was above the spider, so this liquid was not flowing downwards with gravity, but instead was moving upwards within the prey's body, presumably by capillarity. Later still it became clear that there was a slight delay between the moment when the liquid appeared on the spider's chelicerae and the fly's abdomen inflated, and the moment when the flow of liquid began in the base of the fly's leg. This delay supports the idea that the liquid moved into the fly by capillarity, rather than owing to increased pressure, as a pressure increase would have produced simultaneous or nearly simultaneous movements in both the abdomen and the leg.

In sum, *L. geometricus* rhythmically regurgitated and ingested liquid; this liquid was not injected into the prey under pressure, but instead flowed into the fly's body, probably by capillarity. Apparently there was so much liquid produced, and the fly's partially digested abdomen was so soft, that regurgitation caused the abdomen to inflate perceptibly, and then to collapse as the liquid was withdrawn. As the prey's internal tissues became digested, the liquid probably moved progressively deeper into the prey when the spider regurgitated.

Misumenoides sp.

Feeding on a relatively large prey (a honeybee), observed under the dissecting microscope in antero-dorsal view, also involved rhythmic cycles of regurgitation and sucking. The duration of cycles averaged 2–3 min/cycle during early feeding, but later became shorter. A clear liquid periodically appeared abruptly between the distal ends of the basal cheliceral segments, remained there unchanged for 11 ± 4 s ($n=9$), and then slowly disappeared. The liquid made small pulsing movements (17 pulses in 7 s, or 2.4/s) as it disappeared. These pulsing movements were accompanied by rhythmic movements of similar frequency of an unidentified structure that was just visible within the spider's cephalothorax; presumably these were associated with pumping movements of the spider's sucking stomach. The last of the liquid disappeared 59 ± 3 s ($n=8$) after the pulses began, and then no liquid was visible for another 89 ± 10 s ($n=8$) until the moment when the next abrupt wetting began. The cheliceral fangs opened slightly at the beginning of each wetting, and closed slightly as the liquid began to disappear. The opening movement of the fangs might have facilitated entrance of the liquid into the prey by widening the holes they made in the prey cuticle. As with *L. geometricus*, the cyclic accumulation and disappearance of liquid on the prey's exterior showed that the spider's mouthparts did not make a seal with the surface of the prey.

Periodically the spider rotated the prey briskly with her palps, then bit it again with her chelicerae and performed further regurgitation–ingestion cycles. Often her chelicerae bit repeatedly at the prey, and at least some of these bites apparently penetrated its cuticle. When the spider had fed at a site, a hole or holes could sometimes be seen in the cuticle. One hole near the base of a femur allowed direct observation of the fluid inside as the spider fed more distally on a partially consumed prey. The liquid inside rose when the spider regurgitated, and fell when she sucked.

Allocyclosa bifurca

Five spiders were observed feeding on ten prey in ventral and anterior views. The chelicerae of this species have teeth, typical for the Araneidae, and the spiders crushed small soft prey into a pulpy mass when feeding on them (Fig. 1a). Large prey, such as calliphorid fly about the size of the spider (20.6 mg) were, in contrast, left largely intact (Fig. 1b), and in these cases feeding behaviour was similar to that described for the previous species. After wrapping a calliphorid and fastening it near the hub, the spider grasped it with her chelicerae and repeatedly opened and closed them, apparently gnawing a hole in the lateral surface of the thorax. After several minutes of gnawing, her chelicerae became less active (in one case one fang was visible, and was inserted into the prey), and she began a long series of wet–dry cycles similar to those described above. Early in feeding on a calliphorid fly, the cycles were relatively short (mean $= 13.7 \pm 2.2$ s, $n=8$), but three minutes later they had become longer (mean $= 40.7 = 16.8$ s, $n=10$). In at

least some cases the spider's endites were not pressed against the prey, but were instead up to about 1/3 the length of the labium away from it. This entire gap between the prey and the endites (whose medial surfaces were separated and did not meet) was filled abruptly with clear liquid when the spider regurgitated, once again showing that there was no seal between the spider's mouthparts and the surface of the prey. The liquid remained more or less motionless for approximately 10 s, and then gradually disappeared. After feeding at one site for many minutes, the spider shifted the prey, gnawed another hole, and fed. In eight calliphorid and muscid flies, feeding occurred at 2–7 sites.

Two details differed from the previous species. During the sucking phase, the endites moved rapidly back and forth laterally at approximately the same rate (50 in 13.4 s, or 3.7/s) as the movement of an object (presumably the palate plate) that was dimly visible within the labium. These probable pumping movements within the spider may have imparted pulsing movements to the liquid as seen in other species, but such movements were not noted, probably because they were masked by the movements of the endites. Secondly, the liquid gradually drained away from the gap between the spider and the prey during each sucking phase. It disappeared first from the posterior surfaces of the chelicerae and eventually dried up completely, thus breaking the liquid connection between the spider's mouth and the prey. However, the endites and the object in the labium continued to vibrate; these movements ceased only when the spider regurgitated again. The period without a liquid connection between the spider's mouth and her prey lasted for about 20–30 s when the spider was regurgitating about every 60 s.

Philoponella vicina

Six spiders were observed feeding on ten prey. As described elsewhere (Eberhard *et al.*, 2006; Weng *et al.*, in press; Barrantes *et al.*, in prep.), and as typical for uloborids in general (Lubin, 1986; Opell, 1988), *P. vicina* wrapped the prey extensively in silk before beginning to feed. During the final burst of wrapping, clear liquid appeared on the anterior surfaces of the spider's chelicerae, and her chelicerae moved actively. As soon as wrapping ended, the spider transferred the prey package from her legs II and III to her palps and chelicerae, and immediately began to turn the package rapidly with her palps and chelicerae and simultaneously regurgitate a clear liquid which was spread over the surface of the package as she turned it. This initial wetting behaviour lasted for only a minute or so with small prey, but up to >20 min for very large prey. By the time initial wetting was finished (when the spider first stopped turning the prey package), the entire surface of the package was wet. It was not always feasible to observe details of the movements of her chelicerae; in the glimpses we obtained of her cheliceral fangs, they were grasping the silk shroud, not the prey. The prey was turned so rapidly and continuously that it seemed unlikely that her fangs had time to penetrate the prey cuticle.

Following the initial wetting, rotation of the prey slowed considerably and became intermittent. Periodically the spider stopped rotating the package and fed for up to >20 min at a given site. At least with relatively small and weak-bodied prey such as *Drosophila* sp., the spider began extracting material from the prey's interior very early during feeding: red granules of eye pigment from the prey began to accumulate on the spider's endites as little as <1 min after she first began feeding over the surface of the eye. As the spider's chelicerae had apparently not pierced the prey, this material probably flowed through cracks in the prey cuticle that resulted from the collapse of the compound eye owing to the compression produced by wrapping (Eberhard *et al.*, 2006). During long pauses at a feeding site, the prey was repeatedly moved slightly, possibly resulting from movements of the spider's chelicerae. We were unable to observe her chelicerae at all times, and never directly observed them penetrating the prey cuticle. However, the discarded body of one large muscoid fly had a hole at each of the two sites at which the spider had spent long periods of time feeding (between the eyes, and at the tip of the abdomen). Other, smaller discarded

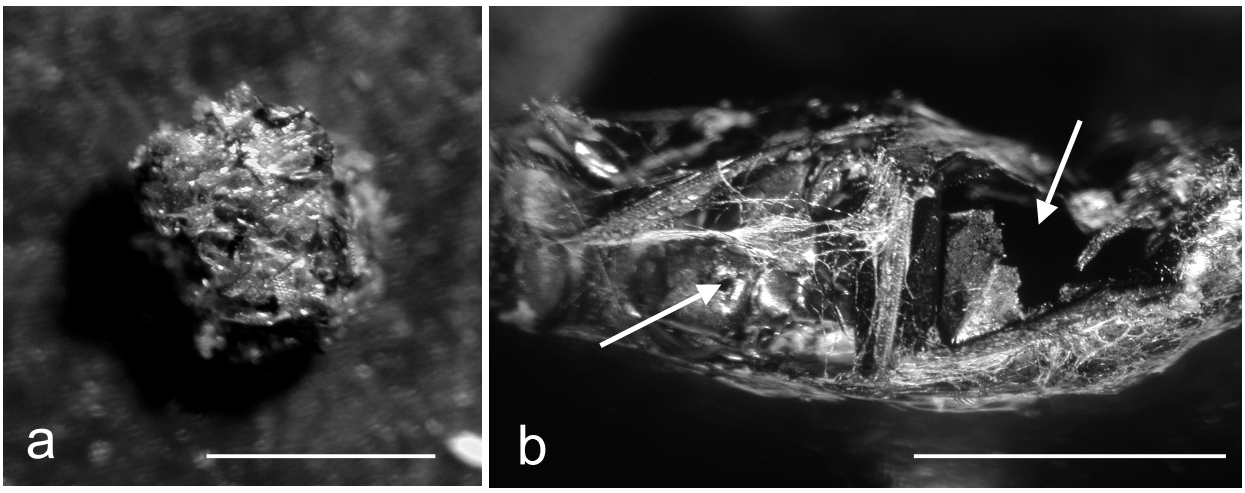

Fig. 1: Extreme forms of the remains of prey discarded by *Allocyclosa bifurca*. **a** A small *Drosophila* sp. fly that was crushed into tiny pieces; **b** A large calliphorid fly that was left largely intact, apart from two holes where the spider fed (arrows). Scale lines = 0.89 mm (a) and 3.2 mm (b).

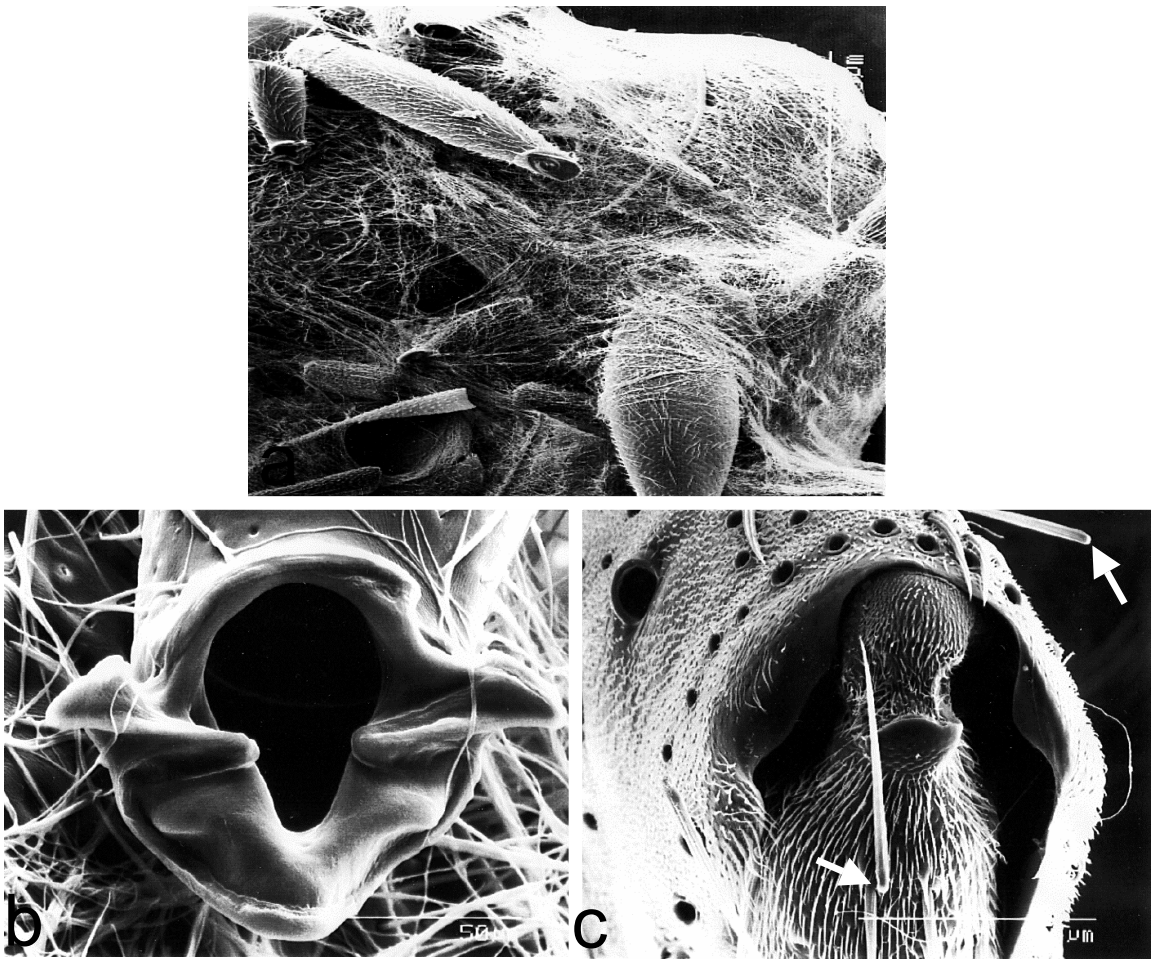

Fig. 2: SEM micrographs of prey discarded by *Philoponella vicina*. **a** Disarticulated pieces of a parasitic wasp protrude through and lie on the outer surface of the silk shroud; **b** The distal end of the trochanter of a parasitic wasp, with the intersegmental membrane entirely missing; **c** Empty sockets and the bases of isolated setae (arrows) from which the membranes are missing in a fly.

prey had no holes. It appeared that during feeding, as during wrapping, the spider's chelicerae and mouth area frequently failed to contact the prey directly, but only contacted the shroud covering the prey.

While feeding, the spider cyclically (approximately once every 30 s) regurgitated clear fluid abruptly, and then more slowly ingested it. As in the previous species, it was clear that the spider's mouthparts did not make a seal with the surface of the prey. As the liquid was regurgitated, it flowed away from the spider's mouth in an expanding circle; this "wave" was visible at distances from her mouth up to approximately the length of her sternum. Following regurgitation, the area on the surface of the prey where the liquid was perceptibly deeper began to shrink gradually in small, barely perceptible pulses of about 5/s (the exact frequency was difficult to measure in video recordings). In one case the spider's abdomen and legs IV pulsed with this same rhythm. At later stages, it was possible to observe movements of the liquid directly by following the movement of small bubbles that formed under the shroud and inside portions of the prey such as inside leg segments: the liquid moved gradually towards the spider as she sucked, and abruptly away from her when she regurgitated. Coordination between regurgitation, ingestion, and rotation of the prey varied: sometimes the spider regurgitated just before rotating the prey and then sucked up liquid from a different spot; on other occasions she rotated the prey immediately after ingesting.

Examination of prey that had been discarded after feeding often showed that portions of their bodies, such as their legs, were disarticulated (Fig. 2a). This raised the possibility that we had missed direct manipulation of the prey by the spider. Closer examination of the ends of disarticulated segments of legs showed, however, that the intersegmental membranes had disappeared completely (Fig. 2b). In addition, free setae, which lacked their basal membranes, were often scattered nearby, sometimes adhering to the inner surface of the shroud (Fig. 2c). The loss of membranes suggests that prey became disarticulated as a result of the spider having digested those membranes. Hard-bodied prey, such as ants and small beetles, had no obvious breaks in their cuticle when they were discarded, but were nevertheless also partially disarticulated and more or less empty inside.

Discussion

Extended cycles of rhythmic regurgitation and sucking occurred in all four species. This may be an ancient and generalised method of feeding in arachnids, as similar cycles have been described in a pseudoscorpion by Schlottke (1933, in Pickford, 1942), and in the agelenid *Tegenaria domestica* (Clerck) (Bartels, 1930).

In none of the four species studied here did the spider's mouthparts form a tight seal against the surface of the prey during feeding. Digestive liquid welled into a pool between and around the distal portions of the spider's basal cheliceral segments each time she regurgitated. This pool spread over the entire prey in the uloborid. The digestive liquid was thus free on the surface of the prey, and was not pumped directly into its interior. The slow subsidence and disappearance of this pool while the spider sucked also indicates that the spiders did not make a seal with the prey's surface to suck liquid directly from its interior. Instead, the spiders sucked only from the pool of liquid on the surface of the prey. As noted in the introduction, these observations contradict standard accounts of feeding by spiders, and necessitate rethinking the mechanism by which spiders extract nutrients from their prey.

A spider's problems of getting digestive fluid into and then out of prey can be appreciated intuitively by imagining the difficulty a human would have in extracting nutrients, spider-style, from a soft drink bottle (representing the hard cuticle of the prey) that was open at one end (the wound produced by the spider's bite) and full of liquid (the prey's blood and internal tissues). One could only add digestive liquid at the mouth of the bottle, and only small quantities of liquid at that. Forcing additional liquid into an unyielding bottle that is already full is not feasible; and in any case it would not be possible to create pressure to force it in, if one's mouth failed to make a tight seal with the bottle (as is the case for spiders). This analogy is somewhat overdrawn, because at least some prey are not entirely rigid (see the description of the abdomen of a prey of *Latrodectus* expanding and collapsing), but it illustrates the basic problem.

It might seem that at least part of the problem of getting digestive fluid into the prey could be solved by first creating several holes in the prey's exterior and then sucking out some blood, so as to create an empty space within the prey, into which the digestive fluid could be added. But feeding did not begin with repeated bites at different sites in *L. geometricus*, *A. bifurca* or *P. vicina* (we did not see its initiation in the thomisid); and at least in the uloborid, spiders routinely regurgitated onto the external surface of their prey before either perforating it or sucking.

The soft drink bottle analogy also illustrates a spider's problems with the second process, sucking up nutrients from the prey. Unless one made an additional hole in the rigid walls of the bottle, one could not suck out fluid from inside, as sucking liquid from a closed-ended container is not feasible unless the walls of the bottle collapse. In addition, when one's mouth does not make a tight seal with the surface of the bottle (as in spiders), negative pressure cannot be produced inside the bottle by sucking; thus sucking could only remove the fluid that had accumulated on the outside of the bottle around the opening. Finally, in contrast with the behaviour of a human who is attempting to extract liquid from a soft drink bottle, spiders did not tip their prey upside down to allow the liquid to run out; some spiders even fed exclusively from the upper half of the prey!

Our observations indicate that fluid flowed into and out of the prey's interior by capillarity, rather than as a result of pressure changes, as suggested by previous authors. Access to the prey's interior was probably provided by holes made when the spider injected venom or, in *P. vicina*, by breaks in the cuticle resulting from compression from wrapping and by the ability of the digestive fluid to digest prey membranes (Eberhard *et al.*, 2006; Weng *et al.*, in press). The low surface tension of the digestive fluid of *P. vicina* compared with tap water (Weng *et al.*, in press) probably facilitates movement of fluid into and out of the prey; the surface tension of the digestive fluid of other species has not to our knowledge been measured.

Given these indications of capillary flow, and the poor design of the relatively thin cheliceral fangs of spiders for pressing more than a small fraction of the liquid from a prey, we doubt that Comstock (1948) was correct in his description of spiders feeding by pressing out fluid when prey is masticated. Simple sucking on such prey is probably enough to extract most of its liquid contents.

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