Eggsac Differences in the Spider Family Uloboridae (Arachnida: Araneae)¹

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Abstract. Scanning electron microscope study of eggsacs produced by representatives of the genera Hyptiotes, Miagrammopes, Octonoba, Philoponella, Tangaroa, Uloborus, and Zosis shows them to contain silk of three diameter classes, the distribution of which does not mirror the family's phylogeny. The eggsacs of some taxa are constructed of a single layer of fine silk fibers having a diameter of about 1.0 μ m and others of two layers of this silk, judged to be of tubuliform gland origin. Others construct eggsacs lined by fine silk and covered by coarse silk fibers having a diameter of about 1.6 μ m. Eggsacs of Hyptiotes are made of two coarse layers covered by tufted silk having a fiber diameter of about 5.6 μ m. Both coarse and tufted silk camouflage eggsacs, tufted silk possibly also serving to collect moisture and protect eggs from mechanical and insect damage. Coarse and tufted silk may be produced by ampullate glands.

The spider family Uloboridae is represented world-wide (Opell, 1979). Its 18 genera show behavioral diversity in the type of capture webs produced and in the shape and placement of silken eggsacs that are spun around egg clusters (Berland, 1932; Comstock, 1913; Eberhard, 1969; Gertsch, 1979; Girault, 1914; Kaston, 1948; Lubin et al., 1978; Scheffer, 1905; Trail, 1982; Wiehle, 1927, 1928; Yoshida, 1981; personal observations). The stellate or elongate, lenticular eggsacs of Philoponella (Fig. 1) often are suspended from the edges of a horizontal orb-web and are guarded by females, whereas those of Octonoba and Zosis are incorporated into the horizontal orb-web and usually are left unattended (Fig. 2). Females of Uloborus also incorporate eggsacs into their horizontal orb-webs, but commonly hang adjacent to one end of an eggsac or chain of several eggsacs. Females of Tangaroa beattyi Opell, 1983 place a chain of 8-12 small eggsacs on one or two of the perimetric framework lines of their orb-webs (Joseph Beatty & James Berry, personal communications). Females of Miagrammopes appear to hold their cylindrical eggsacs until spiderlings emerge (Fig. 3) and, during this time, do not construct their singleline capture webs. By contrast, the triangle-web spider, Hyptiotes cavatus (Hentz, 1847), produces cryptic, planoconvex eggsacs attached directly to twigs

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FIGS. 1-4. Eggsac types. Fig. 1. Female of *Philoponella tingena* with eggsac. Fig. 2. Orb-web of *Zosis geniculatus* showing female at hub (right) and eggsac incorporated into web. The spherical egg mass can be seen at the center of the thin-walled eggsac. Fig. 3. Female of *Miagrammopes* unipus with cylindrical eggsac. Fig. 4. Eggsacs of *Hyptiotes cavatus*. Upper eggsac produced on a dowel rod in the laboratory, others on hemlock twigs in the field. Scale bar in Fig. 1 represents 0.5 cm; 1.0 cm in other figures.

(Fig. 4). *Hyptiotes* also is distinguished by the fact that its eggsacs are produced in the autumn and the eggs are protected until spiderlings emerge the following spring (Opell, 1982). The family's other temperate species produce summer eggsacs from which spiderlings emerge in about 20 days to feed for about two months before passing the winter as juveniles. Such diversity suggested there also may be microscopic differences in uloborid eggsacs and lead to this study which attempts to characterize the layers and fiber diameters of eggsac silk produced by representatives of these seven genera.

MATERIALS AND METHODS

Eggsacs produced by at least two individuals of each of the following species were examined: Tangaroa beattyi from Yap, Caroline Islands; Hyptiotes cavatus from Giles Co., Virginia; Uloborus glomosus (Walckenaer, 1847) from Allegan Co., Michigan and Montgomery Co., Virginia; Zosis geniculatus (Olivier, 1789) from Balboa, Panama; Octonoba octonaria (Muma, 1945) from Tompkins Co., New York and Douglas Co., Kansas; Philoponella tingena (Chamberlin & Ivie, 1936) from Valle de Cauca, Colombia and Barro Colorado Island and Gamboa, Panama; Philoponella oweni (Chamberlin & Ivie, 1924) "stick-" and "bag-morphs" (unnamed sibling species distinguished by Trail, 1982) from Cochise Co., Arizona; undescribed species of Miagrammopes from Heredia, Costa Rica; and Miagrammopes unipus Chickering, 1968 from Valle de Cauca, Colombia. Following collection, eggsacs were kept in dry, stoppered vials. Except for T. beattyi and P. oweni, at least one eggsac from each species contained unhatched eggs.

Eggsac layers were defined as uniform sheets of silk which could be easily and repeatedly peeled from underlying layers. Scanning electron micrographs were made of outer eggsac surfaces, surfaces with successive layers removed, and of inner eggsac surfaces. Samples were vacuum-evaporator-coated, first with carbon, and then with gold-palladium, photographed at 500 or $540 \times$, and contact prints representing 20.3 mm² of eggsac surface made from the 9.0×11.5 -cm negatives. Mean silk diameter was computed from 50 in-focus silk strands measured with the calibrated ocular micrometer of a dissecting microscope. Before being measured, the entire visible length of a fiber was examined. If anastomosis occurred, only the diameter of a constituent fiber was measured. This accounts for the fibers shown in some micrographs being larger than the maximum fiber diameter reported for that layer. Transverse sections of eggsacs made with iris scissors were examined by scanning electron (SEM) or compound light microscopy in order to determine total wall thickness. The entire edge of one or more samples was examined and measurements taken in regions that did not appear to have been compressed by cutting.

RESULTS

The silk used for eggsac construction falls into three classes based on fiber diameter (see Table I).

Fine silk. This white, tan, or light-pink silk has a fiber diameter of $0.93-1.17 \mu m$ (Figs. 9, 10) and lines all eggsacs examined, except those of *Miagrammopes unipus* and *Hyptiotes cavatus*. Eggsacs of *Zosis geniculatus* and *Octonoba octonaria* are composed of only a single light-pink or purple layer of this fine silk, whereas those of *Tangaroa beattyi* and *Philoponella oweni* have an outer covering layer of smoother, more compressed fine silk.

Coarse silk. This white, light-pink, or gray silk has a fiber diameter of $1.41-1.88 \mu m$ and forms the primary platform of eggsacs of *H. cavatus* as well as the two layers of the convex portion of these eggsacs (Figs. 6, 8). In Uloborus glomosus and Philoponella tingena, coarse silk forms the outer eggsac surface (Fig. 7). Despite fiber diameter differences between the outer and inner eggsac

TABLE I

Fiber diameter (μm) , fiber distribution, and wall thickness of uloborid eggsac silk—mean and standard deviation

	Fine silk		Coarse silk		Tufted	Wall
	Lining	Covering	Lining	Covering	silk	ness
Zosis geniculatus	1.08 (0.31)			_	—	_
Octonoba octonaria	1.11(0.08)		_			22
Philoponella oweni s.m.*	0.93(0.09)	0.99(0.14)				24
Philoponella oweni b.m.*	1.01(0.15)	1.14 (0.19)	_		_	29
Tangaroa beattyi	1.03(0.09)	1.04 (0.19)				18
Philoponella tingena	1.17(0.14)	_		1.65(0.28)		
Uloborus glomosus	1.14(0.23)		_	1.75(0.43)		42
Miagrammopes sp.	1.08(0.18)			1.45(0.33)		12
Miagrammopes unipus			1.60(0.34)	1.88(0.43)		
Hyptiotes cavatus		—	$1.41 \ (0.25)^{b}$	1.81 (0.44) ^b	5.60	51°

* Eggsacs of stick- and bag-morph sibling species distinguished by Trail (1982).

^b Coarse lining silk forms the platform. The dome covering is composed of two layers of coarse silk.

 $^{\circ}$ Wall thickness less tufted silk. Total wall thickness 150 μ m.

surfaces of M. unipus, these thin-walled eggsacs appear to be composed of a single layer of coarse silk.

Tufted silk. This dark gray silk is drawn into 5.6- μ m diameter pointed tufts that extend about 100 μ m above the eggsac's surface (Figs. 5, 6), are arranged in parallel rows, and usually extend a short distance onto the underlying twig's surface (Figs. 4, 5).

Comparisons of the inner surfaces of eggsacs from which spiderlings emerged with those containing unhatched eggs show that spiderlings deposited little, if any silk within the eggsac.

DISCUSSION

The simplest uloborid eggsacs, and those of one of the family's most primitive genera, *Tangaroa* (see Opell, 1979), consist only of fine silk. Similar silk lines more complex eggsacs, and therefore is the first silk deposited in most eggsacs. The partial sequences of eggsac construction I have observed in *Uloborus glomosus*, *Octonoba octonaria*, and *Philoponella tingena* indicate that orb-weavers first deposit a silk platform in the web, place eggs under the platform, and then cover them with another silk sheet. Females confined to a vial sometimes place the primary silk platform on its cotton stopper. This pattern is similar to that described for members of other families (Foelix, 1982; Gertsch, 1979; Kullmann & Stern, 1981).

Figure 11 imposes eggsac silk layer distribution on a phylogeny of included genera as determined by the cladistic analysis of Opell (1979) with a more recent reevaluation of the position of *Hyptiotes* and *Miagrammopes* (Opell, in preparation). If fine lining silk is considered plesiomorphic for the family, the minimum number of evolutionary steps required to explain the distribu-

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FIG. 11. Phylogeny of uloborid genera whose eggsacs were included in this study, showing the distribution of eggsac silk layers.

tion of eggsac silk is four. However, the most parsimonious explanation of the pattern shown in Fig. 11 requires 10 steps: independent loss of fine lining silk in *H. cavatus* and *M. unipus*; convergent addition of fine covering silk to *T. beattyi* and *P. oweni* eggsacs; loss in *Miagrammopes* sp. of the coarse lining silk synapomorphic for the *Hyptiotes-Miagrammopes* lineage; loss in the *Zo-sis-Octonoba* lineage and in *P. oweni* of the coarse covering layer synapomorphic for the *Hyptiotes-Philoponella* lineage; and acquisition by *Hyptiotes* of the tufted silk autapomorphy. In addition to being inconclusive, even such conservative attempts as this to explain the distribution of eggsac silk suggest that it is a highly plastic feature that does not clearly reflect family phylogeny.

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FIGS. 5-10. Eggsac silk layers. Fig. 5. Outer tufted layer of eggsac of *Hyptiotes cavatus*. Fig. 6. Transverse section of eggsac wall of *H. cavatus*. Fig. 7. Outer eggsac surface of *Uloborus glomosus*. Fig. 8. Lining of convex portion of eggsac of *H. cavatus*. Fig. 9. Outer surface of eggsac of *Octonoba octonaria*. Fig. 10. Lining of eggsac of *Philoponella tingena*. Scale bar in Fig. 6 represents 100 μ m; 10 μ m in other figures.

Zosis and Octonoba are the only genera correctly united by an eggsac similarity, and the presence of only fine lining silk in their eggsacs may be symplesiomorphic. Silk layers may have been added or deleted from eggsacs several times by addition or deletion of swathing sequences using silk of different diameters.

Generally, tubuliform (cylindrical) glands located on the median and posterior spinnerets are associated with production of eggsac silk (Foelix, 1982; Forster, 1967; Kovoor, 1977; Mullen, 1969; Witt et al., 1968), although Forster (1967), Foelix (1982), and Kovoor (1977) allow that the aciniform glands may also serve this role in some spiders. Kovoor's (1977) finding that uloborid aciniform and tubuliform glands have excretory canal diameters of 6 and 20 μ m, respectively, allows the source of fine eggsac silk to be identified. SEM study of wrapped prey taken from *Miagrammopes* shows it to be swathed by silk with a diameter of about 0.5 μ m. This agrees with Kullmann's & Stern's (1981) SEM (p. 91, top) of "Uloborus" (probably Zosis) wrapping silk and with light microscope measurements of U. glomosus wrapping silk. In the latter case, a few 0.8-um diameter silk strands were also present. Because wrapping silk is smaller in diameter than fine eggsac silk, the former is probably of aciniform gland origin and the latter of tubuliform gland origin. Coarse and tufted silk may be spun by ampullate glands, because these are shown to have spigots capable of aperture control (Breed et al., 1964; Wilson, 1969). Coarse silk diameters correspond roughly to those Work (1977) presents for minor ampullate glands of araneids. If tufted silk is formed of coalesced coarse silk (Figs. 5, 6), it also may be produced by ampullate glands.

Coarse covering silk gives the eggsacs of *P. tingena* and *U. glomosus* a mottled or darker appearance that renders both the eggsac(s) and attending female less conspicuous. The linear shape of *Miagrammopes* and its cylindrical eggsac combine to create stick mimicry that is enhanced by complementary coloration (Fig. 3). *M. unipus* and its eggsac are tan to brown, whereas *Miagrammopes* sp. and its eggsac are green.

Eggsacs of Hyptiotes cavatus were first described by Scheffer (1905), who noted their cryptic form and the parallel rows of silk loops that cover them. In addition to giving the eggsac a dark, velvety appearance that enhances its crypsis, tufted silk may retain water droplets from dew and rain and, in this way, help to retard egg desiccation. The outer layer could also cushion the blows and reduce the abrasion that occur when twigs and needles strike and scrape the eggsac's surface. Because eggsacs of Hyptiotes are attached rather than suspended, they may be more frequently encountered by insects, and by making it difficult for insects to walk on the eggsac, tufted silk may reduce the chance of an eggsac being eaten or damaged. If a hymenopteran egg parasitoid alights on the eggsac, it rests on the top of the tufts, approximately 100 μ m above the eggsac's true surface. This texture may prevent the wasp from gaining a solid purchase, or significantly increase the distance through which the ovipositor must pass before penetrating the eggsac wall, thereby reducing egg parasitism. Egg parasitoids are common in many tropical uloborids; the small species, Arachnopteromalus dasys Gordh, 1976, has emerged

from eggsacs of the temperate species O. octonaria (see Gordh, 1976) and U. glomosus (personal observations). Although I have found this small species in eggsacs of U. glomosus collected in southwestern Virginia, I have not observed it in over 35 eggsacs of H. cavatus collected in the same region. Eggsac composition may reduce the incidence of egg parasitism in Hyptiotes, but differences in habitat and egg deposition times between temperate orb-web and triangle-web uloborids also may play an important role.

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