

THE ORIGIN OF THE SPINNING APPARATUS IN SPIDERS

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I. INTRODUCTION

The purpose of this paper is to review our understanding of the evolutionary biology of spiders pertinent to the problem of the origin of the spinning apparatus. My goal is to generate hypotheses that are both congruent with the historical hypotheses favoured now and which are capable of predicting the outcome of future inquiry. The accuracy of the predictions may serve as a test of the hypotheses I generate.

I will address three interrelated historical problems: the origin of spinnerets, the origin of silk glands and the original selective pressure(s) which favoured the evolution of fibroin silk. Information relevant to each of these problems will be obtained from three different frames of reference: (1) In-group Analysis – information obtained from comparative morphology and ontogeny of Araneae, (2) Out-group Analysis – information obtained from examination of other arachnid orders, especially Amblypygi and Uropygi, (3) Convergence Analysis – information obtained from examination of other terrestrial arthropods (myriapods, hexapods). While the in-group and out-group analyses used here are similar to those methods commonly employed by systematists

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in hypothesizing and testing character polarities (information that establishes directionality within the evolution of a taxon) (see Stevans, 1980), convergence analysis can only be useful when constructing hypotheses about the history of a particular adaptation. Convergences provide examples of how evolution may operate but do not eliminate the possibility of multiple evolutionary pathways to a given adaptation. Therefore, convergences can be used in hypothesis construction but not hypothesis testing (Fisher, 1985).

The great importance of the spinning apparatus to the evolutionary success of spiders has inspired several workers to compose historical narratives in an attempt to explain the evolutionary origin of this unique feature. These notions usually rely heavily on conjecture. For example, Savory (1952) has envisioned the spider ancestor as making brief forays from a burrow while trailing a stream of excrement. At some point, the excrement somehow evolves into silken threads. This crucial transformation, coupled with the ancestral foraging strategy, would then generate the first web. Historical narratives such as this are not uncommon in the scientific literature and continue to crop up as biologists attempt to fill the gaps in evolutionary history. Dissatisfaction with this practice has increased with the general acceptance of the Popperian philosophy which states, in essence, that truly scientific hypotheses must be open to refutation; they must be falsifiable. While it may be impossible to devise such an hypothesis for every evolutionary transformation (such as the origin of a particular structure or taxon), the successful incorporation of phylogenetic reconstruction into the Popperian framework gives added incentive to abandon imaginative story-telling or reliance on expert opinion and to search for a more structured approach to the formulation of testable historical hypotheses.

The evolutionary transformation responsible for the origin of a particular character or taxon represents a unique series of events, no portion of which is available for direct examination. From our vantage point, we can never be certain as to the true nature of the transformation, even if we had the correct hypothesis in hand; no mechanism of absolute verification exists. Still, there is only one true transformational sequence leading to the origin of a feature and, if characteristics of organisms reflect their evolutionary history, one would expect information derived from careful analysis of such features to reveal something of their past. Those hypotheses which accommodate the most information and which generate specific expectations for the kind of information to be found in the future are likely to be the ones which approximate reality most closely. So, while hypothetical evolutionary transformations are not open to direct testing, an evaluation of their predictive powers can serve as a method of indirect testing (Platnick, 1978).

Biological information relevant to the construction and testing of historical hypotheses can be gathered from several lines of inquiry – developmental biology, palaeontology, comparative morphology and biogeography. Historical hypotheses can be derived from evidence gathered from within a single area of investigation or, when congruences are found among results derived from different lines of inquiry, they may be integrated to form more robust hypotheses. If biological information reflects evolutionary history, we should expect the process of evaluation and integration of congruent historical hypotheses to provide ever increasing insight into the causes, consequences and relative timing of specific evolutionary events. Therefore, if we wish to understand the

evolutionary history of a specific feature, such as the spinning apparatus of spiders, we should strive to produce historical hypotheses which are (1) consistent with current biological knowledge, (2) congruent with other well-founded historical hypotheses (e.g. phylogenetic reconstructions, character polarities) and (3) capable of generating predictions that will guide future inquiry and provide a rationale by which the value of the hypotheses may be assessed.

The importance of congruence (or compatibility) among different lines of evidence in formulating historical hypotheses has been discussed by systematists (Meacham & Estabrook, 1985 and references therein) and evolutionary morphologists (Lauder, 1981). It is also not absent from the minds of arachnologists interested in the evolutionary origins of the spinning apparatus of spiders. Decae (1984), for example, realized that his hypothesis on the evolution of silk should be congruent with reconstructions of arachnid phylogeny. He proposed that silk was originally adapted to line the burrows of a marine ancestor, noting that many 'primitive' spiders live in burrows and that marine burrowers often use secretions of various kinds to support the walls of their retreats. The best supported hypothesis of chelicerate phylogeny to date (Weygoldt & Paulus, 1979*a*, 1979*b*) maintains that arachnids are monophyletic and primitively terrestrial (see next section for details), a scenario inconsistent with Decae's. Instead of modifying his hypothesis, however, Decae assumed that the constraints of his untested notion should supersede those of Weygoldt & Paulus' cladogram and then modified arachnid phylogeny accordingly. He did not falsify the relevant portions of Weygoldt & Paulus' hypothesis, and one is left with the impression that Decae has merely manipulated arachnid phylogeny to accommodate his idea. Needless to say, no new information is gained by this methodology, and he simply concludes that the phylogeny he proposes is "...no less fictitious than any extant hypothesis..." (p. 27). Well-founded historical hypotheses should be perceived as guidelines in the construction of new historical hypotheses. They must be rejected or modified when they do not conform to the facts but not simply because they pose an inconvenience.

II. ARACHNID PHYLOGENY

An understanding of the interrelationships of spiders (order Araneae) with the other arachnid orders is essential for generating testable hypotheses about the evolution of the spinning apparatus. A convincing phylogenetic reconstruction places constraints on the kinds of historical hypotheses that can be considered reasonable by specifying a sequence of events in the diversification of a clade. Although the number of hypotheses that fit these specifications may be large, it is certainly lower than the number of 'just-so' stories a totally unrestrained imagination could produce. Most importantly, such phylogenetic hypotheses provide a framework in which testable predictions can be made.

Unfortunately, there is little agreement among systematists about the relationships of the ten living arachnid orders. Due to a paucity of convincing synapomorphies, some workers favour a polyphyletic origin of Arachnida, perhaps from different marine ancestors (Kraus, 1976; van der Hammen, 1977). According to this view, arachnids represent a grade of terrestrial chelicerates and not a natural taxonomic entity. On the other hand, it is possible that the arachnids are derived from a single common ancestor and the large interval of time since the initial radiation (over 350 million years) has

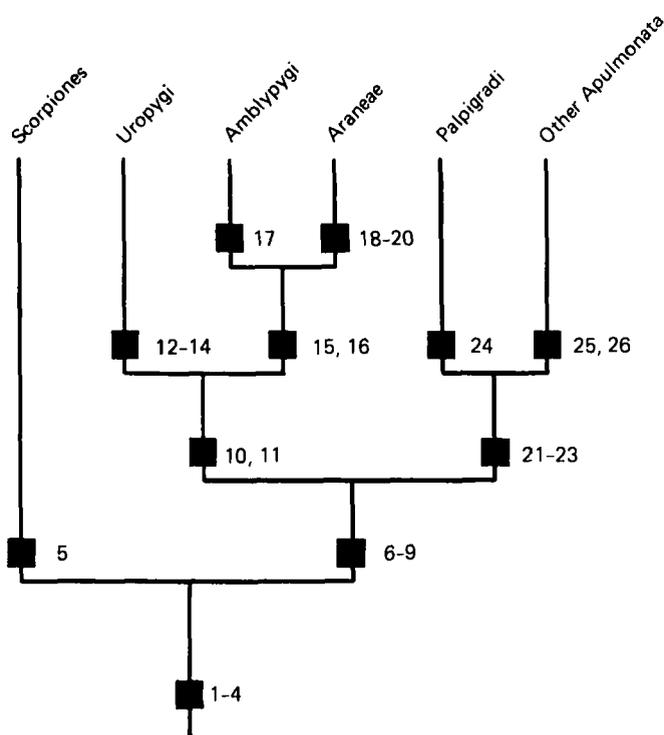


Fig. 1. A cladogram showing the relationships of the arachnid orders (modified from Weygoldt & Paulus, 1979*b*). See Table 1 for characters and their polarities.

obliterated many obvious synapomorphies, a situation that requires a more intensive analysis. Some systematists do, in fact, favour a monophyletic origin for arachnids (Firstman, 1973; Yoshikura, 1975). Perhaps the most convincing and useful of these hypotheses is that of Weygoldt & Paulus (1979*a, b*), a phylogeny constructed with cladistic methodology (Fig. 1, Table 1). This cladogram will serve as the framework within which information relevant to the evolution of the spinning apparatus will be interpreted and integrated. The viability of any hypothesis generated from this information will be subject to modification or falsification of relevant portions of Weygoldt & Paulus' phylogenetic reconstruction.

There are weak spots in this phylogeny which the authors themselves recognize, the most apparent being the interrelationships of the apulmonate orders (Palpigradi, Pseudoscorpiones, Solifugae, Opiliones, Ricinulei, Acari). Fortunately, the precise arrangement of the apulmonate taxa among themselves does not appear to be crucial to the question at hand. However, whether the Palpigradi should be placed among the apulmonates at all is debatable and potentially significant to the present discussion. Several authors associate this taxon with Megoperkulata (Araneae, Amblypygi, Uropygi) because of similarities with uropygids (Savory, 1971; Yoshikura, 1975). The basis of this dispute appears to be uncertainty as to whether the terminal opisthosomal flagellum in palpigrades and uropygids represents a symplesiomorphy, synapomorphy or convergence. To be on the safe side, I will give some special attention to palpigrades when conducting out-group comparisons.

Table 1. *Polarities of characters used in the construction of Weygoldt & Paulus' (1979a, 1979b) cladogram of Arachnida (see Fig. 1)*

Apomorphic state	Plesiomorphic state
1. Pre-oral digestion	Intraintestinal digestion
2. Malpighian tubules	No Malpighian tubules
3. Compound eyes reduced to 5 pairs of lateral eyes	Compound eyes well developed
4. Slit sense organs	No slit sense organs
5. Pectines, etc.	No pectines
6. Retinula cells form a network of connected rhabdomeres	Closed rhabdomeres, star-like in cross section
7. Coiled spermatozoa	Elongate, flagellate spermatozoa
8. Lyriform organs	Only single slit sensilla
9. First leg pair used as feelers	—
10. Chelicerae subchelate with 2 articles	Chelicerae chelate with 3 articles
11. Spermatozoa with 9 + 3 flagellum	Spermatozoa with 9 + 2 flagellum (retained only in pseudoscorpions)
12. Camarostome	Palpal coxae not fused
13. Prenymph and 4 nymphal instars	Number of instars larger, variable
14. Female grasps male opisthosoma during mating	No such mating behaviour
15. Petiolus	Pro- and opisthosoma broadly fused
16. Post-cerebral pumping pharynx well developed	Post-cerebral pumping pharynx not well developed
17. 1st leg pair antenniform	1st leg pair not antenniform
18. Spinnerets	4th and 5th opisthosomal segments without appendage rudiments
19. Copulatory palpal organs	No copulatory organs, indirect sperm transfer
20. Chelicerae with poison glands	Chelicerae with no poison glands
21. Reduction of body size	Body size not reduced
22. Reduction of book-lungs	Book-lungs present
23. Lateral eyes reduced to 2 or 3 pairs	5 pairs of lateral eyes
24. Simple coxosternal region with terminal mouth	Smaller number of sternites, mouth not terminate
25. Tracheae (?)	No respiratory organs
26. Caudal flagellum lost	Caudal flagellum present

With respect to the origin of the spinning apparatus in spiders, the most important conclusions of Weygoldt & Paulus' hypothesis are

- (1) Arachnida is monophyletic.
- (2) Scorpiones is the sister group of all other arachnids.
- (3) Uropygi, Amblypygi and Araneae form a monophyletic group (Megopericulata).
- (4) Megopericulata is the sister group of Apulmonata.
- (5) Amblypygi is the sister group of Araneae.

The claim that Arachnida is a natural taxon is perhaps the most controversial of these conclusions. This hypothesis is based on the presence of four synapomorphies: pre-oral digestion, Malpighian tubules, slit sense organs and five pairs of lateral eyes representing the remnant of a compound eye. One might also include the presence of book-lungs (Størmer, 1977). Three of these features (pre-oral digestion, Malpighian tubules, book-lungs) are associated with a terrestrial lifestyle, thus leading to the conclusion that arachnids were derived from a common terrestrial ancestor. Decae (1984) has argued that pre-oral digestion should not be considered a terrestrial adaptation since many marine invertebrates use similar mechanisms without substantial dilution of the chemicals involved. However, this observation does not falsify the hypothesis of common terrestrial ancestry of arachnids.

There is little reason to doubt that Megoperculata is a natural taxonomic group. The synapomorphies uniting the Araneae, Amblypygi and Uropygi are quite convincing and no one has seriously questioned this relationship. In the past, there has been some confusion over whether Amblypygi should be considered the sister group of Uropygi or Araneae, although most recent authors favour the latter (Savory, 1971; Yoshikura, 1975; Platnick & Gertsch, 1976; Kraus, 1976; van der Hammen, 1977). Recent studies of the spermiogenesis and sperm structure in Megoperculata support the sister group status of Amblypygi and Araneae (Tripepi & Saita, 1985). (Traditional use of the post-cerebral pumping pharynx in uniting Araneae and Amblypygi may not be justified. There is evidence that such a mechanism is present in a vestigial state in Uropygi (Pocock, 1902; Millot, 1949*d*), Scorpiones (Millot & Vachon, 1949*a*), and Solifugae (Millot & Vachon, 1949*b*). An apparent post-cerebral pumping pharynx in palpigrades has been described by Rucker (1901), although Millot (1942*a*) believes this interpretation may be in error. These observations suggest that a post-cerebral pumping pharynx is plesiomorphic in Megoperculata and therefore inappropriate for use in determining relationships among the orders.)

III. ORIGIN OF SPINNERETS

(1) *In-group analysis*

Spinnerets appear to arise embryologically from the same longitudinal series of 'limb buds' which give rise to the prosomal appendages (chelicerae, pedipalps, walking legs) (Dawydoff, 1949). Therefore, these extremities can be considered iteratively (metamerically) homologous as derivatives of segmental appendages. As a result, there have been several inconclusive attempts to homologize the muscles of the spinnerets with those of the prosomal appendages (Brown, 1945; Whitehead & Rempel, 1959). Interestingly, the spinnerets of tarantulas can be seen to move in time with the walking legs during locomotion (Seyfarth in Foelix, 1982), implying that these appendages share a serially arranged motor control mechanism as well as similar developmental origins.

The spinnerets of most spiders are located at the posterior end of the opisthosoma near the anus. However, these structures actually originate on the fourth and fifth opisthosomal segments (there are twelve in all) and migrate rearward during development (Marples, 1967). The orientation of setae and coloration in some spiders provide external evidence of this displacement (Foelix, 1982; personal observations). A few spiders retain a more anterior placement of the spinnerets throughout life. Members of the suborder Mesothelae are thought to represent a primitive grade in spider evolution, retaining a clearly segmented opisthosoma as well as a more anterior position of the spinnerets (Fig. 2). This evidence suggests that the spinnerets of the ancestral spiders were positioned closer to the genital opening (second opisthosomal segment) than to the anus.

The number of spinnerets varies from group to group. *Liphistius* (Mesothelae) has the most, two pairs on both the fourth and fifth opisthosomal segments, and this is considered the primitive condition. Each segment bears a large pair of lateral spinnerets and a small pair of medial spinnerets. The anterior medial pair are apparently functionless in the Mesothelae and essentially absent in all other spiders. Mygalomorph (tarantula-like) spiders tend to lose the anterior lateral pair, as well (see Marples, 1967

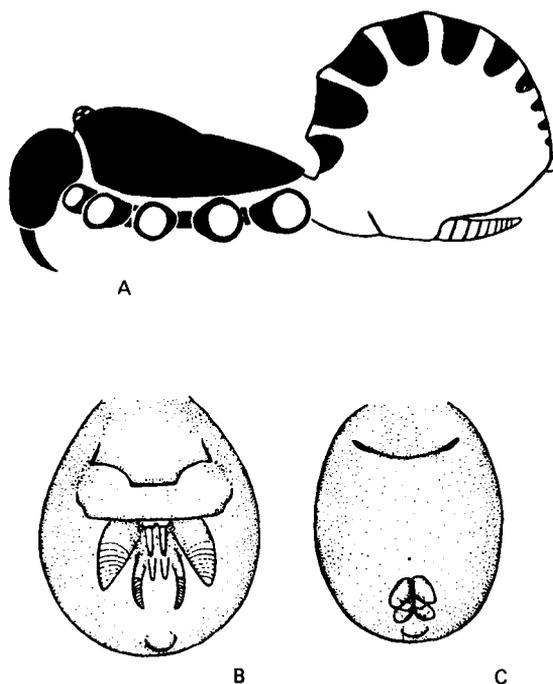


Fig. 2. (A) A lateral view of a 'primitive' spider, *Liphistius* (suborder Mesothelae) showing segmentation of the opisthosoma and anterior placement of the spinnerets (based on Foelix, 1982). (B) Ventral view of the opisthosoma of *Liphistius* showing the number and arrangement of spinnerets (after Marples, 1967 and Platnick & Sedgwick, 1984). (C) Ventral view of the opisthosoma of a generalized araneomorph spider showing the posterior placement of the spinnerets and the absence of the anterior medial pair.

for details). Some araneomorph ('modern') spiders have a special spinning structure, the cribellum, located between the anterior lateral spinnerets which may represent a functional derivative of the anterior medial spinnerets. Other spiders have a small protuberance, the colulus, that is thought to be the remnant of the anterior medial spinnerets or cribellum. Marples (1967) has suggested that the medial spinnerets are not homologous with the segmental appendages but are instead special features associated with the evolution of silk glands. However, these spinnerets do arise from the same limb buds as the lateral spinnerets and share appendicular musculature with them (Machado, 1944; Brown, 1945; Whitehead & Rempel, 1959).

(2) Out-group analysis

The spinnerets of spiders are thought to represent evolutionary derivatives of exopodites and endopodites of biramous opisthosomal appendages similar to those still found in certain arthropods (Petrunkevitch, 1942; Kaston, 1964). Well-developed posterior appendages are common in primitively aquatic arthropods, such as *Limulus* and crustaceans, where they function in generating water currents for swimming, respiration or filter-feeding. Terrestrial arthropods, however, tend to lose segmental extremities not involved in locomotion or manipulation of food. Spinnerets are an obvious exception to this trend. No adult arachnid other than spiders bears such 'primitive' appendages on the fourth and fifth opisthosomal segments, yet spiders are

considered a derived arachnid taxon and the possession of spinnerets is generally regarded as their most apparent autapomorphy. As argued above, it seems likely that arachnids are monophyletic and primitively terrestrial, and this is a virtual certainty for Megoperculata. This situation suggests that the first arachnids had opisthosomal appendages and all but spiders lost them subsequent to the divergence of scorpions, apulmonates, uropygids and eventually amblypygids from the evolutionary path leading to the Araneae (see Fig. 1).

What selective pressures maintained opisthosomal appendages for eventual specialization as spinnerets? Perhaps the opisthosomal spinning apparatus evolved very early in arachnid history and was lost by all taxa but spiders. Fossil tarsi equipped with specialized setae and median claw like those of modern spiders imply that arachnids were handling silken threads as early as the Devonian (Shear *et al.*, 1984), but even this was after the radiation of most or all modern arachnid orders (Størmer, 1969; Shear *et al.*, 1984). However, there may be other possibilities.

Spiders are not the only arachnids with opisthosomal structures derived from segmental appendages. Such structures can be categorized as either sensory appendages or gonopods. Only the pectines of scorpions can be categorized as sensory organs. These paired comb-shaped structures are derived from appendages of the second opisthosomal segment (Weygoldt & Paulus, 1979*a*). All other examples of retained opisthosomal extremities function in the handling of genital products and are correspondingly derived from the second opisthosomal (genital) segment.

Appendages or appendage-like structures associated with the genital opening are widespread among arachnids. In the Amblypygi (the sister group of spiders), both sexes bear gonopods hidden beneath the genital operculum, a ventral plate-like structure thought to represent a modification of the base of the primitive chelicerate appendage (Weygoldt, 1975*b*). In males, each gonopod develops from the fusion of two appendage-like lobes, a medial and lateral lobe (Weygoldt, Weisemann & Weisemann, 1972). Thus, these structures pass through a stage reminiscent of the medial and lateral spinnerets of spiders. The male gonopods function in the formation of the spermatophore. Similar organs, although much reduced, may be present in male uropygids (Weygoldt, 1972). The gonopods of female amblypygids are similar to those of the male in gross position but are composed of only one lobe each. These structures appear to serve in manipulating the spermatophore and in forming the parchment-like egg sac which the female carries on the ventral surface of her opisthosoma. In some species, the female gonopod terminates with a claw-like sclerite which may aid in opening the spermatophore (Weygoldt, 1972).

Female pseudoscorpions are similar to female amblypygids in having a pair of gonopods and using them in constructing the egg sac and, perhaps, receiving the spermatophore. Males do not retain recognizable genital appendages, although the muscles of the genital region responsible for shaping the spermatophore are of appendicular origin (Legg, 1974).

The evolutionary origins of accessory genital structures (genital papillae of male scorpions, penis and ovipositor of opilionids, appendage-like structures in palpigrades) are more problematical, but there is a possibility that some of these were also derived from segmental appendages.

In summary, no arachnid other than spiders bears appendages on the fourth and fifth

opisthosomal segments. While there are no direct homologues to the opisthosomal extremities of spiders among their living relatives there are numerous serial homologues. The primary selective force retaining these appendages is the need to manipulate genital products.

(3) *Convergence analysis*

The spinnerets of spiders are known to be derived from segmental appendages and, so, it is probably not worthwhile enumerating the probable origins of all appendage-like structures involved with the manipulation of silk in non-arachnid arthropods. In some cases, these are also of appendicular origin – for instance, the prolegs of certain chironomid (Diptera) larvae (Webb, Wilson & McGill, 1981) – or are relatively unspecialized locomotory appendages, as in Embioptera or female hydrophiloids (Coleoptera). These convergences, while interesting, add no new information to the problem of spinneret origins in spiders.

On the other hand, the evolutionary morphology of Uniramia (myriapods, hexapods) may be useful in a different sense. Uniramians apparently descended from ancestors with numerous appendages, a condition retained in myriapods (Weygoldt, 1986). Like arachnids, the hexapod classes rely on a few pairs of anterior segmental appendages for feeding or locomotion and tend to eliminate posterior (abdominal) appendages. Exceptions to this trend may provide insight into the kinds of selective pressures that maintain non-locomotory posterior appendages. This information could be useful in formulating hypotheses about why opisthosomal appendages of the spider ancestor were available for specialization as spinnerets.

The non-locomotory abdominal appendages of hexapods can be classified into three groups: styli, sensory structures, gonopods. Styli are small paired appendicular derivatives found on certain anterior abdominal segments in several groups of apterygote hexapods (Protura, Archaeognatha, Thysanura, Diplura) (Chapman, 1982). They are typically associated with eversible vesicles, thin-walled protrusible sacs thought to function in water absorption (Edney, 1977). (Palpigrades and amblypygids possess eversible vesicles which may be derived from appendages, as well (Weygoldt & Paulus, 1979a).) The eleventh abdominal segment of many hexapods bears a pair of sensory appendages, the cerci. These are modified or lost in many 'higher' pterygote orders (Chapman, 1982). Segmental appendages of the eighth and ninth abdominal segments, when present, are modified as organs of sperm transfer in males or ovipositors in females (Snodgrass, 1935; Scudder, 1971; Chapman, 1982). Thus, the selective pressures serving to retain posterior segmental appendages in hexapods (sensing the environment and manipulating genital products) are essentially the same as those already suggested for arachnids.

IV. ORIGIN OF SILK GLANDS

The evolutionary derivation of silk glands in spiders is a mystery. While most workers accept the notion that spinnerets are derived from segmental appendages and are thus, in some sense, iteratively homologous with prosomal appendages, there are no known phylogenetic or iterative homologues of silk glands. As a result, ideas concerning the origin of these structures are highly speculative. Below I will outline two suggestions for the origin of silk glands and explain why I consider them to be inadequate.

(1) *Hypotheses for the origin of silk glands*

(a) *The coxal gland hypothesis*

Coxal glands are paired, segmentally arranged organs characteristic of chelicerates and certain other arthropods. Each coxal gland is composed of a thin-walled filtration chamber (saccule) which is drained by a convoluted tubule (labyrinth). The labyrinth is continuous with a cuticular duct that opens to the exterior through a pore located near the coxa of certain segmental appendages. A simple metameric arrangement was probably the primitive condition, but the number and position of coxal glands among living arachnids varies from group to group. Mygalomorph spiders have two interconnected pairs of glands which exit at the bases of the first and third walking legs. In most other spiders, only those coxal glands associated with the first leg pair are retained, and there is a tendency toward greater simplification in these (Buxton, 1913). Coxal glands appear to function in ion and water balance. The saccule acts to filter the haemolymph and the labyrinth appears to concentrate the coxal fluid (Edney, 1977).

Several arachnologists have suggested that the silk glands of spiders are derived from coxal glands associated with the opisthosomal appendages that were eventually to evolve into spinnerets (e.g. Bristowe, 1958; Kaston, 1964; Gertsch, 1979). Although proponents of this idea do not usually provide a rationale to support their view, there are several reasons why one might believe that silk glands evolved from coxal glands. For instance, both coxal glands and the ampullate silk glands of some spiders exit the body via cuticular ducts that are supplied with dilator muscles of appendicular origin (Whitehead & Rempel, 1959). Also, the coxal glands of certain mites are often suggested as being the site of silk production in these animals (e.g. Woodring, 1973). Perhaps the primary attraction of this notion is its congruence with historical narratives which maintain that silk evolved from a waste material (e.g. Savory, 1952; Bristowe, 1958).

Several lines of evidence speak against this reasoning. (1) The saccule and labyrinth of coxal glands are derived embryologically from evaginations of the coelom (coelomoducts) and are therefore composed of tissue of mesodermal origin (Beklemishev, 1969; Clarke, 1979). Silk glands, however, are derived from ectoderm (Foelix, 1982). (2) The ampullate glands, those silk glands bearing some similarity to coxal glands, do not appear to be the most primitive type of silk gland (see below). (3) Using mites as an example of how silk glands might evolve from coxal glands may not be appropriate. The silk of bdellid mites emerges from the podocephalic canal, a duct which drains a number of different glands. Although a true coxal gland is associated with this complex, Alberti (1973) does not consider it to be involved with silk production. He has identified several other podocephalic glands as probable silk glands. (4) Although one could consider nitrogenous waste to be a potential silk precursor (Rudall & Kenchington, 1971), coxal glands do not appear to be a primary site of nitrogenous waste excretion as some authors imply (e.g. Meglitsch, 1967). Instead, these organs are used for osmoregulation and ion excretion in most chelicerates (Edney, 1977; Towle *et al.*, 1982) and this is probably the primitive function (Clarke, 1979). In any event, it would seem a large evolutionary leap for an osmoregulatory organ to acquire the ability to manufacture silk. How might an ionic excretion evolve into a proteinaceous secretion with an amino acid sequence dictated by the genetic apparatus of the cells composing a coxal gland?

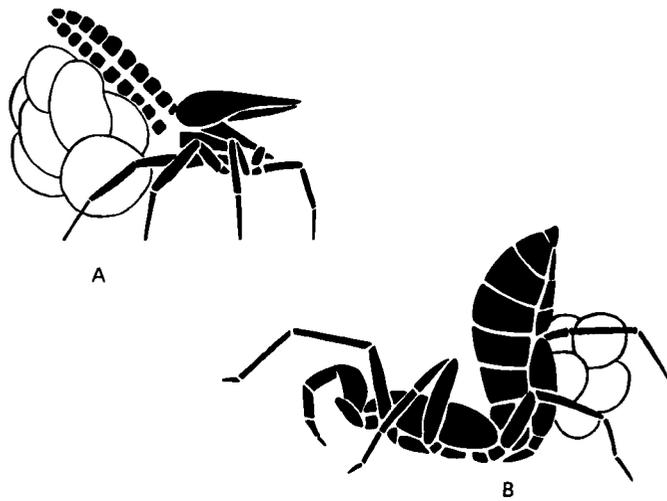


Fig. 3. Female pseudoscorpion (A) and schizomid (*Uropygi*) (B) with brood sacs attached to the ventral surface of the opisthosoma at the genital opening (after Vachon, 1949 and Millot, 1949*d*).

(b) *The amblypygid egg sac hypothesis*

Females of several arachnid orders brood their eggs within a protective sac attached to the ventral surface of their opisthosoma. This behaviour is characteristic of amblypygids (Millot, 1949*a*; Alexander, 1962), uropygids (Millot, 1949*d*; Rowland, 1972), pseudoscorpions (Weygoldt, 1969) and perhaps ricinuleids (Millot, 1949*c*) and may prove to be a synapomorphy of the non-scorpion arachnids (Weygoldt & Paulus, 1979*b*). Egg sacs of uropygids and most pseudoscorpions are membranous and relatively large (Fig. 3). The female is typically immobile while brooding and remains within a burrow (*Uropygi*) or silken chamber (*Pseudoscorpiones*). In amblypygids and some pseudoscorpions (Cloudsley-Thompson, 1958), the egg sac is smaller and tougher, allowing the female to remain active while protecting the eggs.

The search for the evolutionary origins of silk glands in spiders should include an examination of the spider's sister group (*Amblypygi*) for possible silk gland homologues. Because the egg sac is the most obvious external construction of the amblypygids, the organ responsible for its formation would seem a likely candidate. Indeed, the walls of the amblypygid egg sac are invested with a filamentous material and the sac is anchored to the female's body by threads. Pocock (1895), realizing the importance of amblypygids to understanding evolution in spiders, hypothesized that the filaments of the amblypygid egg sac were in some way homologous with the silken threads of spiders. Thus, he concluded that silk was originally used by spiders for protecting the eggs.

Comstock (1912) knew the potential significance of the amblypygid egg sac, as well, but was not so bold in his interpretation, noting that the source of the material had not been determined. (Although Bernard (1896) claimed to have found the spinning glands of amblypygids, Börner (1902: 91) dismissed Bernard's observations as being "...ein Product seiner Phantasie.") More recent studies have shown that Comstock's caution was warranted. Weygoldt *et al.*, (1972) have investigated the source of the filaments associated with the amblypygid egg sac and found them to be the product of certain

cells within the ovary and oviducts. Like coxal glands, the reproductive tract of arachnids develops as a coelomoduct and its tissues are of mesodermal origin. Since silk glands in spiders are derived from ectoderm, it is very unlikely that the filaments produced by female amblypygids are homologous with the silk of spiders. (Interestingly, Balbiani (1897) has reported that the ovaries and oviducts of spiders secrete granules composed of a substance similar to fibroin silk. He suggests that the granules adhere to the surface of the eggs and cement them together while in the egg sac. These granules are probably the same structures discussed more recently by Humphreys (1983).)

(2) *In-group analysis*

The silk glands of spiders occur in a variety of types which differ in shape, function and histochemistry. Some types are virtually universal while others are characteristic of a single family. No single species possesses all forms. The kinds of silk glands which predominate among araneomorph spiders have been classified according to their general shape and function (Table 2), but this classification does not accommodate all types known.

The simplest, and perhaps most primitive, complement of silk glands occurs in certain mygalomorph spiders (*Antrodiaetus*, *Euagrus*, some theraphosids). The glands are simple spherical to pear-shaped structures. Each consists of a wall formed by a single-layered columnar epithelium surrounding a central lumen, which serves to store the proteinaceous secretion of the epithelial cells. The secretion leaves the glands through cuticular ducts that open to the exterior via specialized hollow setae (the spigots or fusules). Two regions can be defined histochemically within the gland, each region producing a different secretion. The proximal hemisphere (the end nearest the cuticular duct) secretes a basophilic protein and the other end produces acidophilic proteins. These substances apparently combine within the duct during silk extrusion and may form functionally distinct components of the silken strand (Palmer, Coyle & Harrison, 1982).

The simple glands of *Antrodiaetus* and the other mygalomorphs are most similar to the aciniform or pyriform glands of the traditional scheme of silk gland classification. These glands are also simple in shape and have two histochemically distinct zones (Glatz, 1972, 1973; Kovoov, 1977; Kovoov & Zylberberg, 1980). They are found in virtually all spider groups. In araneomorphs they are used principally in the construction of egg sacs and sperm webs (aciniform) or egg sacs, attachment discs and swathing silk (pyriform) (Kaston, 1964; Richter, 1970; Foelix, 1982). Interestingly, Richter (1970) has noted that, in the earlier stages of their development, the tubuliform glands of lycosid spiders are virtually indistinguishable from aciniform glands. This observation suggests that the aciniform type is the more generalized of the two.

Many adult male spiders have additional silk glands which are not associated with the spinnerets but occur on the anterior margin of the genital furrow (Marples, 1967). They are termed epiandrous glands by Marples, but authors of more recent studies prefer to call them epigastric glands (Legendre & Lopez, 1971, 1981; Legendre, 1972). These glands are found in all major groups: liphistiomorphs (Mesothelae) (Legendre & Lopez, 1981), mygalomorphs (Melchers, 1964; Marples, 1967; Legendre, 1972) and araneomorphs (Machado, 1951; Marples, 1967; Foelix, 1982). Like 'true' silk glands, the epigastric glands exit the body through cuticular ducts which usually lead to specialized hollow setae. Although there is some diversity in the shape, placement and,

Table 2. *A general list of the types of silk glands found in araneomorph spiders (modified from Foelix, 1982)*

Silk gland	Associated spinnerets	Function of Silk
Pyriiform	Anterior lateral	Attachment disc
Ampullate	Anterior lateral	Drag-line, frame thread
	posterior medial	
Aciniform	Posterior medial	Swathing silk, parts of sperm web,
	posterior lateral	outer wall of egg sac
Tubuliform	Posterior medial	Inner wall of egg sac
	posterior lateral	
Epigastric	None (associated with	Parts of sperm web
	male genital opening)	
Aggregate*	Posterior lateral	Viscid droplets of spiral
Flagelliform*	Posterior lateral	Ground thread of spiral

* In orb weavers (Araneidae, etc.).

perhaps, function of these glands, several lines of evidence suggest that their primitive function is the production of silk and that they are iteratively homologous with 'true' silk glands (Legendre & Lopez, 1971; Legendre, 1972). Their shape is reminiscent of the aciniform glands. The epigastric secretion appears to form that portion of the sperm web on which the seminal fluid is deposited (Melchers, 1964) and may be analogous to the primitive arachnid spermatophores.

(3) *Out-group analysis*

Pseudoscorpions and certain mites (Bdellidae, Tetranychidae) are the only living arachnids other than spiders to have developed the ability to spin silken threads. Unlike spiders, the silk glands in these animals are associated with the mouthparts (chelicerae in pseudoscorpions and pedipalps in mites). The differences in the positions of the glands and the great phylogenetic distances between spiders, pseudoscorpions and mites make it unlikely that the silk-producing organs of these three taxa are homologous as silk glands. However, Bristowe (in Kaston, 1964) has hypothesized that the venom glands of spiders are remnants of a cheliceral spinning apparatus, such as occurs in pseudoscorpions. It has been suggested that the gummy secretion used by the spitting spiders, *Scytodes* (Scytodidae), represents a sort of transitional stage between cheliceral venom glands and the primitive silk glands. Also, salivary secretions are used by some spiders in the construction of brood chambers and pseudoscorpions build brood chambers with their cheliceral silk (Kaston, 1964). Again, such a scenario is confounded by the phylogenetic distance between spiders and pseudoscorpions, but this does not mean that cheliceral venom and silk glands are not homologous at some level, perhaps as salivary glands.

Opisthosomal glands of various types occur in several arachnid orders. The functions of some are known (such as the defensive glands of uropygids), but the adaptive value of some of the more intriguing forms is not. Females of some palpigrade species, for instance, have ventral opisthosomal glands which resemble certain silk glands of spiders (Millot, 1942a). The glands are arranged into two groups, one associated with the ventral surface of the fourth opisthosomal segment (anterior ventral glands) and the other with the sixth opisthosomal segment (posterior ventral glands). Each set of glands

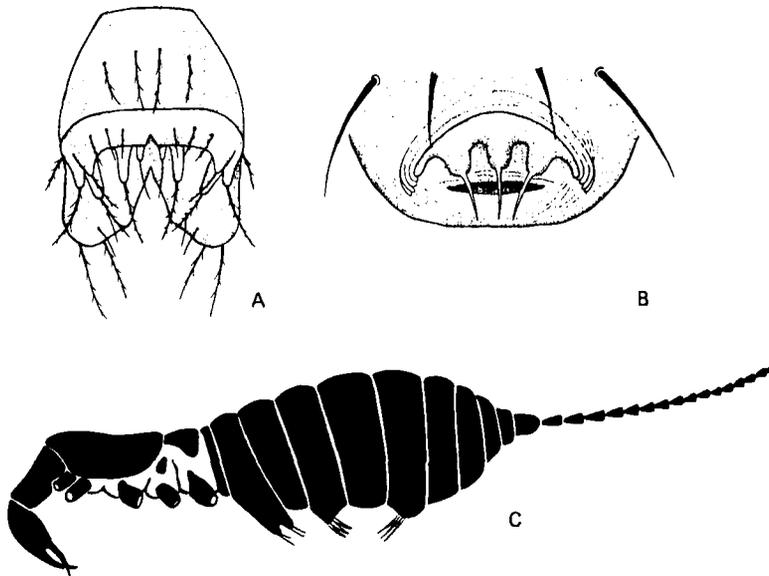


Fig. 4. (A) Ventral surface of genital segment in a male palpigrade showing fusule-like structures surrounding the genital opening (after Rucker, 1901). (B) Ventral surface of the opisthosoma of a male spider (Ochyroceratidae) showing fusules associated with epigastric silk glands (after Machado, 1951). (C) Lateral view of a female palpigrade showing fusule-like projections on the ventral surface of opisthosomal segments four and six (based on Millot, 1949*b*). Glands similar in structure to the silk glands of spiders are associated with these projections.

is associated with a field of stout hollow setae through which the glandular product is released (Fig. 4). The setae associated with the posterior glands are longer than those of the anterior glands. The composition and function of the glandular product is unknown. The cells of the anterior glands appear to have both acidophilic and basophilic properties, while those of the posterior glands are always acidophilic. In addition, Machado (1951) has noticed a similarity between the fusules associated with the epigastric glands of some male spiders and the genital papillae of male palpigrades (Fig. 4). Although these similarities are interesting, virtually nothing is known about the evolutionary morphology or reproductive habits of Palpigradi. Because many systematists consider palpigrades to be the sister group of Megoperkulata, investigation of ventral opisthosomal glands of the female and genital papillae of the male may prove valuable in understanding the evolution of spinning in spiders.

In some solifugids, the ventral surface of the opisthosoma is dotted with fields of glands strikingly similar to the ventral glands of palpigrades and certain silk glands of spiders (Millot, 1942*b*). Each gland is composed of cells which secrete a granular substance into a central lumen. The drawings that accompany Millot's description appear to show two different cell types, one type located at the distal hemisphere and the other located proximally. The lumen of each gland opens to the exterior through a hollow seta or spine. The glands are most numerous on the second (genital), third, fourth and fifth opisthosomal segments. Millot did not investigate sexual differences but considers the glands to be homologous with the ventral opisthosomal glands of female palpigrades. I am not aware of any information on the function of any of these structures.

Glands of various types are also associated with the genital opening of many arachnids. Accessory genital glands in the males of some arachnid orders are used, in part, for the production of spermatophores. The spermatophore typically consists of a supporting stalk with a terminal capsule containing the sex cells. The structure of the capsule can be quite complicated; the shape may be species-specific (Weygoldt, 1975 *a*). Stalked spermatophores are used for indirect sperm transfer by scorpions, uropygids, amblypygids, pseudoscorpions and some mites, indicating that the ancestors of spiders probably did so, as well. Alexander & Ewer (1957) have suggested that sperm webs replaced the use of spermatophores during the evolution of the two-step mating process (sperm induction and copulation) in spiders. Is it possible that the spermatophore and the sperm web are homologous in some way? Interestingly, the spermatophore stalk produced by male pseudoscorpions has been found to be composed of a fibroin or fibroin-like protein (Hunt & Legg, 1971; Legg, 1975). Unfortunately, the composition of the spermatophore used in those orders most closely related to spiders (Amblypygi and Uropygi) is not known.

As I noted before, it has been hypothesized that the material used by female amblypygids for constructing the egg sac may provide a homologue to spider silk. I have argued that this is unlikely. Weygoldt (personal communication) considers the egg sac of amblypygids to be a specialization that allows mobility of the female while brooding. He suggests that the soft egg sacs of uropygids and pseudoscorpions may be more useful in this context. However, few details are available concerning the formation of these structures.

(4) *Convergence analysis*

The silk-producing organs of myriapods and hexapods have tended to evolve from three primary sources: salivary (labial) glands, colleterial (genital) glands and Malpighian tubules (Rudall & Kenchington, 1971). This classification does not include all silk glands found among the uniramian arthropods, but it accounts for the majority (see Table 3 for a more complete list). In general, the larvae of holometabolous hexapods produce silk for cocoons from organs derived from labial glands or Malpighian tubules. A few use a silk-like substance produced from a modified peritrophic membrane. Many adult arthropods have glands associated with the genital opening which produce a variety of materials for protecting eggs (Hinton, 1981) or transferring sperm (Schaller, 1971). Silk in mature myriapods and hexapods is produced almost exclusively by such genital glands.

V. ORIGINAL SELECTIVE PRESSURES FAVOURING EVOLUTION OF SILK

(1) *In-group analysis*

It is disappointing that spider silk does not seem to fossilize well. However, we can console ourselves with the fact that even if we had the first silken thread in hand fresh from some Devonian swamp, we would probably be no closer to understanding the function for which it was intended, that is, the selective pressures which brought about its evolution. So, investigators are forced to survey the uses of silk among living spiders (Table 4) in the hope that one of these uses will somehow reveal itself as being the most primitive. Conclusions are often drawn from such analyses, but they are not always satisfying. For instance, several arachnologists have hypothesized that the original

Table 3. *A list of arthropod taxa other than spiders which are known to produce silken threads or fibroin-like proteins along with sites of silk production and the function of the secretion*

Taxon	Gland type	Function	Source
Arachnida			
Pseudoscorpiones (all)	Cheliceral glands	Moult, brood chambers	Weygoldt, 1969
<i>Chthonius</i> (male)	Genital glands	Spermatophore*	Hunt & Legg, 1971
<i>Serianus</i> (male)	Anal glands	Sperm web	Weygoldt, 1966
Acari			
Tetranychidae	Podocephalic glands	Egg protection, humidity regul., etc.	Gerson, 1979
Bdellidae	Podocephalic glands	Prey capture, egg protection, moult chamber	Alberti, 1973
Myriapoda			
Pauropoda (male)	Genital glands	Sperm web	Schaller, 1971
Diplopoda			
Pselaphognatha (male)	Genital glands	Sperm web	Schaller, 1971
Nematophora (female)	Pre-anal glands	Egg sac	Enghoff, 1984; Barnes, 1980
Chilopoda			
Geophilomorpha (male)	Genital glands	Sperm web	Lewis, 1981
Scolopendromorpha (male)	Genital glands	Sperm web	Lewis, 1981
Lithobiomorpha (male)	Genital glands	Sperm web	Lewis, 1981
Hexapoda			
Apterygota			
Archaeognatha (male)	Genital glands	Sperm thread	Schaller, 1971
Thysanura (male)	Genital glands	Sperm thread	Schaller, 1971
Pterygota			
Dictyoptera			
Mantidae (female)	Genital glands	Egg sac*	Rudall & Kenchington, 1971
Psocoptera (all)	Labial glands	Protect eggs & early instars	Wigglesworth, 1975
Embioptera (all)	Tarsal glands	Tunnels in soil	Imms, 1929
Thysanoptera (larvae)	Abdominal glands	Resting chamber	Lewis, 1973
Neuroptera (larvae)	Malpighian tubules	Cocoon	Rudall & Kenchington, 1971
<i>Chrysopa</i> (female)	Genital glands	Egg stalk*	Rudall & Kenchington, 1971
Coleoptera (larvae)	Malpighian tubules labial glands	Cocoon, burrows	Rudall & Kenchington, 1971; Crowson, 1981
Hydrophiloidea (female)	Genital glands	Egg sac	Crowson, 1981
Diptera			
Empididae (male)	Tarsal glands	Prey wrapping (courtship)	Oldroyd, 1965
Simuliidae, Tipulidae, Chironomidae (larvae)	Labial glands	Cocoon	Oldroyd, 1965
Mycetophilodae (larvae)	Labial glands	Cocoon, tunnels, webs, snares	Oldroyd, 1965
Siphonaptera (larvae)	?	Cocoon	Imms, 1929
Lepidoptera (larvae)	Labial glands	Cocoon, cases, webs, drag lines	Chapman, 1982
Trichoptera (larvae)	Labial glands	Cocoon, cases, webs, drag lines	Wiggins, 1984
Hymenoptera (larvae)	Labial glands	Cocoons	Chapman, 1982
<i>Psenolus</i> (female)	?	Brood cell cover	Wigglesworth, 1975

* Indicates a fibroin not in the form of threads.

Table 4. *A listing of some general uses of spider silk (modified from Kaston, 1964)*

- I. Linear constructions
 - (A) Drag-lines
 - (B) Parachute or ballooning threads
 - (C) Signal threads or 'fishing' lines
- II. Ribbons or two-dimensional structures
 - (A) Attachment discs or anchors
 - (B) Prey wrapping
 - (C) Hackle-band of cribellate spiders
 - (D) Sperm web
- III. Three-dimensional structures
 - (A) Snare or web
 - (B) Egg sac
 - (C) Nest or retreat
 - (1) Simple tube
 - (2) Silk-lined excavation
 - (3) Retreat near web
 - (4) Hibernating chamber
 - (5) Moulting chamber
 - (6) Nursery for spiderlings

function of silk was protection of the eggs (Pocock, 1895; Comstock, 1912; Bristowe, 1958; Gertsch, 1979). This conclusion is often based on the fact that females of virtually all spider species wrap their eggs with at least a few silken strands, and one would expect the most primitive state of a feature to be the most widespread ('commonality principle').

Whether the egg protection idea is valid or not, the logic typically used to support it may be faulty. The construction of egg sacs is not the only use of silk common to a wide variety of spider groups. For example, use of a sperm web of some sort is probably universal among male spiders since the pedipalps cannot reach the genital opening directly (Petrunkevitch, 1952). The use of sperm webs has been observed in liphistiomorphs (Haupt, 1979), mygalomorphs (Melchers, 1964; Minch, 1979) and araneomorphs (Foelix, 1982). The drag-line is also used by a variety of spiders, including liphistiomorphs in some situations (Bristowe, 1976). The lining of burrows or construction of silken tubes or chambers is also widespread (Decae, 1984; Rovner, in press). The 'commonality principle' (common equals primitive) does not provide criteria for choosing among several equally widespread alternatives. In fact, most systematists have abandoned this principle for use in determining character polarity (e.g. Watrous & Wheeler, 1981). There is no reason to believe that a common attribute is necessarily primitive, especially if the feature is highly adaptive. The egg protection hypothesis requires corroboration from other lines of inquiry.

One might also be tempted to approach the problem by examining the spinning habits of spiders which retain primitive morphological features in the hope that these species will display primitive behaviours (Decae, 1984). The reasoning behind this method ('correlation analysis') has been criticized, as well (Stevans, 1980). But even if we assume this reasoning to be valid, those living spiders generally considered most primitive (Mesothelae) use silk for a variety of functions: egg sacs, sperm webs, burrows and tubes, 'fishing lines', securing trapdoors, drag-lines (Klingel, 1967; Bristowe, 1976; Haupt, 1979; Platnick & Sedgwick, 1984). Which adaptation should be chosen

as most primitive and thus indicative of the original selective pressure favouring the evolution of silk? It is my opinion that the kinds of in-group analyses conducted to date (commonality and correlation analysis) do not provide a satisfactory answer to this question.

(2) *Out-group analysis*

Those taxa most closely related to Araneae do not produce silk and are therefore of little value in the attempt to understand the selective pressures which brought this ability into being. The great phylogenetic distances between spiders and the only other arachnid spinners (pseudoscorpions and certain mites) indicate that discussion of these animals should take place in the following section (Convergence analysis). For continuity, however, I will deal with these arachnid taxa here.

Silken threads or fibroin-like proteins have evolved at least three times in pseudoscorpions (Table 3). The primitive function of the cheliceral silk is not known. Here again, there are several alternatives. Among modern pseudoscorpions, this silk is involved primarily with the construction of chambers used in moulting, hibernation and brooding (Weygoldt, 1969). Interestingly, cheliceral silk glands are often reduced or absent in mature males, suggesting that some activity of females (construction of the brood chamber, perhaps) is the most important use of cheliceral silk in adult pseudoscorpions (Snodgrass, 1948). On the other hand, the fibroin or fibroin-like protein which composes the stalk of the spermatophore obviously evolved to enhance manipulation or protection of the spermatozoa (Hunt & Legg, 1971). The anal silk of *Serianus* is apparently used only for guiding the female to the spermatophore (Weygoldt, 1966). Thus, silk has evolved at least twice in pseudoscorpions for use in reproduction.

The silk of mites (spider mites and snout mites) also has a variety of uses: humidity regulation, predator avoidance, egg protection, prey manipulation (Alberti, 1973; Gerson, 1979). But, while the more derived forms are versatile in their use of silk, those thought to be more primitive use silk only for protecting the eggs. "Web production by the Tetranychinae apparently first served to cover and thus protect the eggs; this is the only spinning activity of the Tenuipalpoidini, regarded as the most primitive tribe in the Tetranychinae (Gutierrez *et al.*, 1970)" (Gerson, 1979: 182).

(3) *Convergence analysis*

A brief list of the functions of silk in different arthropod taxa is given in Table 3. This list is not exhaustive but probably provides a good indication of general trends in the use of silk. As in spiders, it is not always possible to identify the original function of silk within a group. However, in many cases, silk is used for only one known function and it seems reasonable to hypothesize that this is the original one. A glance at Table 3 reveals several trends. First, those non-arachnid arthropods using silk to the greatest extent are the larvae of holometabolous hexapods (Neuroptera, Coleoptera, Diptera, Siphonaptera, Lepidoptera, Trichoptera, Hymenoptera). A common feature of these orders is the need to produce a protective covering (cocoon) for the prolonged period of inactivity during metamorphosis. Some groups are quite versatile in their use of silk, but the production of the cocoon appears to be the primitive function.

Silk use among adult arthropods is less common, but when it occurs it is used almost exclusively for reproductive needs. Males in many myriapod and a few apterygote hexapod taxa use silk exclusively for transferring sperm. Because of the close phylo-

genetic relationships of these groups, it would not be surprising if this feature evolved only once. Those female arthropods with the ability to produce silk use it primarily for protecting the eggs. This adaptation has apparently evolved independently within each taxon possessing it. In summary, the selective pressures responsible for the origin and maintenance of silk in most non-arachnid arthropods are the need for protection during prolonged periods of inactivity (e.g. pupation), the need to manipulate male sex cells in those taxa practising indirect sperm transfer and the need of females to protect their eggs.

VI. CONCLUSIONS

In the introduction, I proposed the axiom that those historical hypotheses which approximate reality most closely should be ones that accommodate the most information and which show congruence with the greatest number of other historical hypotheses. From the evidence and reasoning presented above, I suggest that the spinning apparatus of spiders evolved initially for reproductive needs. The rationale for this conclusion is summarized below.

(1) The spinnerets represent modified segmental appendages of the fourth and fifth opisthosomal segments and were therefore originally located nearer to the genital opening (second opisthosomal segment) in the ancestral spiders than their position in most recent adult spiders would suggest.

(2) Those opisthosomal appendages retained by arachnids other than spiders are used primarily as gonopods, manipulating spermatozoa, ova or their containers (spermatophores, egg sacs).

(3) Posterior non-locomotory appendages in terrestrial arthropods other than arachnids are used as sensory structures (cerci) or gonopods.

(4) The primitive silk glands of spiders were probably simple structures similar to the modern aciniform and pyriform types. These gland types appear to be the most generalized and are used, in part, for producing portions of the egg sac and sperm web.

(5) The epigastric (epiandrous) glands of male spiders are used in building sperm webs. They are located on the anterior margin of the genital furrow but are similar to the aciniform glands associated with the spinnerets. Epigastric glands are probably iteratively homologous with 'true' silk glands.

(6) The closest relatives of spiders (Amblypygi and Uropygi) produce spermatophores. Although the composition of these structures is unknown, the spermatophore stalk of pseudoscorpions is composed of a fibroin silk.

(7) Among adults of terrestrial arthropods other than spiders, the use of silk is limited almost exclusively to the production of sperm webs or egg sacs. In those adult arthropods which use silk for multiple functions, the handling of genital products is usually one of them. The primitive function of silk in tetranychid mites was probably for covering the eggs. These facts are evidence for strong selective pressures favouring the use of silk for manipulating or protecting genital products.

There is no reason to deny that this hypothesis fails to explain all relevant facts. It is important, however, to distinguish those facts which do not corroborate this hypothesis from those that falsify it. I do not consider any 'unexplained' facts discussed here to be sufficient for falsifying this hypothesis, although some criterion of falsification must exist. As mentioned before, those historical hypotheses capable of predicting the

outcome of future investigation are ones we might expect to reflect reality. If the predictions are incorrect or impossible to test, the hypothesis should be rejected.

I have generated two hypotheses which are consistent with the proposal that silk evolved for reproductive needs. This is necessary to make the predictions of the hypothesis more concrete.

Spermatophore – sperm web hypothesis

The glands and secretions involved in construction of the spermatophore in the spider ancestor were modified for production of silken threads for use in the construction of sperm webs. Thus, portions of the sperm web and the spermatophore are homologous.

Predictions. (1) The spermatophore of amblypygids and/or uropygids will be found to be composed of a fibroin or fibroin-like protein. (2) The ontogeny of those glands producing spermatophores in amblypygids and uropygids will be found to be similar to that of silk glands in spiders (e.g. they will be derived from ectoderm). (3) Further investigation of epigastric glands will suggest that they are homologous as silk glands in all spiders and that they are iteratively homologous with silk glands associated with the spinnerets.

Egg sac hypothesis

The glands and secretions involved in construction of the egg sac in the spider ancestor were modified for production of silken egg cocoons that could be detached from the opisthosoma. The membranous egg sacs of some arachnids and the egg sacs of spiders are homologous.

Predictions. (1) Comparative studies will lead to the hypothesis that egg sac construction is a synapomorphy of the non-scorpion arachnids or a plesiomorphic feature of Megoperkulata. (2) The egg sacs of uropygids will be shown to be composed of a fibroin or fibroin-like protein. (3) The ontogeny of the glands producing the egg sac in uropygids will be found to be similar to that of silk glands in spiders (e.g. they will be derived from ectoderm).

Critics of these hypotheses may be tempted to argue that each is specific to a particular sex and therefore fails to explain the presence of the spinning apparatus in both male and female spiders (e.g. Decae, 1984). I do not consider this a problem. Sexual dimorphism is typically brought about by the effects of hormones or epigenetic factors on the genetically programmed somatic plan characteristic of a species. In some cases, even the reproductive organs may be virtually identical in both sexes, as in oribatid mites (Woodring, 1970). It is also well known that under certain conditions one sex may manifest the features of the other to various degrees. Thus, if a feature originates in one sex with potential adaptive value for the other, selection may favour the expression of the feature in both. Sexual dimorphism is not a barrier to evolution, but, in fact, may be a source of novelties upon which natural selection can act. The ovipositor–penis complex of opilionids may be the outcome of such a process. The problem, then, is not explaining the transfer of features from one sex to the other but how one determines the sex in which the feature initially arose, a difficulty which I have tried to take into account when formulating the predictions of the hypotheses proposed here.

In conclusion, it is certainly possible that both of the hypotheses I have proposed

will be found wanting or rejected altogether. If so, other hypotheses should be erected from which specific testable predictions can be made. In any event, progress in the problem of the evolutionary origin of the spinning apparatus in spiders can only be made through further research. Additional lines of investigation which may prove useful in this regard include the phylogenetic position of Palpigradi and the apulmonate orders; a greater appreciation for the diversity of behaviour, morphology and natural history in all arachnid orders, especially Amblypygi, Uropygi and Palpigradi; and the ontogeny, morphology and function of ventral opisthosomal glands in palpigrades and solifugids.

VII. SUMMARY

(1) Previous attempts to explain the evolution of spider silk have relied heavily on conjecture. The formulation of testable historical hypotheses to replace such speculation is discussed.

(2) The importance of phylogenetic reconstructions and other historical hypotheses for use in generating and testing hypotheses concerning the evolution of specific adaptations is examined. Recent ideas on arachnid phylogeny are reviewed and their relevance to the problem of silk evolution in spiders is explored.

(3) Evidence from the analysis of three historical problems (origin of spinnerets, origin of silk glands, original selective pressure favouring evolution of silk) is reviewed from three different frames of reference (in-group analysis, out-group analysis, convergence analysis). Several lines of evidence are found which suggest that silk use originated in spiders due to selective pressures associated with reproduction (specifically, the transfer of sperm or the protection of eggs).

(4) The prevalence of segmental appendages retained for use in manipulating genital products in both arachnids and non-arachnid arthropods and the probable placement of spinnerets near the genital opening in ancestral spiders suggest that spinnerets represent modified gonopods.

(5) The most primitive types of silk glands are retained in virtually all spiders, in part, for use in the construction of sperm webs and egg sacs. Similar silk glands are found near the genital opening in many male spiders and used in building a portion of the sperm web.

(6) The silk of adult arthropods other than spiders is used largely in manipulating or protecting sex cells. If there are multiple functions, use in reproduction is typically one of them. Thus, there is evidence for strong selective pressure favouring the evolution of silk for use in reproduction.

(7) Two hypotheses are proposed which are consistent with the conclusion that silk in spiders evolved for reproductive needs (the spermatophore-sperm web and egg sac hypotheses). Testable predictions of each hypothesis are proposed.

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