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A THEORY ON THE ORIGIN OF SPIDERS AND THE PRIMITIVE FUNCTION OF SPIDER SILK

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ABSTRACT

The primitive function of spider silk is commonly thought to have been associated with any of three typical behavior patterns seen in the bulk of spiders today: (1) egg protection, (2) prey capture, and (3) shelter building. It is argued here that a primitive function in egg protection and prey capture must be regarded as very unlikely. Silk production and application is hypothesized to have originated in relation to shelter building and burrowing habits of ancestral spiders then still living in a littoral environment.

INTRODUCTION

Spiders (order Araneae) are commonly referred to as one of the highly successful groups of animals. The statement might be based on either or both of two observations: (1) spiders are ancient and can be recognized as a group since the Devonian period, and (2) representatives of the Araneae are abundant in almost any type of terrestrial habitat. Unquestionably the success of spiders is largely founded on their ability to produce silk and to apply this material in various situations to serve a range of vital purposes.

Since Pocock (1895), theories on the primitive function of spider silk have regularly appeared in arachnological literature (Comstock 1912, Gerhardt and Kaestner 1938, Bristowe 1958, Kaston 1964, Savory 1960, 1977, Gertsch 1979). All such theories are inevitably highly speculative since no paleontological evidence of early spider silk usage is available. The theory presented here is based on recent ideas on arachnid phylogeny and on studies of mygalomorph spiders. In this approach it differs from foregoing theories.

RECENT IDEAS ON ARACHNID PHYLOGENY

According to Savory (1977) the Araneae are one of the seventeen orders that make up the class Arachnida. The taxonomy of the Arachnida has always been complicated because it appears to be impossible to group the orders confidently in a system that would reflect their mutual relationships indicating the course that evolution has followed as the different taxa came into existence. This difficulty in relating the various orders to each other suggests that the Arachnida cannot be seen as a homogeneous group of de-

scendents from one terrestrial ancestor. Nevertheless, using the cladistic method, Weygoldt and Paulus (1979a, 1979b) have recently worked out a classification of Chelicerata which suggests that all arachnid orders in fact stem from one terrestrial ancestor. The key assumption behind their idea is that external digestion of food is a synapomorphous character of the Arachnida. They state that such a feeding-method cannot function in an aquatic environment because digestion products would readily be diluted. Examples of external digestion however are not at all uncommon among marine animals. In particular generalist invertebrate predators such as the Asteroidea are well-known for their capability of digesting prey outside their bodies (Feder 1955, Anderson 1978, Barnes 1980). Active use of abrasive chemicals (enzymes and acids) to "drill" holes or tunnels in hard chalky substrates is a practice that, according to Weygoldt and Paulus' argument, would also suffer seriously from dilution in an aquatic environment. Still, representatives of virtually every phylum use such methods in the sea (Biezenaar 1981). Of course all animals using chemical methods to dissolve or digest material under water show particular adaptations to prevent dilution. There is no reason to believe that early ancestors of the various arachnid orders did not have such adaptations. Most other extant theories on arachnid phylogeny (Kraus 1976, van der Hammen 1977, Savory 1977) proceed from the idea that the class must have been derived from several successful land invasions by different although related forms.

Given this supposed polyphyletic origin of the Arachnida, characteristic features of the constituent orders, unless obvious adaptations to some terrestrial habitat, might well have been present in the particular aquatic forebears. In the case of the Araneae, the spinnerets are believed to be derived from abdominal biramous limbs (Kaston 1964). Such structures, if not modified to respiratory organs, are generally lacking in other Arachnida. Preserving these apparently ancient structures so conspicuously and in association with the very characteristic function of silk production and application is unique and must have separated the spiders at a very early stage from related early arachnids, probably long before the first attempts to colonize the land were undertaken.

AN ETHOLOGICAL REASON TO STUDY 'PRIMITIVE' SPIDERS

Why study spiders? Obviously a large number of different but all very good reasons could be thought of depending on one's interests and attitudes. One very good reason might be that the order Araneae offers an excellent and possibly unique opportunity to study behavioral evolution. Representatives occur in a variety of habitats spread over all the continents in a great abundance of individuals and species (according to recent estimates approximately 35,000 species of spiders exist). It is particularly in the Araneae that we find a score of rather generalized forms that have persisted alongside groups that show intermediate to highly specialized and often spectacular adaptations. The majority of arachnologists working on behavior to date have concentrated on the intricate ways of specialists like orb-weavers, bolas-spiders, jumping spiders etc. However, if one wants to study the roots of spider behavior, it may be more opportune to study primitive forms like the Liphistiomorphae and Mygalomorphae.

THE CONSPICUOUS COMMON HABIT OF PRIMITIVE SPIDERS

The Liphistiomorphae, with about ten recent species, are generally regarded as a superb example of living fossils. They occur in a relatively small area in south-eastern

Asia. The Mygalomorphae, which share a number of obvious primitive characteristics with the former group (Platnick and Gertsch 1976), on the other hand, are spread over the habitable world with a variety of forms. Among the nine families (Savory 1977) composing the Mygalomorphae, we find a remarkable basic uniformity of behavior. This basic behavior is shared with those truly primitive Liphistiomorphae as well as with many Araneomorphae, particularly those forms which are regarded as generalized. It consists of building a home retreat in the form of a silken tunnel in which the spider normally lives its entire life. In the majority of species such a retreat is built within a self-dug burrow in the ground.

THEORIES ON THE ORIGINAL FUNCTION OF SPIDER SILK

The question, "what was the original function of spider silk?" has traditionally been posed and answered in attempts to find a plausible basis for theories on the evolution of the spider web. In these theories early spiders are invariably seen as wandering creatures and the development of silk as an adaptation to a terrestrial existence.

Pocock (1895), Comstock (1912), Gerhardt and Kaestner (1938) and Bristowe (1958), all state that spider silk was first used as a protective cover of the eggs. The argument underlying this statement comes from the supposition that other spinning arachnids, the mites and the pseudoscorpions, use silk solely for this purpose (Kaston 1964). In summarizing the above authors Kaston (1964) concludes: "the web itself evolved from a mass of threads distributed around the egg-sac, or from a tube constructed as a retreat in which the spider hid with its eggs." In a recent publication Gertsch (1979), along the same lines speculates that "the earliest spiders were cautious hunters that grouped around on the ground and made little effort to establish a permanent station of refuge. Only during moulting and egg-laying was it desirable to be concealed from wandering predators. The first step on a life dependence on silk was the coating of the eggs."

Serious weaknesses in the above "egg protection theory" lay firstly in the fact that neither mites nor pseudoscorpions use silk solely for egg protection, but rather build structures in which the spinning individual itself might pass through vulnerable stages (Schuster 1972, Alberti 1973, Forster and Forster 1973, Gabbutt and Aitchison 1980), secondly that the "egg protection theory" cannot explain why all male spiders are perfect spinners.

Savory, in taking an entirely different point of view than the above authors, "prefers to consider that the protection of eggs or young is not normally a primitive habit of any group of animals" (Kaston 1964). In his view (Savory 1960, 1977), the drag line is the most original manifestation of spider silk. "The earliest of all spiders cannot be supposed to have been a web spinner, probably like other arachnids it was a wanderer, devouring what it was able to catch, but, because it was a spider trailing a thread behind it" (Savory 1977:303).

This "drag line theory" is based on the assumption that, "like their earliest ancestor, the archearaneid, all spiders lay a drag line behind them as they move" (Savory 1960). What should have been the function of the early drag line is not consistently clear. It might have served as a guide line "helping the wandering spider find its way back to its crevice" (Savory 1960), although this becomes somewhat unlikely when he then states that the ancestral spider performed only short range hunting. "From here (some crevice or other hiding place) short sallies to pounce upon passing unfortunates would be an obvious

way of life, and a return to safety would be guided by the action of the lyriform organs" (Savory 1977). Seyfarth and Barth (1972) have shown the existence of kinesthetic orientation in spiders in which the lyriform organs play a vital role. Other, more serious objections to the "drag line theory" are: (a) silk is not known to be used in this fashion by any other spinning animals than spiders, and (b) at least some mygalomorph spiders do not always lay down a drag line as they move. (Observations were carried out with the Ctenizidae *Cyrtocarenum cunicularium*, *Nemesia caementaria*, *Nemesia dubia* and an unidentified west African theraphosid.)

POSSIBLE FUNCTION OF SILK IN AN AQUATIC HABITAT

Given the earlier stated ancestry of the spiders' spinning apparatus, it could be that the fundamental tenet of both theories is incorrect and that the original use of spider silk is to be sought in adaptation to a sedentary existence in the ancestral aquatic environment and not in a later adaptation to a wandering life on the land.

What use could silk or its direct forebear have had in an aquatic environment? To answer this question one does not have to search very far. A common feature of many animals living in the littoral zone is the fact that they burrow in the sediment. Many bivalves make deep burrows with mucus-compacted walls (Barnes 1980). Among polychaetes burrowing is very common and many forms build tubes or line their burrows with hardened material which is secreted from special glands (Myers 1972, Brenchly 1976). Within the aquatic arthropods, the Crustacea, burrowing is also wide-spread. In this respect the behavior of stomatopods (mantis-shrimps) is very interesting. Most of these live in self-dug burrows, the walls of which are cemented with a layer of mucus mixed with sediment material. Except for a small central opening the burrow's entrance is frequently covered with a thin sheet constructed from mud, mixed with secretion presumably produced from glands in the mouth region (Caldwell and Dingle 1978).

There are many more examples of littoral invertebrates showing comparable habits. In this light it is not unlikely that ancestral spiders also have been animals of the littoral zone, that dug holes in the sediment and reinforced the walls with some protein rich secretion. In fact, the earlier mentioned molluscs, annelids and crustaceans that burrow in the tidal zone are faced with a range of problems that could be conveniently solved if the burrows are, or could be closed off at the entrance when necessary. For example, according to Caldwell and Dingle (1978) the mud and secretion caps of the stomatopods mentioned above also make the burrows almost invisible. Such an adaptation could function to reduce location by visual hunting predators or in providing a camouflaged ambush site. The tube caps of annelids of the genus *Diopatra* seem to function as a barrier against the burrow being filled-up with sediment material moving in the water current and as a predator detection system (Brenchly 1976). Fiddler crabs (fam. Ocypodidae) are known to plug their burrows with mud during the high tide. The crab *Cardiosoma guanhumi* on the other hand frequently closes its burrow with a similar plug during the dry season presumably thus reducing the chance of dehydration (Gifford 1962).

Burrow entrance ornamentation such as silken collars, tubes and trapdoors seen commonly in primitive spiders today could well have originated from early adaptations connected with life in the littoral zone. Indeed the possession of a burrow that can be closed off from the outside could well have been conditional for spiders to become terrestrial animals. The ability to spin silk, a protective device against hostile physical and

biological factors operating in the tidal zone, could have opened the way on the land to achieve the often wonderful and spectacular adaptations we see in spiders today.

Although early on the scene, many Araneae have preserved a form and associated behavior that probably has remained virtually unchanged throughout the ages. The order appears to have had sufficient genetic potential to largely maintain the original niche without the need for dramatic changes. The great success of the spiders considering the number of species and the wide geographical distribution today, is based on those forms which are endowed with highly specialized adaptations. Study of the primitive Liphistiomorphae and Mygalomorphae can show along which lines such adaptations have been derived. Their success in persisting through the ages gives us the opportunity to study an extremely wide range of behavioral evolution.

CONSEQUENCES FOR ARACHNID PHYLOGENY

Although the aim of this paper is in the first place to stimulate behavioral research on primitive spiders rather than to present an alternative classification of Arachnida, the here proposed theory has some consequences for extant views on arachnid phylogeny. In particular the relationships between the living orders of Savory's (1977) infra-class Arachnoidea are affected. These orders are the Uropygi/Schizomida, Amblypygi and Araneae.

If one takes primitive silk or protosilk usage as an adaptation to life in an aquatic environment, the stem species of the Arachnoidea might be visualized as follows. The animal burrowed in soft substrates within the littoral zone, it possessed appendages on the fourth and fifth opisthosomal segment and flagellum-like extension at the terminal segment. Such an animal might have looked very much like Weygoldt and Paulus' (1979b) stem species of the Lipoctena which was furthermore characterized by retinula cells that formed a network of connected rhabdomeres, coiled spermatozoa and lyriform organs. It could indeed have been the form of which the above authors state "Die erste Aufspaltung der Lipoctena führte wahrscheinlich zu einer Gruppe, die ihre Grösse, Zahl der Atmungsorgane und der Augen zunächst wenig veränderte," and which they propose as the stem species for the Megopericulata Börner, 1902 (Weygoldt and Paulus 1979b).

The recent orders belonging to the Megopericulata were collectively named Arachnoidea by Savory (1977) and it must have been the stem species of this group in which the appendages on the fourth and fifth opisthosomal segments evolved into silk or protosilk producing organs. Being burrow dwellers the species consumed its prey in an environment in which severe dilution of external digestion products was reduced. This could have led to a change in the chelate chelicerae. No longer was it necessary to tear off small pieces of a prey in order to bring them in the pre-oral cavity, it was now sufficient to hold a prey against the mouth opening with strong hooklike chelicerae. Another important adaptation to life in a narrow burrow would have been the reduction of the first opisthosomal segment allowing the body to hinge centrally. This made it possible for the animals to pivot in their narrow holes.

An inability to follow prey animals is associated with a strict sedentary, predatory existence. In certain circumstances however it might well be adaptive to develop mobility. This would depend upon the selection pressures operating, for example, migratory prey, intra- or interspecific competition. A tendency to roam might have led to the separation of the early Arachnoidea into two groups.

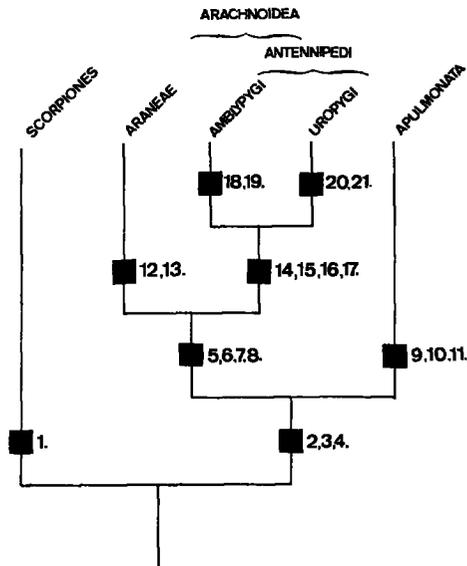


Fig. 1.—Cladogram indicating the probable relationships within the Arachnoidea (Savory 1977) and their relation to other Arachnids based on the work of Weygoldt and Paulus (1979b). Black squares denote apomorphic character states. The numbers refer to the character states mentioned in Table 1.

Table 1.—Character states used in the cladogram to indicate the supposed monophyly of the respective arachnid groups. Character state numbers preceded by a dash are taken from Weygoldt and Paulus (1979b).

apomorph character state	plesiomorph character state
- 1 pectines etc.	no pectines
- 2 retinula cells form a network of connected rhabdomeres	closed rhabdomeres, star-like in cross section
- 3 coiled spermatozoa	elongate, flagellate spermatozoa
- 4 lyriform organs present	only single slit sense organs
- 5 spermatozoa with 9 + 3 flagellum	spermatozoa with 9 + 2 flagellum
6 1st opisthosomal segment reduced	1st opisthosomal segment broad
7 opisthosomal spinning or pre-spinning organs	no opisthosomal spinning or pre-spinning organs
- 8 chelicerae with 2 articles	chelicerae with 3 articles
- 9 reduction of body size	body size not reduced
-10 reduction of book lungs	book lungs present
-11 lateral eyes reduced to 2 or 3 pairs	originally 5 pairs of lateral eyes
12 copulatory palpal organs	palps without copulatory organs
-13 chelicerae with poison glands	chelicerae without poison glands
14 opisthosomal spinning or pre-spinning organs lost	spinning or pre-spinning organs present
15 1st legs antenniform	1st legs not antenniform
16 strong grasping palps	palps leg-like
17 subchelate chelicerae	"pocketknife" chelicerae
18 flat body shape	body not flat
19 1st pair of legs extremely elongated	1st pair of legs of moderate length
-20 camarostome	palpal coxae not fused
-21 pre-nymphal and 4 nymphal instars	number of instars larger and variable

Firstly, the Araneae remained in the old burrowing habit. They developed such apomorphies as palpal copulatory organs and cheliceral poison glands. An early branch of the Araneae led to the, what I would call, Antennipedi. These Antennipedi left the plesiomorphic burrowing habit still living in an aquatic environment. Food consumption in the "free-hunting," externally digesting Antennipedi would be more efficient if small pieces could be torn from a prey and brought into the pre-oral cavity. This could have led to the development of the pedipalpi into organs for grasping and holding the prey and the chelicerae into subchelate organs suitable for tearing off pieces.

Because the early Antennipedi originated from burrowing ancestors it seems reasonable to suggest that they showed shelter seeking tendencies. Competition for shelter places might have caused a branching of the Antennipedi, in which one species became adapted to life in very narrow crevices. This event might have or might not have taken place after the Antennipedi had colonized the land. It led to the separation of the Amblypygi from an old uropigid stock. The Uropygi must then be seen as the plesiomorph sistergroup of the Amblypygi in which autapomorphies developed such as a camarostome and the typical number of nymphal stages Weygoldt and Paulus (1979a, 1979b) report.

The possible temporal derivation of the above discussed groups, defined by their respective apomorphic character states, is schematized in the cladogram of Fig. 1.

This hypothesis of Arachnoidea phylogeny leads to the acceptance of the following characters as convergent:

- 1) Terrestrial existence. The Arachnoidea must have originated from at least two forms which have independently colonized the land.
- 2) The reduction of the flagellum must have occurred independently in the Araneae and the Amblypygi.
- 3) Typical terrestrial adaptations such as the development of malpighian tubes and trichobothria must have originated at least twice in the Arachnoidea and more often in the Arachnida.

It is realized that the above sketch of arachnid history is rather speculative. Still in my opinion, interpretation of the observable facts along these lines is certainly no less fictitious than any extant hypothesis on the phylogeny of these very early colonists of the land.

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