Reprint Series
27 October 1989, Volume 246, pp. 479–481

SCIENCE

A Devonian Spinneret: Early Evidence of Spiders and Silk Use

WILLIAM A. SHEAR, JACQUELINE M. PALMER, JONATHAN A. CODDINGTON, AND PATRICIA M. BONAMO

A Devonian Spinneret: Early Evidence of Spiders and Silk Use

William A. Shear, Jacqueline M. Palmer,
Jonathan A. Coddington, Patricia M. Bonamo

A nearly complete spider spinneret was found in Middle Devonian rocks (about 385 to 380 million years old) near Gilboa, New York. This is the earliest evidence yet discovered for silk production from opisthosomal spigots, and therefore for spiders. Two previously known Devonian fossils described as spiders lack any apomorphies of the order Araneae and are probably not spiders. The spigots of the Devonian spinneret resemble those of members of the living suborder Mesothelae, but the number of spigots and their distribution are like those of members of the suborder Opisthothelae, infraorder Mygalomorphae. The Devonian spider belonged to a clade that may be the sister group of all other spiders, of Mesothelae, or of Opisthothelae.

Spiders (Arthropoda: Chelicerata: Araneae) are among the most important terrestrial predatory animals. Among the arachnids, they alone produce silk from opisthosomal (abdominal) glands that open through modified setae called spigots, which in turn are located on reduced abdominal appendages, the spinnerets. This character complex is the most diagnostic apomorphy of spiders. We report here on the earliest evidence yet discovered in the fossil record of spinnerets, of spiders themselves, and of silk production by animals.

Although two spider fossils have been reported from the Devonian Period, in neither of these cases can any apomorphies of the order Araneae be demonstrated. *Paleoctenіza crassipes* (*1*), from the Lower Devonian (404 million years old?) Rhynie Chert, is a minute, crumpled exoskeleton that is undoubtedly arachnid, but is more likely from one of the trigonotarbids that are the most abundant animals in that deposit. Spinnerets, characteristic patterns of leg jointing, eye arrangement, and other spider apomorphies that are potentially present even in very small, immature animals cannot be detected in this fossil or are certainly not there (*2*). *Archaeometa devonica* (*3*), from the slightly later Alken-an-der-Mosel, West Ger-

---

W. A. Shear, Department of Biology, Hampden-Sydney College, Hampden-Sydney, VA 23943, and American Museum of Natural History, New York, NY 10024.
J. M. Palmer, Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138.
J. A. Coddington, Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560.
P. M. Bonamo, Center for Evolution and the Paleoenvironment, State University of New York, Binghamton, NY 13901.

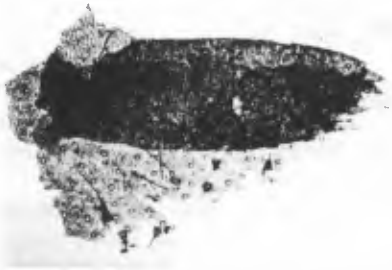

Fig. 1. Fossil spinneret, slide 334-1b-AR34. The greatest length of the specimen (not including the terminal spigots) is 0.94 mm. Note the numerous spigots scattered along the anatomically median surface. Magnification, ×40.

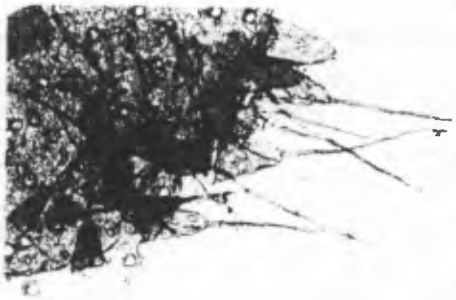

Fig. 2. Distal portion of the fossil spinneret, showing denser clustering of spigots at tip. Magnification, ×200.

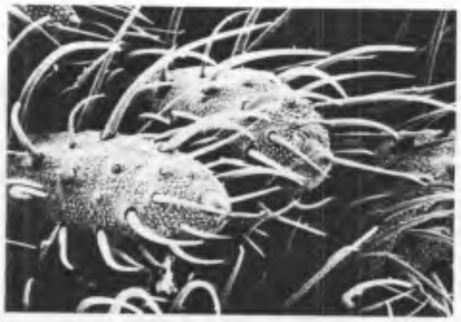

Fig. 3. Posterior median spinnerets of *Liphistius malayanus* (Mesothelae: Liphistiidae). Note the single, terminal spigots, and the scaly cuticle. Scanning electron micrograph (SEM), ×92.

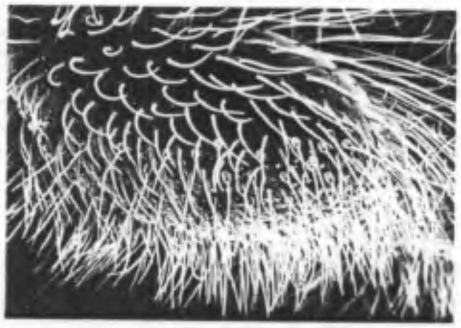

Fig. 4. Posterior median spinneret of *Neocteniza* sp. (Opisthothelae: Mygalomorphae: Idiopidae). The spigots are numerous, occupy the median surface, and are more densely clustered near the tip. SEM, ×92.

many, judging from the published photographs, is not a spider and perhaps not even an animal fossil, rather a vertebrate coprolite. Again, no spider apomorphies are visible on the specimen, which is simply an elongate blob with vague cross-striations at one end. In our opinion, it must be rejected as a possible spider fossil.

The earliest known terrestrial arachnids in North America occur in Middle Devonian rocks near Gilboa, New York (*4, 5*). An extraordinarily diverse fauna of arthropods, some not yet identified, are found in this *Konservat Lagerstätte* (a fossil deposit remarkable for fine preservation, preservation of an entire community, or both). Among recently obtained specimens is a single spider spinneret.

Recent views of spider evolution (*6*) divide the order Araneae into two suborders. Mesothelae includes a small number of species today restricted to southeast Asia, Indonesia, and Japan; they are united by a number of synapomorphies, including a peculiar sense organ between the tibiae and metatarsi of the legs (*7*). Mesotheles are better known for their primitive characters, including an externally segmented opisthosoma and the possession of eight (rarely seven) spinnerets, which are located not at the end of the opisthosoma, but near the middle of its ventral surface. Suborder Opisthothelae includes all other spiders, in which the number of spinnerets has been reduced to six, four, or two and moved to the posterior end of the opisthosoma, which is not externally segmented. Within this group, Mygalomorphae ("tarantulas" in the North American sense) have lost all vestiges of the anterior median spinnerets, while Araneomorphae carry a cribellum (repeatedly lost in many lines) homologous to the anterior median spinnerets of mesotheles, and have chelicerae rotated to the labidognath position, so that the fangs point toward one another.

Aside from the Devonian examples mentioned above, all Paleozoic fossil spiders come from Pennsylvanian rocks, and with two possible exceptions (*8*) are mesotheles, though spinnerets are not preserved in the majority and this assignment by paleontologists has been based on the combination of spider-like general morphology and a segmented opisthosoma. Some of these fossils are not spiders (*9*). A gigantic Carboniferous arachnid from Argentina has been assigned to Araneae (*10*) but may represent an unnamed order or a ricinuleid (*11*). In any case, this fossil, *Megarachne servinei*, suggests undetected Paleozoic araneid or arachnid diversity.

The Devonian spinneret (Figs. 1 and 2) is nearly complete, consists of a single article, and carries 19 or 20 spigots that are in most ways characteristic of mesotheles. The spigots are arrayed along the medial surface and are more densely clustered distally. Slit sense organs and setal sockets are scattered over the cuticle between spigots, and a few of the sockets retain setae, which may be either smooth or serrate. The cuticle itself has a scaly appearance, as does that of living mesotheles. However, in mesotheles the large lateral spinnerets of each pair are pseudosegmented, with spigots in ranks of two, three, or four on the mesal surface of a pseudosegmental ring, and the smaller, single-articled median ones bear only a single spigot (*Liphistius maylayanus*, Fig. 3). Because the Devonian spinneret is not pseudosegmented, yet bears more than one spigot, it could not have come from a mesothele spider similar to those living today.

We have ruled out araneomorph spiders since the spigots of their spinnerets are strongly differentiated from one another and from those of mygalomorph spiders in characteristic ways (*12*), and all spigots on the fossil specimen are of the same size and shape.

Mygalomorph spiders have single-articled posterior median spinnerets with numerous spigots (*Neocteniza* sp., Fig. 4) arranged as in the fossil. The presence of undifferentiated, or only slightly differentiated, spigots that are more densely clustered near the tip of the spinneret is consistent with mygalomorph spider posterior median spinneret anatomy. However, both mygalomorph and araneomorph (but not mesothele) spinnerets have peculiar nipple-shaped structures called tartipores, which represent the positions of spigots in previous instars (*12*). Tartipores are not present on the Devonian spinneret. In addition, mygalomorph spinnerets usually have two types of spigots present. The form of the spigots themselves does not, in detail, agree with that of mygalomorph spigots (Table 1).

Mesothele spigots (Fig. 5) are uniform in morphology, with a broad, conical base and a long, gradually tapering, unsculptured distal shaft that merges smoothly into the base. The spigots of our fossil (Fig. 6) are of this type.

Mygalomorph spigots usually have an articulated shaft, which joins the base by means of a well-defined, sleevelike fold. At least the distal third of the shaft is sculptured. However, the rastelloid clade of mygalomorphs have nonarticulated shafts and extremely fine sculpture, visible only when viewed with a scanning electron microscope. Diagenetic changes in the fossil spinneret may have made it impossible to resolve such fine detail as the distal shaft sculpture of *Neocteniza*. Considering the absence of tarti-

Table 1. Comparison of spinnerets.

Character	*Liphistius* (mesothele) posterior median spinneret	Devonian fossil spinneret	Mygalomorph posterior median spinneret
Spigot arrangement	Single apical spigot	19–20 on mesal side of spinneret, not ranked, clustered at tip	Numerous on mesal side of spinneret, not ranked, clustered at tip
Spigot types	One	One	Rarely one, usually two
Cuticle texture	Scaly	Less pronounced scales	Slightly scaly
Shaft sculpture	Absent	Apparently absent	Present on at least distal third
Shaft-base union	Smoothly graded	Smoothly graded	Collar-like articulation
Tartipores	Absent	Absent	Present

pores and the possibility that distal sculpture is absent, not eroded by postmortem changes, the spigots are more like mesothele spigots than mygalomorph ones.

As already discussed above, the combinations of apomorphies found in spinnerets of the three living clades would seem to exclude the fossil from all of them. The question then becomes placement of the Devonian spider as a sister group of one, two, or all of these clades. The presently accepted three-taxon statement for the groups of spiders so far discussed is (Mesothelae (Mygalomorphae (Araneomorphae))). The spider that bore the fossil spinneret is probably not a member of the sister group of either Araneomorphae or Mygalomorphae, because to place it in either of those positions would require the ad hoc secondary loss of tartipores in the fossil clade. Thus the fossil may be a representative of the sister group to all other spiders, to Mesothelae, or to Opisthothelae. Additional evidence from other parts of the Gilboa spider is required to further refine its position, since all observable character states of the spinneret are plesiomorphic.

However, the early appearance of every physical modification required to produce silk at a level of sophistication paralleling that of some modern spiders is striking. If relatively constant rates of evolution are assumed, it suggests a long period of pre–Middle Devonian evolution for spiders and their relatives, and that even Devonian fossils will not shed much light on the origins of spider spinning (*13*). While mesotheles may have achieved their modern form by the Pennsylvanian, definitively opisthothele fossils do not appear until the Mesozoic [Triassic (*14*), Jurassic (*15*), Cretaceous (*16*)], and nearly all of these fossils can be assigned to families still extant—they are in every detail (the preservation is exquisite) the equivalent of living species.

Fig. 5. Terminal spigot on posterior median spinneret of *L. malayanus*. SEM, ×510.

Fig. 6. Spigot base from fossil spinneret. Oil immersion, Nomarski interference contrast optics, ×1000.

To what use Devonian spiders put their silk is unclear. Living mesotheles do not make aerial webs but use silk only as a burrow-and-door lining, as trip lines extending from the mouth of the burrow, and as the material for egg sacs. However, when spiders make trap doors, there are specific adaptations present to shorten and broaden the spinnerets (*17*), which are not present in our specimen. Rudimentary aerial webs are made by a few mygalomorphs (*18*), and many araneomorphs weave highly derived ones (*19*), a habit that may be correlated with their well-differentiated spigots. Flying insects, against which aerial webs would have been directed, do not appear in the fossil record until much later [Carboniferous: Namurian (*20*)] but may have had a long history previous to that appearance. The report (*21*) of an archaeognath insect from the Lower Devonian (Emsian), and the presence in the later (Givetian) Gilboa fauna of similar material (*4*) establishes an early origin for insects. Devonian material of winged (pterygote) insects may well be found in the near future.

The Devonian spider, therefore, was perhaps a sit-and-wait, tunnel or tube-dwelling predator on cursorial arthropods, but may just possibly have made an aerial web.

REFERENCES AND NOTES

1. S. Hirst, *Annu. Mag. Nat. Hist.* 9, 455 (1922).
2. W. A. Shear, unpublished observations. The specimen was studied intensively using Nomarski optics; 35 serial optical sections were photographed, digitized, and reconstructed on a computer. The resulting image could be examined from all angles; no spider apomorphies were found.
3. L. Størmer, *Senckenb. Lethaea* 57, 121 (1976).
4. W. A. Shear *et al.*, *Science* 224, 492 (1984).
5. W. Shear, P. Selden, W. D. I. Rolfe, P. Bonamo, J. Grierson, *Am. Mus. Novit.*, no. 2901, 1 (1987); R. Norton, P. Bonamo, J. Grierson, W. Shear, *J. Paleontol.* 62, 259 (1988); W. Shear and P. Bonamo, *Am. Mus. Novit.*, no. 2927, 1 (1988).
6. N. Platnick and W. Gertsch, *Am. Mus. Novit.*, no. 2607, 1 (1976); R. Raven, *Bull. Am. Mus. Nat. Hist.* 182, 1 (1985).
7. N. Platnick and P. Goloboff, *J. NY Entomol. Soc.* 93, 1265 (1985).
8. W. A. Shear, unpublished observations. *Archaeometa nephilina* Pocock and *Arachnometa tuberculata* Petrunkevitch [both Late Carboniferous; British Museum of Natural History (BMNH), specimens In15863, In31259, and In13914, respectively] may be araneomorphs.
9. W. A. Shear, unpublished observations. *Practeniza brittanica* Petrunkevitch (Late Carboniferous; BMNH specimen In22834), for example, has the ventral opisthosomal surface very well preserved, but shows no spinnerets. It is probably an amblypygid.
10. M. Hünicken, *Bol. Acad. Nacl. Ciencias, Cordoba, Argentina* 53, 317 (1980).
11. P. Selden, personal communication.
12. J. Coddington, *J. Arachnol.* 17, 75 (1989); J. Kovoor, in *Ecophysiology of Spiders*, W. Nentwig, Ed. (Springer-Verlag, New York, 1986), pp. 160–186.
13. J. Schultz, *Biol. Rev.* 62, 89 (1987).
14. J.-C. Gall, *Mem. Service Carte Geol. d'Alsace Lorraine* 34, 1 (1971).
15. K. Eskov, *N. Jahrb. Geol. Palaeontol. Monatsh.* 11, 645 (1984); *N. Jahrb. Geol. Palaeontol. Abh.* 175, 81 (1987).
16. P. Selden, personal communication; J. McAlpine and J. Martin, *Can. Entomol.* 101, 827 (1969).
17. R. Raven, *Bull. Am. Mus. Nat. Hist.* 182, 12 (1985).
18. F. Coyle, in *Spiders: Webs, Behavior, and Evolution*, W. A. Shear, Ed. (Stanford Univ. Press, Stanford, CA, 1986), pp. 274–279, figures 10.6 and 10.7; *Bull. Am. Mus. Nat. Hist.* 187, 205 (1988).
19. W. A. Shear, in *Spiders: Webs, Behavior, and Evolution*, W. A. Shear, Ed. (Stanford Univ. Press, Stanford, CA, 1986), pp. 364–400; W. Eberhard, *ibid.*, pp. 72–75; J. Coddington, *ibid.*, pp. 326–334.
20. R. Wootton, *Annu. Rev. Entomol.* 26, 320 (1981).
21. C. C. Labandeira, B. S. Beall, F. M. Hueber, *Science* 242, 913 (1988).
22. We thank A. Robble, who prepared the specimen, N. Platnick, who loaned material of *Liphistius*, and P. Selden, for commenting on the manuscript, and for discussions with W.A.S. of fossil spiders. The comments of two anonymous reviewers improved the manuscript. Supported by NSF grants BSR 85-08442 and BSR 88-180-27 to W.A.S. and P.M.B., and by a research grant from the Power Authority of New York State to P.M.B.

30 June 1989; accepted 29 August 1989