Fossil evidence for the origin of spider spinnerets, and a proposed arachnid order

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Silk production from opisthosomal glands is a defining characteristic of spiders (Araneae). Silk emerges from spigots (modified setae) borne on spinnerets (modified appendages). Spigots from Attercopus fimbriunguis, from Middle Devonian (386 Ma) strata of Gilboa, New York, were described in 1989 as evidence for the oldest spider and the first use of silk by animals. Slightly younger (374 Ma) material from South Mountain, New York, conspecific with A. fimbriunguis, includes spigots and other evidence that elucidate the evolution of early Araneae and the origin of spider silk. No known Attercopus spigots, including the original specimen, occur on true spinnerets but are arranged along the edges of plates. Spinnerets originated from biramous appendages of opisthosomal somites 4 and 5; although present in Limulus, no other arachnids have opisthosomal appendage homologues on these segments. The spigot arrangement in Attercopus shows a primitive state before the reexpression of the dormant genetic mechanism that gave rise to spinnerets in later spiders. Enigmatic flagellar structures originally described as Arachnida incertae sedis, are shown to be Attercopus anal flagella, as found in Permarachne, also originally described as a spider. An arachnid order, Uraraneida, is erected for a plesion, including these two genera, based on this combination of characters. The inability of Uraraneida precisely to control silk weaving suggests its original use as a wrapping, lining, or homing material.

Araneae | Chelicerata | Devonian | Paleozoic | silk

he defining adaptation of spiders is the production of silk from highly modified appendages called spinnerets, located on the posterior division of the body (opisthosoma). Silk emerges from spigots (modified setae) arrayed on the spinnerets and connected to internal silk glands capable of producing, in the most advanced spiders, several kinds of chemically and physically distinct fibers. Silk is used not only to create webs of various types, but also to produce egg-sac material, for prey wrapping, lining burrows, and to aid in navigation and communication, among other uses. Because of the importance of silk and spinnerets in the lives of spiders, clues to the origins of the spinning apparatus are of great importance in understanding the evolution of the group. Although silk is important in other animals (e.g., moth cocoons), no other arthropod group relies so heavily on its use in so many ways. Here, we reinterpret old and assess recent fossil evidence, and combine our analysis with developmental genetic studies, to clarify how silk use may have evolved. An unexpected result of the study was the discovery that some Paleozoic fossils thought to be spiders represent a hitherto undiagnosed order of Arachnida.

The Fossil Evidence

The oldest known silk-producing spigots are from the Middle Devonian of Gilboa, New York (1). This specimen (slide 334.1b.AR34, Fig. 1A), was described as a nearly complete, fusiform spinneret, consisting of a single article, bearing ≈ 20 spigots arrayed along the presumed medial surface but more clustered distally. On the basis of the single, simple spigot type

and the lack of tartipores (vestigial spigots from earlier instars), the fossil spinneret was compared most closely with posterior median spinnerets of the primitive spider suborder Mesothelae. The distinctiveness of the cuticle enabled us to associate the spinneret with remains previously referred tentatively to a trigonotarbid arachnid (2). Restudy of this material resulted in a fuller description of the animal as the oldest known spider, *Attercopus fimbriunguis* (3). The appendicular morphology of *Attercopus*, but little of the body, is now known in great detail. In this article, morphological information on *Attercopus* is described, which significantly alters these earlier interpretations, and provides insights into the evolution of the spider silk system.

Collections made in 1993 and 1996 in Middle Devonian strata [lower Frasnian, lowermost Onteora Formation, 374 Ma (4)] at South Mountain, Schoharie County, New York (74°16′30″E/ 42°23'55″N) yielded material that is indistinguishable from *A. fimbriunguis* from Gilboa, and thus presumed to be conspecific. This material includes 3 pairs of chelicerae (therefore, at least 3 individuals), numerous podomeres including a palpal femur showing the distinctive patch of spinules on the inferoanterior surface (Fig. 1*B*), and two slides with specimens showing spigots. The last are numbered sequentially (SM 1.11.3 and SM 1.11.4), which means they were extracted from the same acid-macerate residue and slide-mounted one after another, and so could be parts of the same animal.

Spigots and Silk

SM 1.11.3a (Fig. 2A) consists of a subrectangular mass of overlapping layers of cuticle with \approx 33 spigots arrayed in an approximate double row along one long edge and an area of unsculptured cuticle along the opposite edge. The folds have their long axes parallel to the shorter edges. These features, together with the setal arrangement, suggest that the preferred orientation is: unsculptured cuticle anterior, spigots posterior, shorter edges lateral. Seven macrosetae and/or their sockets are present on SM 1.11.3a. One posterolateral corner is missing; spigots are most numerous at the opposite posterolateral corner. Because of the presence of spigots, we interpret SM 1.11.3a as part of the opisthosoma. Living and fossil mesotheles have macrosetae at the rear of each large tergite (5), and other spiders that lack tergites commonly bear large setae on the opisthosoma that reflect original segmentation; thus, the macrosetae on Attercopus SM 1.11.3a could also reflect at least 4 sclerotized plates and the transverse lines could represent plate boundaries (note: both dorsal and ventral surfaces are present).

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Fig. 1. Attercopus fimbriunguis, Devonian of New York (localities: G, Gilboa; SM, South Mountain), macerated from matrix with HF and slide-mounted. (A) First-described "spinneret," G 334.1b.34; darkness of cuticle reflects number of layers, so this fragment is folded over twice. (B) Palpal femur, SM 1.11.12; arrow indicates patch of distinctive spinules. (C) Piece of cuticle from corner of opisthosomal ventral plate showing setae, spigots, and possible silk strand, SM 1.11.4. (D) Close-up of *E* showing possible silk strand emerging from spigot shaft, SM 1.11.4. (*E*) Flagellar structure with 12 segments (including possible distalmost) from original Gilboa locality; segments show distal collars and setae, G 334.1a.4. (*F*) Close-up of cheliceral fang showing a number of holes (arrowed), the most distal of which had been interpreted as a venom-gland opening, G 329.22.9. (Scale bars: 0.5 mm, except *F*, 0.25 mm.)

SM 1.11.4 (Fig. 1 *C* and *D*) is a smaller piece of cuticle than SM 1.11.3a. The distribution of setae and spigots enables orientation of the piece. At one lateral side is an even fold that conforms to the curved outline of the posterolateral margin; this is interpreted as a doublure along the margin of the plate. It is folded at the lateral side and bears \approx 15 spigots in an approximate double row along the posterior edge; the anterior and opposite lateral edges are torn. If SM 1.11.4 were once joined to SM 1.11.3a, then it is likely that it is the missing posterolateral corner of SM 1.11.3a, with its posterolateral concentration of spigots. Of especial interest on SM 1.11.4 is the long, winding filament emerging from the distal end of one spigot (Fig. 1*E*). Detailed study shows that this is a single strand that is inseparable microscopically from the tip of the spigot, thus leading us to hypothesize that this is a strand of silk. No other silk strands have been seen in *Attercopus* material, but silk from modern spiders is identical in size and appearance under the light microscope.

From our reevaluation of 334.1b.AR34 we conclude that the original description is essentially correct, but note that the specimen consists of a sheet of cuticle folded over twice; thus, the resemblance of the piece of cuticle bearing spigots to a "semifusiform" spinneret (3) is fortuitous. In summary, the specimens of *Attercopus* bearing spigots are plate-like in morphology, with 2 rows of spigots along the presumed posterior edge. The spigots are not borne on appendage-like spinnerets.

Ventral Opisthosomal Plates

Although mesothele spiders and a few mygalomorphs have opisthosomal tergites that can be attributed to the original segmentation of the opisthosoma, no spiders living or fossil have ventral opisthosomal plates. However, these plates are present in all other arachnid orders, including the Pedipalpi (orders Amblypygi, Uropygi, and Schizomida), sister group to spiders. There is no evidence for the origin of these plates from genetic studies; the patterns of expression of hox genes has only been studied in some spiders and mites [in the latter, with focus on head segmentation, not expression of appendage-determining genes (6)]. It has been suggested, on the basis of paleontological and developmental evidence (7), that, in scorpions, these plates are not true sternites but are the fused remnants of paired opisthosomal appendages, as indeed seems to be the case for the epigastric plate and book-lung covers of spiders, and the homologous anterior opisthosomal opercula in Uropygi (8) and Amblypygi (9). In mesotheles the first 2 pairs of book-lung covers are part of continuous sclerotization across the opisthosoma, with distinct posterior margins.

It seems unlikely that the spigot-bearing plates in *Attercopus* are tergites, and much more probable that they represent ventral plates, because in spiders the spinnerets are invariably ventral. If the ventral plates are appendage-derived, the reactivation of genes (such as *distalless*) that would extend these plates once more into segmented appendages would carry along with them



Fig. 2. Attercopus fimbriunguis, Devonian of South Mountain, New York, macerated from matrix with HF and slide-mounted. (A) Part of opisthosoma with rows of spigots, SM 1.11.3a. (B) Two flagellar segments emerging from posterior part of opisthosoma, SM 1.11.3b. (Scale bars: 0.5 mm.)



Fig. 3. Paleozoic Araneae and Uraraneida. (A–C) Permarachne novokshonovi, Permian of Russia, PIN 4909/12. (A) Holotype part in rock matrix. (B) Explanatory drawing of A. (C) Close-up of flagellum showing whorls of setae. ch, chelicera; cx, coxa; fe, femur; mt, metatarsus; pa, patella; pl, ventral plate; st, sternum; ta, tarsus; ti, tibia. (D) Palaeothele montceauensis, Carboniferous of France, In 62050a, X-ray CT scan showing appendages buried in the rock matrix; note, anal tubercle (arrowed) is not a flagellum. (Scale bars: B, 1 mm; C and D, 0.1 mm.)

the spigots observed in *Attercopus* to be distributed along the posterior margins of those plates. We suggest that developmental genetic studies to determine the homologies of the ventral plates in the pedipalp orders could provide evidence to resolve this question. Further evidence that silk spigots are associated with appendages comes from the recent finding that at least one species of mygalomorph spider has silk spigots on its leg tarsi that produce threads that help the spider cling to smooth surfaces (10).

In *Permarachne*, from the Permian of Russia, a series of 6 opisthosomal plates are clearly seen (11) (Fig. 3 A and B). In the original description these were interpreted as tergites (as seen in mesotheles) even though all other visible structures in the fossil are ventral, a fact originally accounted for by assuming that the specimen represented a molt from which the carapace had been displaced, thus revealing ventral structures in the prosoma. However, these structures are in ventral, not dorsal, view. It now seems more parsimonious to interpret the series of plates as

ventral plates, conforming to the ventral view of the rest of the fossil. Thus, there is a real probability that, unlike spiders, both *Attercopus* and *Permarachne* bore a series of ventral plates.

Flagellum

Specimen SM 1.11.3b (Fig. 2B) shows overlapping layers of undoubted Attercopus cuticle with both small setal and large macrosetal follicles but no silk spigots. Slightly darker and lighter bands of cuticle are interpreted, as in SM 1.11.3a, as plate edges and interplate membrane, respectively. The few macrosetal follicles are interpreted as those present at the posterior edges of plates (and the largest of these occurs adjacent to a darker plate edge). The plates taper and become narrower to one side; the widest plate is torn along most of its width and laterally, whereas the narrower ones are more complete. Setae on the specimen point toward the side of the specimen with narrower plates, and \approx 3 plates are present. We interpret this specimen as the posterior end of the opisthosoma where the plates narrow.

Both tergite and sternite remains could be present on this specimen, but the posteriormost, at least, appears to be a complete ring. The importance of this specimen is that emerging from the posterior end are two annular segments with thickened posterior collars that bear a row of ≈ 12 prominent setal follicles. These are clearly part of the same flagellar organ found in association, but hitherto not in direct organic connection, with Attercopus (2). Despite the virtually identical cuticle pattern, including slit sensilla, between these flagella and Attercopus, we described them as Arachnida incertae sedis because no flagella are known from spiders. The evidence provided by specimen SM 1.11.3b shows unequivocally that Attercopus did, indeed, bear a postanal flagellum of at least 12 segments. In two of the Attercopus specimens (e.g., Fig. 1E), a distinctive terminal article appears that is 2-3 times as long as the more proximal articles and densely set with setal sockets.

A flagellar structure was described in *Permarachne* (11), but because such a structure was previously unknown in spiders, yet all other morphological features suggested that Permarachne was a mesothele, the structure was interpreted as an elongate, multiarticled spinneret. However, close examination of the specimen shows a complete absence of spigots; the structure appears to emerge from the posterior of the opisthosoma along the median line (Fig. 3 A and B), not laterally as would be expected for a spinneret, and is not matched by any corresponding paired structure on the specimen. Spider spinnerets are always paired, except where the anterior median spinnerets are fused into a single cribellar plate or nonfunctional colulus (12). In Permarachne the flagellum shows setal whorls (Fig. 3C), but only a few segment collars are distinct, because of the poor preservation; those preserved are similar to the segments of Attercopus. Extrapolation from the lengths of the more distinct segments, \approx 12 articles appear to be present, but the distal end is not preserved.

Many other characters demonstrate that both *Attercopus* and *Permarachne* are spider-like in their morphology, without features of other known pulmonate arachnids (3, 11). Among pulmonate orders, only uropygids and schizomids have a postanal flagellum, and only in uropygids is the flagellum long and multisegmented. In other pulmonate orders (amblypygids, trigonotarbids, and spiders), the pygidium is a 1- to 3-segmented preanal structure with a postanal tubercle. The multisegmented flagellum may be a plesiomorphy of Pantetrapulmonata (13) that has been retained in Uropygi (where it appears to function as a sensory structure used for aiming shots of the acetic/caprylic acid repugnatorial secretion), and in our proposed order where the function is unknown, or it could be a homoplasy.

Genetic Developmental Studies

Spider spinnerets are homologs of biramous opisthosomal appendages, still present in the primitive chelicerate Limulus, as demonstrated by expression of the developmental genes pdm/ nubbin and apterous in embryos of spiders and Limulus (14). In Limulus these appendages consist of a segmented median branch and a lateral branch with a plate covering lamellate gills. In spider embryos, distalless gene expression shows 4 pairs of spinnerets (anterior and posterior median and lateral pairs) represented by 2 pairs of appendage buds on opisthosomal somites 4 and 5 (15). The appendage buds each later divide in 2 to produce potentially 4 pairs of spinnerets, although in nearly all spiders some of these buds do not develop into functional postembryonic spinnerets. The full complement of 8 spinnerets is today seen only in the primitive mesotheles Liphistius and Heptathela (even in these animals the anterior median pair bears no silk-producing spigots) (16). Other homologs of opisthosomal appendages in spiders are the book-lung opercula (2 pairs in mesotheles and mygalomorphs, on somites 2 and 3) and tracheae derived from appendage apodemes in araneomorph spiders on somite 3. In other arachnids, homologs of opisthosomal appendages can be seen in the gonopods, book-lung opercula, and ventral sacs of pantetrapulmonates, and other organs in diverse groups (13). Only spiders show expression of appendage homologs on somites 4 and 5 [although structures in other orders could be silk gland homologs, such as the fusules in female palpigrades (17)]. Silk glands also occur in many adult male spiders along the anterior edge of the epigastric furrow (somite 2). These are termed epiandrous or epigastric glands (12), and open through simple spigots (fusules). Because of their medial position in relation to the more lateral book-lung opercula, epigastric fusules could be serial homologs of the median spinnerets of somites 4 and 5.

The advantage of spigots on spinnerets is that silk production can be controlled to produce complex linear structures, rather than simple, sheet-like masses of threads. Our interpretation of spigot location in *Attercopus* suggests that the original use of silk in protospiders was to produce such sheets, perhaps used as burrow linings, to cover egg masses (17), or as trails that would allow hunting animals to return to the safety of a retreat (18).

Loss and reappearance of wings in stick insects suggests that genes for appendage development can be suppressed, perhaps by a single disabling mutation, and later reactivated, again perhaps by a reversal of the original mutation or an offsetting mutation that restores gene function (19). Once these genes were reactivated in the ancestors of spiders, it would be a clear advantage to have the spigots on them as this would confer significantly more control over the use and distribution of silk, as seen in the orb-weaving Orbiculariae of today in the construction of their architecturally precise webs.

A Proposed Arachnid Order

Taking the evidence from Attercopus and Permarachne together, we conclude that both lacked spinnerets but possessed rows of spigots along the margins of sclerotized ventral plates, and a long, multiarticled postanal flagellum. These characters, while evidently plesiomorphic, would exclude Attercopus and Perma*rachne* from the order Araneae as presently defined. Removal of Permarachne from the Mesothelae leaves only one other described mesothele in the fossil record: Palaeothele montceauensis from the Late Carboniferous of France (20). A number of other Paleozoic fossils have been referred to Araneae; some of these are not spiders at all (21), whereas others can be referred to Mesothelae with confidence (P.A.S., unpublished observations). The external mold of the London specimen of Palaeothele shows an anal tubercle, and to ascertain whether this continued into a flagellum (which could place *Palaeothele* as an intermediate between Araneae and the order), an X-ray computed tomography (CT) scan was performed on the specimen by M.D.S. (Fig. 3D). This showed without doubt that there is no flagellum, and therefore *Palaeothele* remains the earliest and only described fossil mesothele spider to date.

In the original description of *Attercopus*, several chelicerae were illustrated and described. In at least one of these specimens (329.22.AR9; Fig. 1F), a hole near the tip of the fang was interpreted as a poison gland pore. Revisiting this specimen raises uncertainty because other apparent holes on the same fang appear to be artefacts of preservation and none of the chelicera specimens show this pore clearly. Mesothele spiders lack poison glands (16), and to infer their existence in *Attercopus* would require their loss and reacquisition (by opithotheles) in Araneae. Because the preponderance of the evidence now suggests that poison glands were also absent in *Attercopus*, it is more parsimonious to assume that they were acquired only once, in the spider suborder Opisthothelae, and are synapomorphic for that taxon, not for spiders as a whole.

Because of the different preservational styles of *Attercopus* and *Permarachne*, it is not clear whether the apomorphies of

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Attercopus (palpal femur spinules, fimbriate tarsal claws, lack of emargination at distal joint of leg patella) are shared by Permarachne. It is possible that the flagellum was uniquely derived and not homologous with that of the pedipalp orders. Although we do not presently have evidence of any synapomorphies for this lineage, we wish to draw attention to its distinctiveness and so establish the ordinal name Uraraneida Selden & Shear ord. nov. (etymology: Greek oura, tail, and Latin, aranea, spider; included taxa: Attercopus and Permarachne). Uraraneida and Araneae are distinguished from the pedipalp orders by 2 characters: the naked (seta-less) cheliceral fang and the presence of opisthosomal silk glands and spigots. The existence of Permarachne alongside mesotheles in the fossil record indicates that Uraraneida was a persistent lineage that only became extinct (if, indeed, it is) some time after the Late Permian.

Methods

Attercopus. A. fimbriunguis specimens were recovered from the rock matrix by digestion in concentrated hydrofluoric acid followed by washing in dilute hydrochloric acid and mounted on plain microscope slides in Clearcol mountant. The specimens were studied by using a Leica DM2500 M microscope and photographed with a Leica DFC420 digital camera attachment. Images of the Attercopus specimens were captured by using Leica FireCam software on an Apple MacBook Pro computer and manipulated by using Adobe Photoshop CS3 software. Drawings were made by using a drawing tube attached to the microscope and also by tracing photographic images in Adobe Illustrator CS3.

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All specimens are deposited in the Department of Invertebrates, American Museum of Natural History, New York.

Permarachne. The holotype and only known specimen of Permarachne novokshonovi, PIN 4909/12, part and counterpart, comes from the Koshelevka Formation, Kungurian Stage, Cisuralian Series (Permian), at the Krutaya Katushka outcrop, left bank of the Barda River, upstream of Matveyevka, Russia, and is deposited in the Palaeontological Institute of the Russian Academy of Sciences, Moscow. The specimen was studied, under ethanol to enhance contrast, by using a Wild M7S stereomicroscope, drawn by using a drawing tube, and photographed with a Nikon D1X digital camera attached to the microscope.

Palaeothele. A specimen of Palaeothele montceauensis, In 62050a housed in the Natural History Museum, London, was submitted to X-ray CT analyses. These were performed on a Phoenix v|tome|x "s" X-ray tomography system in the Engineering Faculty, Imperial College, London. X-ray source energy was 160 kV; the detector was a 16-bit flat panel 512 imes 512 pixel-direct digital detector using a stepping mode to double initial resolution. Analysis and reconstruction of tomographic slices was performed by using the custom SPIERS software suite; visualizations are ray-traced isosurfaces of data, manually prepared to remove artefacts and extraneous material.

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