The Spinning Apparatus of Geometric Spiders.

By

Cecil Warburton, B.A.,
Christ's College, Cambridge.

With Plate V.

THE familiar circular snare constructed by the "geometric" spiders has always been an object of interest to naturalists, but it is remarkable how little has been known until lately of the highly complicated organs which compose the spinning apparatus of these animals.

Thanks mainly to the labours of Blackwell,[1] Emerton,[2] Bertkau,[3] and lastly Apstein, a tolerably complete knowledge has now been obtained of the structure and general arrangement of these organs.

Apstein's excellent paper,[4] recently published, contributes much that is new and valuable, and fairly represents our present knowledge of the subject. Recent researches, however, have led me to dissent from some of that author's conclusions as regards the functions of the various spinning glands, conclusions based upon evidence for the most part too indirect to be entirely satisfactory.

Before discussing this matter, some description of the

[1] "On the Mammalæ of Spiders in Spinning," 'Trans. Linnean Soc. London,' 1839, vol. xviii, pt. ii.

[2] 'The Structure and Habits of Spiders,' Boston, Cassino & Co., 1883.

[3] "Cribellum und Calamistrum," 'Archiv für Naturgeschichte,' 1882, p. 316.

[4] "Bau und Function der Spinnendrusen der Araneida," 'Archiv für Naturgeschichte,' 1889, p. 29.

morphology of the organs in question will be necessary. The large garden spider, Epeira diadematа, is taken as the most convenient type of the family, but the following remarks apply in the main to all its orb-weaving congeners.

External Spinning Organs.

These occupy a small round area on the under surface of the abdomen towards the posterior end, where, when at rest, they present a bluntly conical protuberance (figs. 1 and 2, *sp.*). If this area be examined under a low power, it is seen to be occupied mainly by four conical spinnerets, their bases forming a quadrilateral, and their apices meeting in the centre of the area (fig. 8). The narrow space which intervenes between the bases of the anterior (or inferior) spinnerets (*a*) is filled by a small tongue-like process (*t*). The wider gap separating the posterior (or superior) spinnerets (*p*) is occupied by a terminal projection of the abdomen (*z*) containing the anus. Each of these spinnerets is two-jointed, and furnished at its extremity with a multitude of hair-like tubes containing the ducts of the spinning glands.

They are possessed of a wonderful mobility, and can be widely separated, or energetically rubbed upon each other with a rotary motion at the will of the animal. Their separation discloses a third and smaller pair of spinnerets consisting of one joint only, and having their apices directed backwards and inwards, so as to lie immediately beneath the apices of the posterior spinnerets (fig. 10, *i*).

These again present a large number of glandular orifices. They will be referred to hereafter as the intermediate spinnerets. Thus we have, in all, three pairs of spinnerets capable of a great variety of movement, and bearing at their extremities, as will be presently seen, about 600 spinning tubes.

Internal Spinning Organs.

Apstein has shown that there are, in this group of spiders, five distinct kinds of glands, to which he assigns the names Ampullaceal, Aggregate, Tubuliform, Piriform, and

Acinate. The first three kinds are few in number and of large size, extending throughout the greater part of the abdomen. The piriform and acinate glands are minute and numerous, and are closely grouped together immediately above the spinnerets.

Their exact arrangement is important and may be summarised as follows:

There are two pairs of Ampullaceal glands (fig. 3) debouching on the anterior and intermediate spinnerets respectively on the inner side.

There are three pairs of Aggregate glands, their three outlets on each side being situate upon the inner surface of the posterior spinneret.

There are three pairs of Tubuliform glands, two opening on the inner side of the posterior spinnerets, and one upon the outer surface of the intermediate spinnerets.

The above glands are comparatively large, and their ducts terminate in distinct tubular prominences.

There are about 200 Piriform glands, all connected with the anterior spinnerets, where their ducts terminate in hair-like tubes.

Finally, there are about 400 Aciniform glands, each posterior and each intermediate spinneret bearing the hair-like terminations of about a hundred ducts.

Or thus, tabulating for one side only:

Glands.	Ant. Spinneret.	Intermediate.	Posterior.
Ampullaceal . .	1 on inner side	1 on inner side	...
Aggregate . .	...	...	3 on inner side.
Tubuliform . .	...	1 on outer side	2 on inner side.
Piriform . . .	About 100	...	...
Aciniform . .	...	About 100	About 100.

The question naturally arises as to the different functions

performed by glands apparently so distinct. Apstein attempts its solution by reasoning which is mainly indirect and, in my opinion, misleading. It occurred to me that the problem might be attacked in a more direct manner, and with this view the experiments to be now described were performed.

A spider of this group usually trails a line from its spinnerets while walking. With a little dexterity it can be quickly seized, and imprisoned in such a manner that the spinnerets from which the line is proceeding can be microscopically examined.

This may be best effected by means of a piece of wood about the size and shape of a microscope slide, with a narrow band of cloth attached by its end to one extremity. The cloth band is then held in front of the crawling animal, which may, with a little practice, be thus trapped between the cloth and the wood, so that the band passes beneath the cephalothorax, leaving the abdomen free for examination with the lately emitted line still attached.

The fourth pair of legs must be kept from interfering with the experiment by pins suitably adjusted. The spinnerets will now be in their quiescent position, and the precise origin of the threads therefore invisible. If, however, it be gently drawn forwards, i.e. towards the animal's head, certain facts with regard to it become at once clear. As, however, the phenomena differ at different times, we must take the various cases in succession.

In the simplest case (fig. 9) one of the anterior spinnerets will be pulled forward with the thread, which will be easily seen to consist of a single line emanating from one large tube.

More frequently (fig. 10) the line will be double issuing from similarly situated tubes on the inner sides of the two anterior spinnerets. This is probably the most usual case, and I have drawn out from a spider many yards of such a double line of silk, its origin being all the time plainly visible.

It is important to note that there is no adherence between the two lines, which remain perfectly distinct throughout their whole parallel course.

The spider will probably tire of having its silk thus drawn out—a process which it can only influence indirectly. Were its hind legs free it would seize the thread and break it. It sometimes contrives to do this by a rapid movement of its spinnerets, but occasionally it decides to strengthen the thread instead. The spinnerets are accordingly actively rubbed together, and a little flocculent mass of silk appears upon the line, which is thereafter seen to consist of four strands, two of finer calibre having made their appearance between the former lines (fig. 11). To see their origin the anterior spinnerets must be kept forward by a gentle strain on the thread, and the posterior spinnerets thrust aside with a needle. The new lines may then be traced to the intermediate spinnerets, and proceed from large spinning tubes on the inner side. Again, the four lines remain distinct and non-adherent.

Should the spider still resolve on strengthening the line a further rubbing together of the spinnerets occurs, and presently a large number of strands are seen to proceed from the numerous hair-like tubes on the anterior spinnerets (fig. 12). The four previous lines are still distinguishable by their greater thickness.

If after drawing out several inches of this compound line it be slightly slacked, a puff of air separates the strands, showing that, though contiguous, they are not adherent.

Lastly, upon rare occasions, the whole battery of tubes seems to be brought into play, the posterior spinnerets contributing their quota to the strengthening of the line. Thus the "trailing line," as I have called it, will be found at any moment to be constituted as indicated in one of the cases above described.

It appears, therefore, that such a line usually consists of either two or four non-adherent threads emanating from what Apstein has shown to be the origin of the Ampullaceal glands, and that it may on occasion be strenghened by contributions from the Piriform and Acinate glands opening upon the anterior and posterior spinnerets respectively.

It was next attempted to apply the same direct method to

the observation of the animal when employed naturally in its various spinning operations. Here the difficulties experienced were considerable, but some results were obtained by the aid of a simple contrivance, consisting of a pair of compasses with the points fixed some two inches apart, and between them a narrow strip of cloth stretched.

A flat piece of wood was held behind the spider while at work, and between this and the strip of cloth the creature was suddenly trapped, the points of the compasses, which projected the eighth of an inch beyond the cloth, being buried in the wood on either side.

Flies were now placed in the various webs, and the spiders seized in the act of binding them up in the usual manner. The fly is held and rotated by means of the jaws, palps, and anterior legs, while the fourth pair of legs draw up from the spinners the bands of silk which are to enclose it. These silken bands were found to be constituted as shown in figs. 12 or 13. There seems no doubt, therefore, that the Aciniform and Piriform glands are mainly used in performing this operation.

The structure of the geometric snare was next investigated. This is a familiar object, and may be said to consist of—

(1) a sort of frame or scaffolding, to which are attached the distal ends of
(2) the radial lines;
(3) the spiral line, extending from the periphery to near the centre.

(1) The thread of the framework was generally found to be composed as exhibited in fig. 11. When necessary the spider strengthened the line by repeating the journey, and laying it down a second time.

(2) The same line, or that of fig. 10, was also employed in constructing the radii of the snare.

Thus the framework and radii of the geometric web are supplied by the Ampullaceal glands.

(3) The spiral line requires a more detailed description.

A low power shows it to consist of bead-like viscid globules

strung upon a thread with remarkable regularity, as shown in fig. 14 *d*.

It was until a few years ago supposed that these globules were separately deposited by the spider, whereas a uniform coating of viscid matter is given to the thread in the first instance, and its subsequent subdivision into globules is an entirely physical phenomenon. Boys[1] well describes the spider's action as follows:

"The spider draws these webs slowly, and at the same time pours upon them a liquid, and, still further to obtain the effect of launching a liquid cylinder into space, he pulls it out like the string of a bow, and lets it go with a jerk."

That this separation into globules is really a secondary phenomenon I have shown by taking upon a slide a portion of such a spiral immediately upon its completion. It readily stains with hæmatoxylin, and on microscopic examination shows the various stages indicated in fig. 14.

We have thus separately to consider the ground-line (Grundfaden, Apstein) and the viscid matter with which it is enveloped.

Apstein imagines the ground-line to be furnished by the Aciniform glands, and to be many-stranded.

I have not yet succeeded in tracing it with certainty to its origin, but have established the following facts with regard to it:

In the first place, it is not many-stranded, but double only.

When engaged upon this line the creature is so absorbed as to allow of pretty close examination with a hand-lens. I have at such times noticed that the posterior spinnerets are partly open, and that the line is, at first, distinctly double, fusing, by virtue of its viscid envelope, where grasped by the leg which draws it forth. Moreover, on staining and teasing the spiral line, the ground thread readily shows its double nature (fig. 15), but no amount of teasing breaks it up into further strands, as would surely be the case if such existed, for their separate

[1] "Quartz Fibres," by C. V. Boys, F.R.S., 'Nature,' July 11, 1889.

existence as threads implies a degree of dryness inconsistent with complete fusion.

As far as I have been able to trace these lines they have appeared to emanate from the intermediate spinnerets. They are much more elastic, however, than the radial lines, and can therefore hardly proceed from the Ampullaceal orifices.

The only other paired orifices on the intermediate spinnerets are those of the Tubuliform glands. Now, an important function of these glands is undoubtedly, as Apstein remarks, the spinning of the egg cocoon, for they are always distended with yellow fluid in the female just before the deposition of ova, and comparatively inconspicuous after, while the cocoon consists of yellow silk.

If, however, they also furnish the ground-threads, this would help to explain their presence in the male spider, which has not hitherto been very easy to understand.

The objections to this view are, first, that cocoon silk is not especially elastic, and secondly, that I have not been able to find threads in the cocoon of the precise diameter of the ground-threads.

In spiders of the species under consideration the following thread-diameters were found to be fairly uniform:

Cocoon line	·006 mm.
Anterior Ampullaceal	·003 „
Ground-line of spiral	·0025 „
Intermediate Ampullaceal	·0016 „

The imperfect view I obtained of the origin of the ground-thread led me to think that though it proceeded from the intermediate organs, it had some subsequent relation to the posterior spinnerets.

It is possible, therefore, that Apstein is correct in supposing that the Aggregate glands, which debouch on the inner side of the posterior spinnerets, deposit the viscid matter above described.

The arguments hitherto adduced in support of this view are, first, the convenient arrangement of the Aggregate orifices for such a purpose, and secondly, the presence of these glands in

such spiders—and such only—on whose threads the viscid matter has been observed. On dissecting out the various glands from a spider, isolating them on slides, and crushing them, I found that the contents of the Aggregate glands retained their viscidity the longest. Evidence was also sought from histological changes in the glands themselves before and after web-spinning, and though a much larger series of observations would be necessary to afford trustworthy results, alterations similar to those known to occur in active serous glands seemed to be taking place (figs. 19 and 20).

This would show that the Aggregate glands are used in spinning the web, in which case they must furnish the viscid matter, all the other structures being accounted for.

The unsafe nature of such indirect evidence is, however, freely admitted, but it may be pointed out that the certainty which now exists with regard to some of the glands gives greater probability of the true function being allotted to the remainder.

One other web structure remains to be briefly discussed. Foundation lines are attached to surrounding objects, and ordinary non-viscid lines are glued to one another by little patches of silk which we may call attachment discs (Haftscheibe, Apstein). The spider rubs its anterior spinnerets against a surface, emitting silk from the Piriform glands, and upon walking away a line is drawn out from the spinnerets.

I have been best able to study these structures in a small bottle in which a spider was obliging enough to deposit its eggs, fixing the cocoon in its place by a multitude of cross threads fixed to the sides of the bottle at their ends, and to one another where they intercrossed. Their appearance is given in figs. 16—18. It was this structure which led to the belief in the highly compound nature of the spider's line.

Summary.

1. Facts newly established.—A spider's line does not consist of many strands fused or woven together, but ordinarily of two or four distinct threads.

The framework and the radii of circular snares are supplied by the Ampullaceal glands.

The Acinate and Piriform glands are those mainly employed in binding up captured prey.

The "trailing line" consists primarily of Ampullaceal threads, sometimes strengthened by contributions from the Acinate and Piriform glands.

The ground-line of the spiral is double only, and the two strands are bound together merely by the viscid matter which envelops them.

2. Corroborative of Apstein.—The "attachment discs" are furnished by the Piriform glands.

The Tubuliform glands supply the silk for the egg-cocoon.

The viscid matter of the spiral is probably the product of the Aggregate glands.

Finally, the origin of the spiral ground-line is uncertain, but it may proceed from the Tubuliform orifices on the intermediate spinnerets.

Morphological Laboratory, Cambridge.

EXPLANATION OF PLATE V,

Illustrating Mr. Cecil Warburton's paper on "The Spinning Apparatus of Geometric Spiders."

FIG. 1.—Profile of Epeira diademata, sp. spinnerets.

FIG. 2.—Ventral aspect of the same species.

FIG. 3.—Ampullaceal gland.

FIG. 4.—Aggregate gland.

FIG. 5.—Tubuliform gland.

FIG. 6.—Piriform gland.

FIG. 7.—Acinate gland.

FIG. 8.—External spinning organs at rest. *a*. Anterior, *p*. Posterior spinnerets. *t*. Anterior tongue-like fold. *z*. Terminal fold of abdomen.

FIGS. 9—13 show the composition of the "trailing-line" under various circumstances. *i*. Intermediate spinnerets.

FIG. 14.—Stages in the formation of the viscid globules. *d*. Shows the final arrangement.

FIG. 15.—Teased spiral line, showing that the "ground-line" is double.

FIG. 16.—"Attachment disc" (Haftscheibe, Apstein).

FIG. 17.—The same, more in profile.

FIG. 18.—Attachment disc, gluing together irregular strands which held an egg-cocoon in position.

FIG. 19.—Section (somewhat diagrammatic) of aggregate gland at rest.

FIG. 20.—Ditto of aggregate gland when the spider had just constructed its web. (The right half only of Figs. 19 and 20 is shaded.)

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

Fig. 6.

Fig. 7.

Fig. 8.

Fig. 9.

Fig. 10.

Fig. 11.

Fig. 12.

Fig. 13.

Fig. 14.

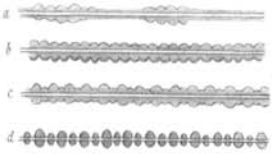

Fig. 15.

Fig. 17.

Fig. 16.

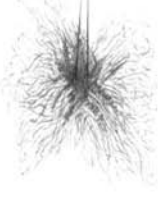

Fig. 18.

Fig. 19.

Fig. 20.