[*From the* Proceedings of the Royal Society, B, Vol. 102, 1928.]

On the Production of Silk by Species of the Genus Hilara *Meig.* (*Diptera*).

By H. ELTRINGHAM, M.A., D.Sc., F.Z.S.

And an Appendix on the Habits of the Species.

By A. H. HAMM, A.L.S., F.E.S.

[*Reprinted from the* PROCEEDINGS OF THE ROYAL SOCIETY, B, Vol. 102.]

On the Production of Silk by Species of the Genus Hilara *Meig.* (*Diptera*).

By H. ELTRINGHAM, M.A., D.Sc., F.Z.S., with an Appendix on the Habits of the Species, by A. H. HAMM, A.L.S., F.E.S.

(Communicated by Professor E. B. Poulton, F.R.S.—Received Oct. 17, 1927.)

[PLATE 22.]

In the *Entomologist's Monthly Magazine* for 1877, p. 126, there is a note by Baron C. R. Osten-Sacken describing certain species of the genus *Hilara* which, in flying, carried with them " bits of white tissue." These objects, on closer examination, proved to be flakes of " opaque, white, film-like substance, oval, about 2 mm. long, and so light that the faintest breath of air could lift them." He describes the appearance of the film as " not unlike the opaque white tissue spun by some spiders." The species of fly was identified as *Hilara alpina*, Loew, by Prof. Loew, who also informed Baron Osten-Sacken that Prof. Zeller had made a similar observation on August 14, 1873, near Bergün.

The foregoing account appears to include the first recorded observation on the habit of silk-spinning in the genus. In regard to the name *alpina*, the original identification of the film-making species is questioned by Becker (*Berlin Ent. Zeit.*, 1888, p. 7) and he gives to it the name of *Hilara sartor*, and appends a full description of the two sexes. He supposes that the secretion is produced from the abdominal glands. In 1889 (*Ent. Nachr.*, p. 220) Girschener described the webs made by *H. maura*, Fab., and *H. interstincta*, Fall., and pointed out that they sometimes contained the insect prey of Hilara. Later, Mik added the species *H. aëronatha* to the list of those which carried prey. Handlirsch (in *Verh. Zool.-Bot. Ges.*, Wien, 1889, p. 624) further described, with much detail of

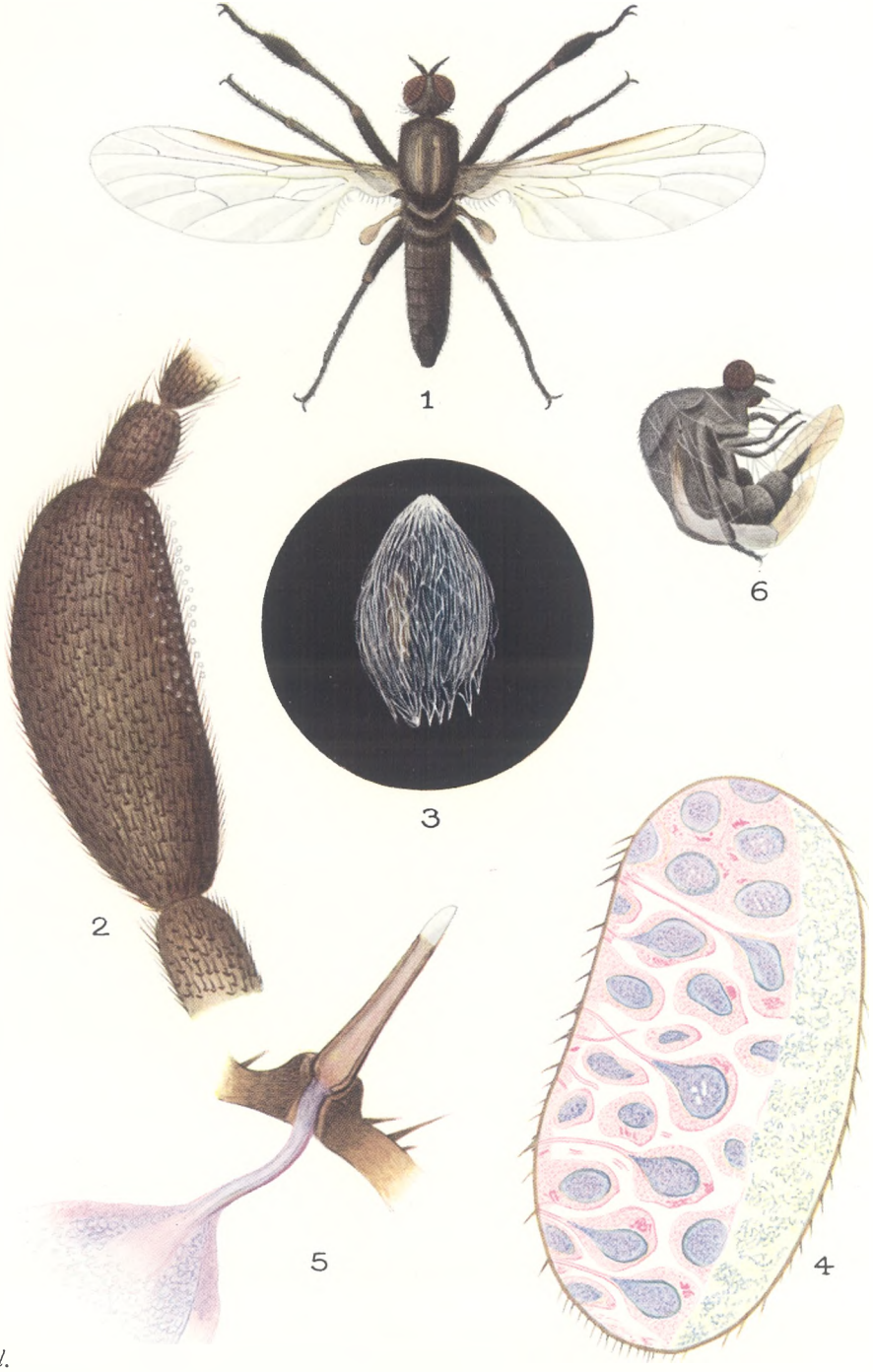
measurement, the webs or veils made by *H. sartor*. He gives the diameter of the threads as 0·001 to 0·0015 mm., and states that the silk is similar in chemical composition to that of caterpillars and spiders.

In *Wiener Ent. Zeit.*, vol. 12, p. 260, Mik published a paper on the biology of certain Diptera, the second part of which is devoted to the spinning of certain Hilaras. He discusses at length the previous work on the subject, and the many opinions that have been expressed as to the use, method of carrying, and origin of the silk, and concludes that it is produced from the mouth. In the *American Naturalist*, 1899, No. 394, p. 809, Aldrich and Turley give an account of a "Balloon-making Fly." The species was identified as *Empis poplitea*, Loew, "or a closely allied species." In this case the balloon is described as composed of sticky globules, which were immediately dissolved by alcohol. The balloons sometimes contained prey.

Evidently in this species we have something of a different nature from the silk produced by Hilara. In the silk-making species of Hilara, the substance hardens so rapidly in the air that it is never found to be sticky, and it consists of threads and not globules. Mr. A. H. Hamm has, however, found a species which carries small globules apparently of a nature somewhat different from the usual silk.*

It would be difficult, even in a paper of much greater length than this, to do adequate justice to the long series of painstaking observations which have been made by Mr. Hamm, of the Hope Department at Oxford, on the habits of the British species of Empidæ, including especially the genus *Hilara*, found near Oxford. The first published account of this work appeared in the *Oxford University Gazette* of 4th June, 1913, being in fact a part of Prof. Poulton's Report upon the Hope Department for 1912. The collections have been generously presented to this Department and are arranged in groups—"first and lowest, as food devoured by both sexes without relation to pairing, then as

* The precise nature of these globules remains in doubt. The species found carrying them has been identified by Mr. J. E. Collin as *Hilara maura*. I have made preparations of the elaborate genitalia both of *maura* and of an individual which Mr. Hamm found carrying a globule, and could detect no difference between them. The globules are of a peculiar viscid substance. So permanent are its qualities that examples mounted on cards fifteen years ago are still as viscid as when first obtained. The substance is soluble in water, rather slowly soluble in xylol, and insoluble in pure alcohol, ether or chloroform. It has a sweet taste. I described these properties to my friend Mr. D. L. Chapman, F.R.S., the well-known chemist, and he is of the opinion that it must be of a sugary nature. Since *H. maura* will pick up any small object, it seems likely that the globules are obtained by it from some external source, but further investigation can only be made during some future season when the fly is obtainable.



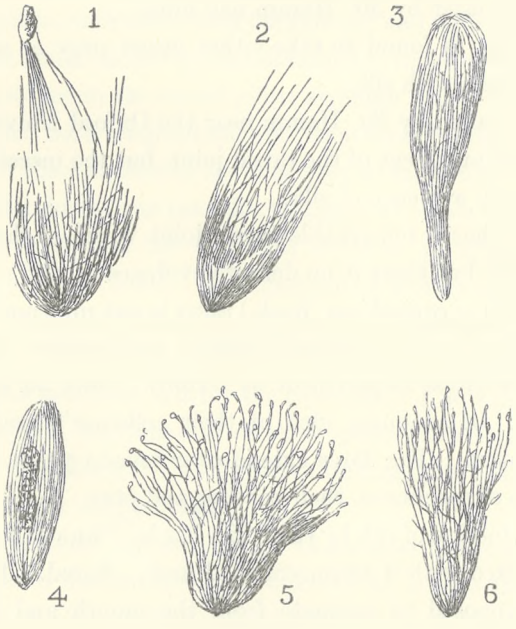
H. Eltringham del.

Production of Silk by Flies of the genus Hilara.

a gift provided by the male and devoured by the female during pairing, finally as it were an ornament or plaything—no longer eaten by the female, but acting as a lure or stimulus. In the last stage the prey is often replaced by some vegetable fragment which is quite unsuitable as food. The climax of this line of evolution is reached in an elaborate cocoon spun by the male around the prey, and replacing the latter as an object of attraction " (see *Ent. Mo. Mag.*, vol. 49, 1913, p. 178, where the report is reprinted).

Amongst the species experimented upon by Mr. Hamm are the following—*H. maura*, Fab. This species makes quite considerable " balloons " of which one is illustrated in fig. 3, Plate 22. This particular example is about 4 mm. long and 2 mm. wide, and contains a small object, probably a particle of vegetable débris. Although there is some irregularity, a general direction of the main threads can usually be detected, running from pole to pole, and where two join towards one end of the cocoon they often fuse into a single thread. The form of these cocoons varies greatly, and almost any shape may be found, from an elongated balloon, pointed at both ends, to a mere tangled, more or less spherical mass.

I have shown in the text-figures six examples of these cocoons. Nos. 1 and 2 were made by *H. pilosa*, Zett., 3 to 6 by *H. maura*. Sometimes a fairly regularly constructed example spreads out spontaneously into quite a large ball of fluff



after it has been mounted on a card. *H. maura* will accept any small object thrown on the water, though it often catches small insects, and even examples of its own species. When such prey is large, it seems to be merely rolled up and tied with a few strands of silk. Fig. 6, Plate 22, shows another Hilara which, after being disabled and thrown on water, was picked up and bound with silk by a male *maura*.

The manner in which *maura* and other species overcome the surface tension of the water in order to pick up a floating object is remarkable. The insect whirls rapidly round and round, and so lifts the prey in a little vortex of its own making.

H. quadrivittata, Mg., was not observed to make any balloon, but takes small insect prey and binds it with silk. It will not accept any extraneous object.

H. curtisi, Collin (= *cilipes*, Meig.), has the usual enlarged tarsal joint but has not been observed to make silk.

H. beckeri, Strobl., has the tarsal joint but slightly enlarged. It takes insects as prey and ties them with silk, but does not appear to make balloons.

H. pilosa, Zett., has been taken by Mr. O. W. Richards, of the Zoological Department, Oxford, and by Mr. Hamm, in very small numbers. It makes a silken structure of great beauty, which may be described as comet-shaped, having numerous threads trailing from a kind of central point or nucleus. The few examples obtained in the first instance (by Mr. Richards) had prey in the silk. Others taken later by Mr. Hamm had none.

H. thoracica, Mcq., is found to take either insect prey or small extraneous objects and bind them with silk.

H. litorea, Fall., taken by Mr. Hamm near the Oxford University Parks, has a well-developed enlargement of the tarsal joint, but the insect prey taken with it does not show any evidence of silk.

H. chorica, Fall., has a remarkable tarsal joint which is short and rounded. It takes insect prey, but there is no definite evidence of silk.

H. fuscipes, Fab. (= *carinthiaca*, Beck.) takes insect prey and ties it with silk.

All the above species, and others collected and observed by Mr. Hamm, can be seen in the Hope Department at Oxford. Only an inspection of the material can give an adequate idea of their collector's great industry and powers of observation. The dates extend over several years, and the mounts contain thousands of specimens, their cocoons and prey.

Though the production of silk by these flies has been known for so many years the organs associated with it have remained undiscovered. The secretion has been variously supposed to emanate from the mouth and from abdominal

glands. Some time ago Mr. Hamm suggested that I should endeavour to find the silk-glands, since such must evidently exist, and I did in fact make sections from material which he kindly obtained for the purpose. I must admit that I also was obsessed with the idea that the glands would be found in the thorax or abdomen of the insect. Indeed one would rather naturally expect to find some modification of the salivary glands. My researches did not then furnish any clue to the mystery, the short season of the imaginal fly was over, and pressure of other work caused the matter to be left in abeyance. Early this summer however (1927) Mr. Hamm again brought me material and suggested that the peculiarly enlarged basal joints of the fore-tarsi in the male might be worth examination. The first species to be taken was *H. maura*, and when this was over the work was continued with *H. quadrivittata*.

On teasing out one of the enlarged tarsal joints, which had been treated with picro-chlor-acetic acid, and examining the mass under a moderate power, there appeared numerous large cells or glands, somewhat pear-shaped, and each having a tube-like structure emanating from its thinner end, like the much enlarged stalk of the pear. Evidently there was some glandular structure in the tarsus.

Fresh examples were then examined. On breaking open the chitin there emerged drops of a clear fluid which, on exposure to the air, hardened with great rapidity. A needle inserted in one of the drops and drawn slowly away carried with it a thread which became dry and more or less rigid in a few seconds, the effect being similar to that obtained in drawing out a thread of molten glass. The substance in the tarsal joints strongly resembled a silk-like secretion.

Sections, both longitudinal and transverse, having been made, the glandular nature of the contents of the modified tarsal joint was no longer in doubt, and the tubular ducts from the cells, though very liable to fracture in section-cutting, evidently ended at the chitinous exterior, principally on the rather narrow edge of the tarsal joint. Examination of a piece of the chitin, flattened-out on a slide, disclosed the fact that close to the base of some of the spines in this area, there was, in the substance of the chitin, a minute pore, at first interpreted as a means of exit for the secretion. I now know, however, that this is incorrect, and the function of these pores remains for the time being undiscovered. The chitin is densely pigmented, and, being rather hard, it is extremely difficult to cut thin sections.

Having determined the part to which most of the gland ducts were directed, and prepared more sections, so oriented as to pass through this area, a careful examination showed that each gland-duct led to the base of a specialised spine.

Most insect spines, though hollow throughout the greater part of their length, are closed at the distal extremity. The poison-spines on the larvæ of Limacodid moths contain glands and are capable of injecting the poison into any wound they make, but this is accomplished by an ingenious arrangement by which the point of the spine becomes detached.* Ordinary examination of the spines on the tarsus of Hilara does not disclose any opening, and yet the gland-duct leads directly into the spine.

A perfectly fresh tarsus was placed on a slide under a medium power and pressure applied by laying over it another slide. Minute beads of the secretion could then be seen to exude from the points of the spines, and, by sliding the upper glass over the lower, these beads could be drawn out on the glass into threads which hardened rapidly in the air, and although thicker, resembled the silk spun by the insect. Sections in which these special spines occurred were examined under a high power, and it was then seen that the hard chitinous tube of the spine ended at a short distance below the extremity, and the point, which is comparatively blunt, seemed to consist of a very delicate membrane. There can be no doubt that the membrane opens at the end under the pressure of the secretion, and probably closes again by its own elasticity. Indeed such a provision would seem to be necessary, since the secretion hardens so rapidly on exposure to the air that an ordinary open tube would speedily be blocked by a film of the solidified substance at its extremity. In many sections ordinary spines can be seen, but in these the deeply pigmented chitin continues to the end, which is sharply pointed, and unprovided with the valve-like structure found on the spinneret-spines, as they may be called.

Reference to Plate 22 will now make these organs clear. Fig. 1 is a magnified view of the male of *Hilara maura*, in which the enlarged basal joints of the fore-tarsi can be distinctly seen. The wings are actually covered with minute hairs, but as these could not be resolved at the power used when making the drawing, I have not indicated them. The actual wing expanse of the specimen from which this was drawn is 11·5 mm. Fig. 2 shows the enlarged tarsal joint under a much higher magnification, and at the upper part of the right side the beads of the secretion can be seen exuding from the spines, as they do when pressed between two glass slips. Fig. 4 is a magnified view of the tarsal joint of *H. quadrivittata* as seen in longitudinal section. The drawing, which represents a reconstruction from several sections, as well as from teased and other preparations, shows the appearance when stained with eosin, methyl-blue orange-G, and light-green.

* See my '*Butterfly Lore*,' Oxford, 1923, p. 50.

It will be seen that the secreting cells consist of an enveloping cytoplasm (stained pink), enclosing a mass of granular, globular, or vacuolated secretion (stained mauve), and where it happens to fall in the plane of the section, the duct of each cell can be traced to its junction with the chitinous envelope. The cells themselves show remarkably little structure, even when stained with iron-hæmatoxylin. The outer cytolasmic envelope appears slightly granular, and portions, occasionally darker, though ill-defined, seem to indicate nuclei. The inner secretory substance varies considerably in appearance. In some cells it is merely granular, in others it shows comparatively large globules, and sometimes quite large vacuoles.

In all the complete and undistorted sections the glandular mass is definitely separated from the chitin of the side opposite to the spinneret-spines by a space containing a finely granular substance (green in the section) which has all the appearance of insect blood after treatment with a fixative. There seems little doubt that there is a large blood-space in this position, and that its pressure, increased by some contractile action in another part of the body, serves to control the exudation of the silk from the spinneret-spines.

Although not showing continuously in any of my sections, I am inclined to think that the proximal ends of the glandular cells lie upon, or perhaps by their fusion form, a delicate membrane lying between them and the blood-space. The diameter of the gland-ducts is about 0·002 mm. Fig. 5 shows a view under the 1/12 inch oil-immersion objective of a single spinneret-spine of *H. quadrivittata* in its socket, with the gland-duct joining it, and part of the cell from which the duct arises. The delicate membranous "valve" can be seen at the end of the spine. The spine itself is about 0·025 mm. in length and about 0·0035 mm. in diameter, although thicker at the base.

Examples of the production of silk by a mature insect are of the greatest rarity. Silk is produced by species of Hydrophilinæ (*Coleoptera*) which make egg-cocoons. Psocids cover their eggs with little silken pads or scales. Embiidæ live in silken galleries. After I had made the foregoing observations on Hilara, Mr. O. W. Richards kindly called my attention to a paper I had not seen,* in which Melander describes the silk-producing glands in *Embia texana*, Mel., and shows that the silk from this species is also produced "in the thickened anterior metatarsi, within chambers,† and conducted outside to the recurved hairs at the edge of the plantar surface."

* Melander, *Zool. Bull.*, vol. 3, p. 16 (1902).

† Melander uses the word "chambers," probably assuming that each silk-gland is multicellular, as indeed they may be in Embia. Those in Hilara are, in my opinion, unicellular.

Melander gives a diagrammatic section of the part of the tarsal joint of *E. texana*, and though differing in detail, the apparatus is in general arrangement similar to that found in Hilara. That silk-glands should be found in the tarsal joints of insects belonging to two such widely separated orders as Embiidæ and Diptera is probably a unique example of parallel development. I have to thank Mr. Hamm for the whole of the material used in the investigation, and also for valuable assistance. Indeed, without his help and co-operation the work could not have been carried out.

Appendix.

On the Epigamic Behaviour of Hilara maura, *Fab., and two Allied Species.*

By Albert Harry Hamm, A.L.S., F.E.S., Assistant in the Hope Department of Zoology, Oxford University Museum.

The following record of observations is offered as a supplement to Dr. Eltringham's researches upon the silk-producing apparatus of the male Hilara.

Hilara maura, Fab.—Around Oxford this species is the commonest and most generally distributed of any in the genus, and is at the same time by far the most interesting because of its extraordinary and remarkably variable habits.

These flies are on the wing from mid-May to mid-June, and in some seasons occur in extraordinary abundance. They are always to be found flying over or near water, although the smaller streams are most favourable for observation. This follows from the fact that the flies collect in incredible numbers on a limited surface, while on rivers or ponds they become so widely dispersed that it is difficult to follow their activities in detail. Hence all my observations have been made on small streams from 3 to 6 feet wide. Sometimes, when one approaches such a stream at the period of maximum abundance, the flies are so numerous that they produce the appearance of a thick haze lying on the water. After rain, the males may sometimes be seen in abundance flying just above the surface of small pools in the roads. I have also seen them in the city itself swarming over the gutters after the passage of a water-cart.

Some of the males are to be seen skimming hither and thither over the water—apparently skating upon it but without touching the surface—and all the time keeping a sharp look-out for any small insect or other object as it comes floating down the stream. Having seized its "prey" a male immediately joins the throng flying from 1 to 3 feet above the water. This swarm, made up of virgin females and males carrying their "prey," flies rapidly for a variable distance

PROCEEDINGS OF THE ROYAL SOCIETY,
SERIES B.

SUBSCRIPTION PRICE 20 SHILLINGS PER VOLUME.

Printed and published for the ROYAL SOCIETY
by HARRISON & SONS, LTD.,
44—47, St. Martin's Lane, London, W.C.2.