XVIII. On the larvæ of the Tenthredinidæ, with special reference to protective resemblance. By P. CAMERON.

[Read June 5th, 1878.]

THE purpose of the following paper is to show that the theory promulgated by Wallace,* in explanation of the colours and markings of caterpillars, namely, that edible larvæ are coloured so as to be invisible as much as possible, and inedible ones so as to be easily seen, holds good with the larvæ of saw-flies. I purpose also showing that caterpillars and saw-fly larvæ have the same style of coloration and arrangement of the markings both in the edible and inedible larvæ, that is to say, that the former are green, either entirely so, or if they bear any markings these take the form of white or pink continuous lines along the back or sides, while the latter have contrasting colours; the markings are usually irregularly-arranged dots, and they feed in exposed positions where they are readily noticed.

I need scarcely point out how widely different the *Tenthredinidæ* and the *Lepidoptera* are, how they belong to two different orders, differing profoundly in almost every detail of structure, and having no very close generic affinity with each other.

Let us first consider those saw-fly larvæ, whose bodies correspond in coloration with the substances upon which they are usually found. Many of these have flat bodies, and rest when feeding upon the lower side of the leaf. In every case they are uniformly green, with the head faintly brownish, or it may be green, like the rest of the body. A beautiful example of the flat green larvæ we find in that of *Camponiscus luridiventris*, which seems indeed to have been specially formed for this mode of life, being very broad and flat. We have other instances in the *luteus* group of the genus *Nematus*, which feed on the lower surface of the alder leaves, and in *Nematus pallescens*,

* See Darwin's "Descent of Man," 2nd ed. p. 325.

TRANS. ENT. SOC. 1878.—PART III. (OCT.)

whose body corresponds in coloration with the leaf of *Salix cinerea*, its food plant. These larvæ are very sluggish.

Another group of harmless larvæ feed along the margin of the leaf. They have cylindrical bodies, the colour green, or if they bear any markings, these take the form of whitish or pinkish dorsal or lateral stripes. We have said that they feed along the outer edge of the leaf. Necessarily, in feeding, they cause indentations in the leaf. The indentations are very regular, are cut clean as if by a pair of scissors, in shape they are oval or semi-circular. When feeding, the larvæ keep their bodies closely pressed to the leaf, and if there be a curve, either a natural one or made by themselves, they follow its shape. We may point out as examples of this habit, *Nematus miliaris*, *N. fagi*, *N. fallax*, and others.

It is a matter of familiar observation to collectors of Lepidoptera, that most caterpillars, which feed on grass or narrow-leaved plants, are green, either entirely so, or with white or reddish continuous stripes, and so it is with the saw-fly larvæ. In Nematus it is the case with N. capreæ, N. conductu which feed on carices and grasses respectively, with N. fallax, which is attached to the little trail-. ing willow Salix fusca, with N. rumicis on Rumex, N. mysoitidis on clover, Taxonus glabratus on Polygonum, and many others. In the Ent. M. Mag. XI. p. 66, the Rev. John Hellins relates how similar in coloration the larva of the moth Erastria fuscula and that of a saw-fly, which feeds on the same grass, are to each other, and he proceeds to say that "he will leave it to some one else to guess which of the two is the first wearer, and which the mimic of the colours of their common dress." But it is clear that here we have no case of mimicry, but rather that both acquired the same garb through its being that which afforded them the greatest protection, similar habits and similar surroundings having led to identity in coloration.

It is equally well known to Lepidopterists that pine-feeding caterpillars assimilate very closely in coloration with the pine leaves. This is so well known that I need scarcely quote instances; it occurs with widely different families of moths. The same thing occurs with the saw-fly larvæ. I may mention as examples *Nematus Erichsoni*, *Lophyrus virens*, and many others.* One of the finest cases

^{*} They feed resting perpendicularly, which is seldom the case with larvæ attached to broad-leaved plants.

of protective resemblance I have seen was with a species of *Nematus* on the juniper. It could scarcely be seen, so much did its body resemble the leaves. I need scarcely say that many caterpillars of moths on the juniper have the same colour.

We have seen that the innocuous larvæ are either flat or cylindrical, the former feeding on the flat surface and the latter along the edge. It is equally so with those which smell badly.* Curiously enough, the flat larvæ in both the groups are uniformly green, and have the same sluggish habits, but there is a marked difference in their ways of feeding. I have said that the edible ones feed on the under side of the leaf. They eat the leaf quite through, so that in a short time it becomes full of square or roundish holes, the creature resting always on the uneaten portions. Now the others rest on the upper side. They do not eat the leaf through and through, but only the upper cuticle, so that when the larvæ have been feeding for any period, the leaf becomes quite white, and the larvæ are then not difficult to see. Now we find that larvæ which have this habit are either covered with a slimy secretion, as some species of *Eriocampa*, or they emit bad odours, as is the case with some Nematides. The larva of *Nematus leucotrochus*,[†] for instance, which feeds on the hawthorn, has an exceedingly bad smell. I tried this larva with a Carabus to see if the beetle would eat it, but it would not do so, although afterwards it ate a bit of a worm.

The inedible larvæ which feed along the edge of the leaf are very different in coloration and habits from the green margin feeders described above. Many of them have a greenish tinge, but it is seldom or never of the same tint as the leaf. Frequently it is bluish or seagreen, or it may be whitish. Instead of the white or pinkish stripes they bear irregular dots and marks, which

* Although I have not made many experiments with the foul-smelling larvæ to see if they are rejected by insectiverous animals, still I think it is allowable to conclude from the bad secretions they give out that this is actually the case.

 \dagger These larvæ are very difficult to rear. I have only bred three females, which unfortunately died in the cocoons before they got entirely rid of the pupal skin. They are thus not easily identified, but the specimens appear to agree in every respect with *N. leucotrochus*. Brischke and Zaddach figure (Schr. Ges. König. XVI. pl. 6, f. 5) a species of similar habits and coloration under the name of *N. xanthopus*, but as the description has not yet appeared, I can't say whether it is the same as mine or not.

do not form regular lines. The markings are usually black and orange, and often fore and aft the body is orange or yellow. Instead of keeping their bodies close to the leaf and following its outline they stick them out into the air, so that they assume the form of a U, the turned-up tail reaching to the head and frequently above Some of them bear black marks on the belly, between it. the ventral legs, and also glands, which they can protrude at will, and from which exude a foetid odour. To make them even more conspicuous, several of them feed on the same leaf, while they keep the posterior part of the body in a state of continual agitation. Most of them are uneaten by birds, and they are also proof against the attacks of insects, for a cockroach would not eat some larvæ of Nematus pavidus with which I supplied it, after having subjected it to a fast of some days, while it devoured those of N. miliaris.

I think that the habit these insects have of whipping the body about is not so much to frighten birds as to intimidate ichneumons from depositing eggs in their bodies. I once observed a Tryphon endeavouring to lay its eggs in some larvæ of Cræsus septentrionalis, which at that time were very common on an alder bush. It tried it on several larvæ. In one case five larvæ were on the same leaf, and whenever the parasite approached them in a moment they were in a state of considerable agitation, and the intruder was driven away by the active lashing of their bodies. It, however, succeeded with a solitary larva which was rather inactive, being apparently about to moult. I may here remark, that every saw-fly larva which I have found "stung," i.e. with ichneumon eggs on its body, had them invariably on the fore region of the body, generally on the thorax, frequently even on the head-a circumstance readily understood when we consider that the posterior part of the body can be easily moved away, while the anterior part can only be removed by the creature letting go its hold of the leaf. The only way it can do this with sufficient swiftness to escape the ovipositor of the ichneumon is by dropping to the ground at once. And this we find to be the case with many larvæ, especially with those attached to grasses and other low-growing plants, e.g., the larvæ of *Dolerus*, *Tenthredo*, which drop down on the slightest occasion. On the other hand, larvæ attached to trees do not readily drop down, but then we have seen that some of them can protect themselves by

means of the flexible abdomen, and others, as we shall see, have especial means of protection.

Take, for example, the larvæ of Trichiosoma; these are among the largest in the family. They are white, which contrasts well with the green of the leaf, and, as they feed openly, they are readily observed. They have the faculty of ejecting from lateral pores an acid greenish liquid to some distance and in some quantity. I have no doubt that this is as much a protection against ichneumons as against birds. We know, indeed, from the observations of Lewis (quoted by Westwood, Intr. ii. 108), that the larva of Perga (an Australian genus closely allied to the *Cimbicides*) carries in its mouth a yellowish gummy matter, which it can vomit in some quantity when there is any occasion for it. That it is of some protection against ichneumons is shown by Lewis finding an ichneumon which preys on the larvæ with its legs and wings covered and glued together by this gummy matter.

Most of the larvæ of the *Cimbicina* feed on trees during the day, and they hold on very firmly to the leaf. They are in coloration white or greenish-white, without any distinct marks, and in some cases are covered with a whitish exudation. An exception to this rule is found in *Abia sericea*, which is found on *Scabiosa succisa*, usually in the evening. It is of a drab colour, with orange lateral marks. When alarmed it drops at once to the ground * in the form of a ball. I always, when searching for this larvæ, was much puzzled to find it when it had dropped down to the ground. Frequently when found I have lost it again by removing my eye for a moment, and yet it could not have changed its position. Indeed, most larvæ which fall readily to the ground in the form of a ball are difficult to find.[†]

It is curious to see how different the larvæ are in the same genus—even a small one—and how interesting it is to find that these differences are explained by their habits, and especially as regards their means of protection. Take, for instance, the genus Cræsus. Two of our species have very distinctly-marked larvæ. C. varus, on the contrary, although it has the form and habits of

^{*} It feeds also on the under side of the leaf, while the tree-feeders rest on the upper side.

[†] This habit of falling down to the ground and remaining there motionless, rolled up into a ball, is analogous to the "shamming dead" of perfect insects.

C. septentrionalis (vide supra), is much less active, has no coloured marks on the belly; it has the ventral glands, but they are rarely protruded, nor has it (so far as I can judge) a very bad odour; indeed, I could not feel any from some specimens which I examined last year. Above all, the larva of varus is of the same green as the alder leaf upon which it feeds, and has no markings beyond some slight black lines along the sides. It is thus less noticeable than the other larvæ, is more solitary in its habits, and hence we can understand how it is not so active, nor has such a bad smell as the others.

I have stated before that many pine-feeding larva are coloured to resemble the pine leaves—either entirely green, or green with a white lateral stripe. But this is not the case with all of them. *Lophyrus pini* has a palecoloured larva with round black marks on the sides. It feeds, too, in companies, frequently two or three dozen, if not more, being found on the same shoot; so that in this way they form, when massed together, very conspicuous objects, the more especially as they strip the branches almost completely of their leaves. The distinction of the *pini* and *virens* larvæ is readily explainable by the fact that the former exudes abundantly a resinous secretion, which sticks firmly to the hand, while the latter does not give out any.

Many of the brightly-coloured saw-fly larvæ have hairs on the body, each issuing from a raised tubercle. These hairs, however, are not very thickly distributed over the body, generally about a dozen or so to a segment, so that they do not in any way obscure or hide the coloration. The larva of *Nematus ribesii* is a case in point, and it is not eaten by birds. A more conspicuous example is found in the larva of *Cladius viminalis*, which is orange with black markings, and they feed in a row, three or four lying abreast and almost touching each other. All the larvæ, however, of this class are not brightly coloured. Thus, most of the larvæ of *Cladius* are pale coloured, or dark coloured on the back and white at the sides.

While there are no hairy larvæ among British sawflies comparable,—for instance, to caterpillars like the tiger moth,—there are some Tenthredous larvæ provided with longish stiff-branched spines, which give their bearers a very curious appearance. These spines are black (as a rule) on the back, with green ones along the sides, and they project straight from the body. The ground colour of these larvæ is green, and the spines are never so thick as to hide the coloration of the body. With some species there are some little white lines between the rows of spines. The larvæ feed on the upper side of the leaf; they are very sluggish and rarely measure more than four lines. I believe these spines standing up from the green body tend to conceal the larvæ, which do not look like living creatures at all; and this inanimate appearance is increased by the small retreating head. One or two species have the spines pale green.

There are many other points of similarity between the larvæ of the *Tenthredinidæ* and *Lepidoptera* which, if time permitted, I should have liked to discuss, as well as some others belonging more particularly to the Hymenopterous section. I may, however, say, that all the conclusions arrived at by Weismann, in his work* on the origin of the forms and colours of caterpillars of the *Sphingidæ* apply with equal force to the *Tenthredinidæ*. That being the case, the cause or causes which produced the general similarity in the markings of the larvæ of saw-flies and of caterpillars must have been the same, and that natural selection was one of the most proficient of them will now, I think, be admitted by the majority of naturalists.

I may add, further, that when young the larvæ of saw-flies are green and devoid of distinctive markings, just as we find among moths.

• Studien zur Descendenz-Theorie, ii.



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