ON THE CHEMOTROPISM OF INSECTS AND ITS SIGNIFICANCE FOR ECONOMIC ENTOMOLOGY.

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In a highly interesting article in a previous number of this journal (vol. iii, p. 343) J. Dewitz discussed "The bearing of physiology on economic entomology," and gave in this connection, amongst other things, an account of the various kinds of tropisms and their use, besides which he also pointed out the necessity for studying these for the purpose of discovering weapons for fighting noxious insects. It strikes me, however, as if the importance of chemotropism had not been emphasised in this survey as in my opinion it ought to have been, and the purpose of these modest lines is partly to draw attention to two important researches in this branch of science, recently carried out independently of each other, partly to point out that with the aid of chemotropism we shall in all probability be able to discover new weapons for the fight against noxious insects.

By the term "chemotropism" is meant, as it is well known, the automatic orientation of the animals to any olfactory sensation in such a manner that both sides of the body are struck by the lines of diffusion at the same angle. Theoretically, when a substance diffuses an odour, fine particles are ejected in straight lines, but in reality the air currents cause the lines to deviate from their straight track, and for that reason we cannot expect insects in the case of chemotropic movements to follow such straight lines as in the case of phototropic movements.

Chemotropism is a very important factor in the life of insects, and its positive action is especially evident in the following circumstances: in the search of the sexes for each other; in their search for food; and in oviposition. On the other hand, the occurrence of negative chemotropism is demonstrated by the fact that many insects protect themselves against their enemies by discharging evil-smelling fluids, and so forth.

Entomologists have been aware for a long time that the males of certain species of moths are attracted from a great distance by the females, and the phenomenon has been confirmed by many experiments. It is perfectly well known also that the antennae of many males are far better developed than those of the females, and that olfactory organs of different kinds are found both in male and female Lepidoptera. All these arrangements go to prove that chemotropism plays an important part amongst the Lepidoptera from a sexual point of view. It is, however, quite obvious that sexual chemotropism cannot be utilised in practice, unless the females were attracted by the males. But this appears to occur only in extremely rare cases (*Hepialus hecta*, according to Degener).

The position is quite different in the case of that form of chemotropism which guides the insects in their search for food, or the females when ovipositing; and the former action has actually been turned to practical use for a long time by

collectors who employ traps with strongly smelling baits. Numerous observations have shown how coprophagous Lamellicornia and carrion-bettles are capable of detecting a long way off the smell of excrement and carrion; similarly in the case of insects, the females of which oviposit upon substances or plants that serve both themselves and their larvae as food, it has been recognised that it is the odour that guides them.

But in the case of insects, the larvae of which have quite another diet from that of their parents, *e.g.*, parasitic Hymenoptera which oviposit upon a certain insect, or butterflies that lay their eggs upon a single species of plant, or upon the plants of a single genus or family, we have been satisfied with saying that their actions were instinctive, without attempting to analyse which definite elementary instinct or instincts, *i.e.* tropism, had guided their apparently purposeful action. One of the reasons for not thinking of chemotropism as one of the active factors in these cases, is probably that it was impossible for a human being to detect any odour. And yet it is evident that it is chemotropism which in the first instance guides the majority of these insects to the right spot for depositing their eggs, even if, after they reach it, their touch or some similar sense guides them, when it is a case of perhaps finding the very spot upon the plant where the egg has to be deposited.

If we consider that there are some ICHNEUMONIDÆ that lay their eggs deep down in the trunks of trees upon *Sirex* larvae, it is of course quite evident that neither sight, nor hearing, nor touch is able to assist them in ascertaining that a larva is living in the tree; but it must be a certain odour given off by the larva which is sensed by the parasitic insect. In the same manner it is probable that those parasites which attack leaf-mining larvae in the first instance are guided by their sense of smell. And finally we have every reason for assuming that it is the same sense which on the occasion of ovipositing guides all those insects whose larvae are herbivorous to their respective food-plants.

This assumption is confirmed by some experiments made during the last few years. In the year 1910 Ed. Verschaffelt² published in Amsterdam his investigations into the factors that determined the choice of food of certain butterfly larvae. He experimented with the caterpillars of *Pieris brassicae* and *P. rapae*, which prefer cruciferous leaves to all others. They eat, however, also leaves of *Tropaeolum* and *Reseda*, and the composition of their bill-of-fare throws a good light upon the determinative factors of their choice, for a group of glucosides, the mustard-oils, is common to all these.

In order to ascertain how strongly the mustard-oil attracted the larvae, Verschaffelt smeared a dough of *Bunias orientalis* upon some leaves of other plants which the larvae had previously refused to eat. Thus treated, the leaves were attacked and devoured with evident appreciation. In some instances the attempts failed, however, *e.g.*, with leaves of *Salvia officinalis* and *Menyanthes trifoliata*; but this was certainly due to the occurrence of other substances* in these leaves which exercised a more strongly negative reaction than the *Bunias*-dough had been able to effect in a positive direction. In order to obtain convincing evidence that it was really mustard-oil and not perchance some other

* In the *Salvia* leaves there occurs a volatile terebene, called tujon.

substances likewise common to the Cruciferae, *Reseda* and *Tropaeolum*, which exercised their attractive force upon the *Pieris* larvae, Verschaffelt took a solution of sinigrin, which forms the glucose part of black mustard, and with a brush spread it upon some leaves of other plants which the larvae had refused to eat without previous treatment. These were then devoured with relish. From these experiments it will be clearly seen that the *Pieris* larvae exhibit a strong positive chemotropism* towards a group of substances, mustard-oils, and that it is the presence of these substances in the leaves of their food-plants which makes them palatable for the larvae.

In the same manner Verschaffelt showed, by experiments with the larvae of a herbivorous Hymenopteron, *Priophorus padi*, which attacks the leaves of some members of the natural order Rosaceae, that in these there occurs a glucoside, amygdaline, which forms the attractive substance. It is hardly too daring to predict that further investigations will merely go to confirm these observations, and that the choice of food by herbivorous insects is determined by the occurrence of certain specific organic substances in the plants. So far only a beginning has been made with this problem; but it is certain that co-operation between vegetable chemists and entomologists in this question will prove highly profitable.

The above-mentioned experiments do not, however, give an answer to the question as to what factors guide the females of the herbivorous species in their ovipositing, and it is a fact that in the majority of cases the larvae have no option in the choice of their food. The selection is made by the females, and were their instinct not reliable, the larvae would perish. I am more especially thinking of the leaf-miners which, at least when quite young, would not be able to quit the plant upon which they had been deposited in the egg-stage.

It has been frequently observed that when moths are trapped with baits—in opposition to what occurs when catching with lanterns—a very large percentage of fertilised, egg-laden females is obtained, and this point seems very suggestive. Dewitz considers that this is due to the fact that the females are in the habit of feeding before ovipositing, and that they are attracted by the bait because the smell of the latter is like the odour of the fluids in their food. This is quite possible; but we might also imagine that the attraction is due to the odour of the bait being like that emanating from the food-plants of the larvae, and it would appear to be an easy matter to solve this question on the basis of Verschaffelt's researches by enticing the females of *Pieris* to oviposit upon other plants than the normal food-plants by means of sinigrin, for example.

No such experiments have, however, as yet been carried out, so far as I am aware, but in some cases where the larvae and adults have nearly the same diet, the attempt has been made to deceive the females into ovipositing by the aid of certain organic substances extracted from their food.

F. M. Howlett last year published the results of some experiments of this kind.³ He succeeded in enticing *Sarcophaga* to oviposit in a bottle containing scatol, a pungent substance found in excrement, and which is the product of

* This term is not used by Verschaffelt, who regarded the problem merely from the standpoint of vegetable chemistry.

decomposition of albuminous substances. Furthermore, he lured *Stomoxys calcitrans* into laying eggs upon a cotton rag drenched with valerianic acid, a substance found in decomposing vegetable matter.

Howlett then goes on to discuss the theoretical significance of these experiments. He points out that our own sense of smell appears to be limited to substances that possess a molecular weight of about 30 or more, whilst we are unable to perceive any smell in substances with a less molecular weight, even if they exercise an irritating influence upon our nasal mucous membrane.

It is probable that the sense of smell in insects has been developed only in certain directions, and that they are extremely sensitive to the odour of certain substances, whereas others do not make any impression on them. In other words, we may assume that every species is adapted merely to react to the odour of certain organic substances, either positively or negatively, and that these are probably substances which under normal conditions play a part in their life. There ought, therefore, to exist a certain correlation between specialising with regard to food and the sense of smell. The odour of organic matters again is due to the occurrence in them of certain specific chemical combinations, *e.g.*, organic acids, amines, terebenes, phenols, glycosides, etc., which are characterised by a certain structure and stratification of the atoms.

Howlett did not know of Verschaffelt's work, but we discover immediately how remarkably well the two researches complete each other, and even if the chain of evidence is not fully perfect as to which factor determines the females of herbivorous species in the selection of the food-plant for their larvae, we may yet be permitted to draw the following hypothetical conclusions. The ovipositing of the females is guided, even in those cases where the larva has a diet different from that of the adult, by chemotropism, and this latter is correlated with the food of the larva in such a manner that, if the larva is a univor, it is only *one* specific organic union in the food-plant which attracts the female. If the food of the larva consists of several species of one and the same genus, or of different genera within one or several families, then it is an organic union or group of such, common to all these, to which the species reacts positively.

As an example of how strongly specialised the sense of smell can be in insects, we may mention the ants. It is a well known fact that the members of the same species attack each other with the greatest fury if they only come from different nests, and this has been proved by experiments to be due to each member of a community of ants possessing its special nest-odour, by the aid of which it is able to distinguish friend from foe.

After this short account of what we know of the chemotropism of insects, we may pass on to the question as to whether it can possess any importance for economic entomology. From a theoretical point of view, we ought, if the above conclusions are valid, to be able to discover in the chemotropical reactions of insects in many cases a superb weapon in the fight against noxious species. For it has always been considered that prevention is better than cure, and of all methods in preventing devastation that is undoubtedly nearest to the ideal in which we succeed in capturing the females ere they have had an opportunity of ovipositing. And we shall probably be able to effect this if we succeed in isolating the organic substances in the food-plants of the larvae, towards which

the females react with a positive chemotropism, and with which a kind of trap might be prepared.

In reality such methods have for a long time been practically utilised without the theoretical foundation of the idea being understood. If, for example, we lay out pieces of freshly pulled bark to act as traps for catching the pine weevil, or make use of trap trees for bark-beetles, we are utilising in reality the specific chemotropism of the animals.

But in no instance has as yet an attempt been made to ascertain what definite organic combination in one plant or another chemotropically influences a certain insect ; still less has an attempt been made to produce the same synthetically and make practical use of it.

In my opinion, however, the investigations of Verschaffelt, Dewitz, and Howlett, if regarded in the light of the researches of physiologists into chemotropism, are of an importance which cannot be overestimated, and will guide practical entomology into new lines. Intimate co-operation between vegetable chemistry and entomology in these questions will surely provide us with good weapons in our fight with many insects, against which we are at present absolutely helpless.

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