THE CORRELATION BETWEEN HABITS AND STRUCTURAL CHARACTERS AMONG PARASITIC HYMENOPTERA

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The problem of insect parasitism has always been a fascinating one from the standpoint of pure science, but during recent years it has become an increasingly important one for the economic entomologist. Indeed it has been discussed so fully and in so many aspects that I feel much hesitancy in adding the present remarks to the writings of many able entomologists better acquainted with the more or less heterogeneous mass of facts so far accumulated on the subject. My only desire is to present the matter in a somewhat different light.

The rapidity of increase among injurious insects which become introduced into new regions where they are not kept in check by their parasites was early noted and commented upon by entomologists, and certain experiences in our own country within the past few decades have brought out very clearly the fact that of all the forces which control the comparative abundance of related insects, the presence of their parasites is the most vital.

The balance maintained by the struggle for existence between species is immediately and violently disturbed if the parasites of any particular species be removed. Such a form suddenly begins to increase in numbers, reproducing itself at a phenomenal rate approaching the geometrical progression, which would theoretically obtain if every individual were permitted to reach maturity and reproduce itself. When the food supply is sufficient it will quickly become dominant over related species. Such conditions of rapid increase occur almost exclusively as the result of the introduction of an insect into a locality where its natural parasites do not occur, and are on this account most often brought to our notice by the rapid spread of injurious species.

Following the acceptance of this principle, was the attempt on the part of economic entomologists to combat accidentally introduced insects by purposely introducing the parasites which prey on them in their native region. The experiment has been tried a number of times under varied conditions and has proven almost universally successful in measure to warrant its trial whenever feasible.

There are vast numbers of parasitic insects, particularly Hymenoptera. These are widely distributed, and a very close relationship exists between allied species and genera inhabiting widely separated regions. It would be natural to suppose, therefore, that the transfer of an insect from one region into another would lay it open to attack from some of the forms closely related to parasites which control it in its native environment. We have abundant proof however that such is not usually the case, and it is a matter of general agreement that the likelihood of any sudden variation appearing in the life history of a parasite, due to an introduced host, is very slight. Such a generalization is not universally true, especially among members of the dipterous family *Tachinidæ,* but seems to ordinarily apply, and does so particularly well, to the groups of parasitic Hymenoptera to which I shall confine most of my remarks.

Upon what, then, does this mutual adjustment between parasitic species and host species depend?

Entering the field of speculation, it is evident that there are a number of possible factors which may determine it, and I shall endeavor to consider the more important in turn.

That the physical form or size of a species has an important bearing on the matter of parasitism is undoubted. Parasites which live singly in the bodies of their hosts must necessarily confine their attacks to species which will furnish them with a proper amount of food to mature. On the other hand, it is imperative that the body of the host be entirely consumed at maturity in the case of parasites which pupate *in situ;* or in the case of species which leave the host for pupation, that the emergence of the delicate parasitic larva may proceed without accident.

Many of the smaller parasitic species, particularly certain *Chalcididæ,* may develop in large numbers within a single host. Such species ofter undergo remarkable multiplication during development, and the number of young is regulated to suit the food supply. The adaptability of certain forms in this respect has often been observed. For example, the well-known and widespread *Pteromalus puparum* attacks a considerable series of butterfly larvæ, ranging in size from rather small to large species, and the number of specimens derived from a single caterpillar is roughly proportionate to its size.

Such species are however decidedly in the minority, and within reasonable bounds, the size of an insect is a limiting factor in the determination of its parasites. This does not necessitate that all of its parasites be of uniform size, since the number of eggs laid in a single host usually determines the number of emerging parasites. For example, there may issue from a parasitized cocoon of the common Cecropia moth, but a single specimen of the large Ichneumon-fly, *Eremotylus macrurus,* while dozens of specimens of the small *Cryptus extrematatis* regularly issue from a single cocoon of the same moth. This sort of adjustment is almost universal, and most insects which have been extensively studied are found to harbor parasitic species of each type. A similarity in form of body or type of structure is generally seen to exist between the hosts in cases where a parasite attacks several different insects. Thus all of the hosts of the aforementioned *Pteromalus* are caterpillars, and the same rule obtains among others, for example, among species of egg-parasites, which always attack insect eggs, although not always those of the same insect. Remarkable exceptions to this are nevertheless to be noted, for instance, the Chalcidid genus *Eupelmus* (*sensu lato*), which attacks both the eggs and larvæ of numerous species belonging to six natural orders of insects.

It is seen, however, that while the hosts of a given species, genus, or larger group are usually of similar form or habitus, that this similarity generally depends upon relationship and is not merely accidental, for we do not find ordinarily that insects presenting the same general appearance will have the same parasites. A species of *Ichneumon, I cyaneus* Cres., which attacks both saw-fly larvæ and caterpillars, is a notable exception.

In other words, dissimilarity seems to act more strongly as a deterrent than similarity does as a persuasive, in regulating parasitism.

Occurrence in a similar habitat acts very evidently in some cases to widen the range of hosts attacked. This is especially noticeable in the case of insects producing galls on plants. We must make allowance for the greater care with which the parasites of these insects have been studied, but it is nevertheless astonishing to see what a wide range of species are often regularly attacked by the same parasite.

The European Chalcid-fly, *Ormyrus tubulosus*, has been minutely studied by Mayr, who has bred it from no less than 27 species of Cynipid galls, and I have from Massachusetts what is apparently the same species, bred from about half as many North American species by the late Dr. M. T. Thompson. The galls formed by the various hosts of this species are many of them entirely dissimilar in form, the only resemblance between them, aside from their gross gall-like form, being their more or less uniform habitat, attached to twigs and leaves.

On the other hand, an isolated environment usually restricts greatly the possible parasites of a given species. A case in point is seen with species living beneath bark or boring into wood. Many groups are represented among the enemies of such insects, but all must come from groups provided with an elongated ovipositor, with which to reach the host for egg deposition. A beautiful case of complete restriction is the Ichneumonid genus *Thalessa,* which attacks certain wood-boring *Siricidæ,* deposting its eggs in the body of its host far within the infested tree by means of its enormously elongated ovipositor. It may perhaps be urged that natural selection will develop a long ovipositor in any group where it may be of service, but the value of the elongated ovipositor for the separation of larger groups shows that it is an organ that is very slightly influenced by specific exigencies.

Seasonal distribution naturally limits the range of parasitism rather closely, since the time of appearance of insect species varies greatly; and as adult parasites are not long-lived, their hosts must appear at nearly the same time as they do themselves. The tendency is for parasitic species to undergo metamorphosis more rapidly than others, probably on account of their easily assimilated food, and with shorter life-cycle they will tend to pass through more generations in a season than their hosts in many instances. Here I believe lies the reason for the acquirement of more than a single host by some species, although it cannot explain the large number of hosts of some species, nor the several closely related hosts of others.

While some of the probable reasons for the association of host and parasite may be found among the foregoing, there seem to be no cases that can be fully elucidated by either one or a combination of all. Indeed, the very fact that there are so many closely related parasites and so little transfer to new hosts, would almost preclude such a supposition *a priori,* and some more subtle hereditary influence must be sought for.

Throughout the entire parasitic group, there are scattered here and there species which are particularly adaptive, in that they attack several or a number of more or less closely related hosts, while others not far removed taxonomically have apparently but a single one. But in nearly every minor group and in some of the larges ones, there is a well-marked tendency to select as hosts species belonging to another homogeneous group. Thus every one of the seven or eight hundred members of the Proctotrypid family *Scelionidæ,* so far as known, with one single exception of doubtful relationship, is an egg-parasite. Almost every species of the family *Alysiidæ* is parasitic on dipterous larvæ; practically all members of the extensive sub-family *Aphidiinæ* of the *Braconidæ* are aphid parasites, and so we might continue to list many more. There are here also very noticeable exceptions, but they only serve to show the strong tendency toward uniformity which exists everywhere.

Small groups do not always show the increased specialization which we might expect from the uniformity exhibited by so many larger groups, and species in particular may occasionally have almost as great a range in choice of hosts as genera or even larger groups. A case in point is the Chalcidid genus *Trichogramma,* which attacks the eggs of insects belonging to four orders, one of its species, *T. pretiosa,* preying upon no less than 12 species belonging to two orders, the Lepidoptera and Hymenoptera.

It has often been customary among hymenopterists to assume that a different host species must almost surely have different parasites from those of a related form, even if sharp differential characters could not be observed, but reliance on this physiological character is gradually giving away to a demand for actual structural characters, and recent investigators place little confidence in host relations for the actual separation of species.

Undoubtedly the explanation for the fixity of habits throughout many of the larger groups, is the common inheritance of specific instincts through long periods of time without any, or with but little change, while the varied genera and species of the group have meanwhile been evolved. A habit thus formed has been handed down from generation to generation as the groups have passed into a more and more intricate interdependence, through the evolution of new species in each group. Such will be the natural trend of evolution, and we can readily comprehend how the habits of a group like the *Scelionidæ, Alysiidæ* or *Aphidiinæ* must have originated. The Alysiid are particularly interesting in this respect, as they form a very compact group distinguished from all its relatives with more than usual ease by a single morphological character, which does not allow of the different interpretations to which the characters of most other groups are subjected at the hands of the systematist. In cases where groups are more opinionative, habits themselves usually have considerable weight in the segregation of their components.

Conversely, that the variations from any uniform or related system are due to some sudden change in the nature of a mutation seems probable, and if so, the antiquity of the mutation should in some degree be traceable from a knowledge of the extent of the present variations.

Turning to view this possibility in the light of paleontological evidence, we find that several well-marked cases of unusually variable habits within a genus or small group are evidently associated with antiquity.

Among over one hundred undescribed species of fossil parasitic Hymenoptera, which I am working over from the Miocene shales of Florissant, Colorado, there are several genera that stand out distinctly on account of their abundance. One is the Ichneumonid genus *Pimpla.* It is represented by four or five species, one of which is the most abundant form in the entire collection. Evidently these were as dominant then as our species are at present. We find also that the recorded habits of *Pimpla* are unusually varied.

Another dominant genus resembles the present-day Chalcidid *Torymus* very closely, but on account of a somewhat less specialized wing venation, I have termed it *Palaeotorymus.* There are at least four distinct species from Florissant, represented by many specimens in the collection. Because of its evident antiquity it has had ample chance to give rise to variations in habits, through mutation or otherwise, and we find that the present species of *Torymus* are parasites of gall insects belonging to both the Diptera and Hymenoptera, and apparently of certain Coleoptera and Lepidoptera as well.

Chalcis (including *Smicra, Spilochalcis,* etc.) is another genus that is well represented at Florissant, and recent species of this dominant group attack insects belonging to at least three orders, Lepidoptera, Coleoptera, and Diptera.

That very persistent types are not always the ones to give rise to variations in habits is shown by the occurrence of many species of *Limneria, Ichneumon, Microgaster, Proctotrypes,* etc., in these same Miocene deposits. None of these particular genera seem to have at present a wide range of hosts.

Correlation between very slight characters and certain host relations is very common, and I shall mention one in closing. The genus *Telenomus* contains nearly 175 species of egg-parasites, and is distinguished from the closely allied *Phanurus* by such evanescent characters that many systematists recognize no generic division. Of the entire series only two are known to breed in the eggs of Diptera. Both attack the eggs of *Tabanus,* one in Europe and the other in America, while taxonomically they exhibit particularly well the slight differential characters of *Phanurus,* although they cannot satisfactorily be segregated from the rest of the genus upon a strictly morphological basis.

To judge, then, from the fragmentary evidence so far adduced, we can only suggest that the single explanation which seems applicable to the constancy of some groups and the variability of others, lies in the assumption of a general evolutionary trend toward gradual elaboration, broken here and there by a mutation in habits which has split off the progenitors of certain groups from the conservative majority. The fact that parasitism has undoubtedly originated independently in a number of groups further enlarges the possibilities of complexity in host relations.

A paper was presented as follows: