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BORDERLINE APHID STUDIES.

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The family Aphididae presents a bewildering array of variation in its biological behavior. This lack of uniformity has usually been explained on the basis of the eccentricity of the individual species or genus, and the matter has often been dismissed as such without further inquiry, rather than to attempt to account for these apparent discrepancies as a result of some natural cause. The belief that certain of these biological characteristics indicate stages in the phylogenetic development of the family, and as such become of interest to the taxonomist, has led to their further consideration.

Aphid taxonomists have largely directed their attention to species where the presence of a large number of excellent morphological characters has made it unnecessary to consider carefully the meaning of any biological characteristics which may be present. Aphidology has now reached the place where considerable time may be profitably spent considering the family as a whole, or divided into groups. When considered in this manner the biological and ecological factors of the family heretofore considered as independent facts peculiar to certain genera or species, become ancient trail blazers to him who would go back of the present to gain some knowledge of the past. To the taxonomist interested in a natural classification this becomes a necessary procedure, for the phylogeny of a group can not be determined by the use of a single factor.

Aphids have departed widely from other insects biologically. The factor or factors responsible for this change have apparently received but little consideration, and few attempts have been made to retrace the path over which the aphids passed in going from the more generalized condition common to other insects to the derived condition which they represent. It is true that this path is no longer fresh; in places it has been obliterated by time so that it must be rebuilt in accordance with facts gathered from other sources. In other places this path lies beautifully preserved in the form of biological characteristics which have been known for a long time

but imperfectly interpreted, hence incorrectly evaluated. By the use of these biological characters, the fragments of the paleontologist, we should be able to reconstruct the various stages in the phylogenetic development of the family. The problem of the day for the aphidologist, and likely to be for many years in the future, is the weighing and evaluating of these biological characteristics in comparison to the value placed upon morphological characters. When this is done, and only when this is done, will we have a natural classification, which is the hope and aim of systematic work.

The fact that aphids have beaks in common with the order to which they belong, makes them admirably adapted to carry on a parasitic life. Leading this kind of an existence, all that is necessary for them to do is to remain attached until the host is sucked dry, or until its sap becomes unsuitable as a source of food. This parasitic habit undoubtedly was present before the Aphididae reached family rank. We would expect this, for it is one of the characteristics of the order Homoptera, although it has perhaps reached its highest development in that order in the family under consideration. Here we have reason to believe that feeding has become a continuous process by reason of the beak being attached at all times, and because of the copious amounts of honey dew produced per individual. The capacity to consume a large amount of easily obtained food and its availability in unlimited quantities, must have been one of the primary factors in bringing about viviparous reproduction. Certain it is that aphids would not be as successful as they are were it not for the fact that their hosts have proven suitable to provide an abundant source of food upon which to develop the large numbers of young per individual, and to mature them in so short a time. The strength of these insects and their success, lies largely in their power to reproduce rapidly; a condition which their method of reproduction and early maturity favors.

Sexual reproduction with the subsequent laying of the eggs by the female is the common method of reproduction in the class Insecta; the progenitors of the family Aphididae undoubtedly reproduced in this manner, for parthenogenetic viviparous reproduction certainly represents a derived condition. The sexual generation which in aphids usually occurs only once a year, where it occurs, must therefore be looked upon as the last vestige of the original method of reproduction of the family, and consequently may be viewed as one of the few biological characteristics that aphids have in common with generalized insects. The dependence of species in northern latitudes upon at least one sexual generation a year indicates that these species have gone as far as they dare in the suppression of the sexual generations. In fact the suppression of the sexual forms has gone so far in northern latitudes, that winter sometimes actually sets in before the sexual forms are produced. Consequently, a year following an early fall or a fall unfavorable to aphids in general, may see many species practically annihilated. Perhaps in such cases winter sets in so suddenly that the physical and biological factors which determine the production of the sexes do not have time enough to act. Such a condition may explain why certain species such as *Toxoptera graminum* (Rondani) migrate northward each spring from their breeding grounds in the south

instead of overwintering in the egg stage in the more northern limits of their range where under natural conditions the sexual forms are not produced. In other words I assume that either a physical or biological impulse acting through a period of time is necessary to bring about the production of the sexual forms, and that in case unfavorable conditions prevent the reaction time being carried to completion that the aphid dies before the sexual forms are produced.

An aphid species completing its cycle of generations upon a single host species must of necessity confine its range within the range of its host. A species having a primary host upon which the sexual forms are produced, and a secondary host upon which the summer generations occur, may extend its permanent range without reference to the range of its primary host as long as it is able to reproduce viviparously parthenogenetically throughout the year within the range of its secondary host. Considering the scarcity of distributional records for the family Aphididae it is quite remarkable that Mordwilko was able to list several species which have extended their range beyond the range of their primary hosts.

Aphid species in the tropics have established complete independence from the sexual forms, for here parthenogenetic viviparous reproduction may be carried on throughout the year. Because of this well known fact, weather conditions have been thought to influence the production of the sexual forms so that the species may be carried through periods in the egg stage which otherwise would be unfavorable to them or their hosts. Aphids are not indigenous to the tropics. The question naturally arises as to how long species in the tropics retain the ability to produce the sexual forms when called upon to do so by a radical change in their environment which threatens them with destruction, due to their inability to maintain themselves further by parthenogenetic means. This question is difficult to answer without subjecting such species to the environmental factors which produce the sexual forms. This can not be done until the environmental factors themselves are known. There are indications, however, that the period of time necessary to bring about the total suppression of the sexual forms is considerable, for apparently not enough time has elapsed since the aphids invaded the tropics to make this suppression complete. Takahoshi has listed several species which still produce one or the other of the sexual forms but never both. This fact indicates very strongly that such species are in what may be called a transitional stage. In this connection it is interesting to note that two of the species listed by Takahoshi as producing only males are cosmopolitan species probably native to Europe.

That the weather and other physical factors are not entirely responsible for the occurrence of the sexual forms at specified periods of the year is evident, for some species produce the sexual forms intermittently throughout the year. Such a habit is to be looked upon as very primitive for it indicates an intermediate step between the time when aphids reproduced wholly by sexual means and the present. Near Taihoku, Formosa, according to Takahoshi, the leaves of young Celtis trees remain green throughout the year. Aphids feeding upon such trees fail to produce the sexual forms. However, older Celtis trees growing in the same locality shed

their leaves and it is upon such trees that the sexual forms are produced. Such a condition as this, and the intermittent production of the sexual forms mentioned previously, would appear sufficient to question physical factors such as temperature and light as factors *directly* influencing the production of the sexual forms.

The capacity to pass through a large number of generations in a given year is a derived condition peculiar to most aphids. Certain species of aphids, however, such as *Mindarus abietinus* Koch and *Georgiaphis ulmi* (Wilson) have not developed this capacity, the number of generations for these species being greatly reduced. These species spend the greater portion of the year in the egg stage, a harking back, as it were, to a time when there were but few generations a year for the class, a condition which is even now the most prevalent.

The problem of aphid migration is extremely interesting, for it is here that many of the apparent discrepancies in the biological behavior of the family Aphididae occur. We shall not concern ourselves with the question whether insects were first monophagous or polyphagous for it would appear to be better to base such conclusions upon the habits of insects lower in the scale of development than the Aphididae, for such a fundamental function as the procuring of food must have been firmly established before these insects reached family rank. As far as aphids are concerned, the evidence is quite conclusive that the direct progenitors of the family were monophagous.

Largely upon morphological grounds the series Lachnea has been looked upon as the oldest series of the family, and there is ample biological evidence to substantiate this view. The series Lachnea has not been a progressive group. It is represented by comparatively few species which show but slight variation in their morphological and biological characteristics. Hence, particular attention may be directed to a study of the biological characteristics of the tribe Lachnini which is considered to be the oldest tribe belonging to the series Lachnea. All of the species belonging to this tribe are intimately associated with species belonging to the family Pinaceae which is an old family of plants—thus fulfilling a necessary condition—for the association of an old species with a comparatively new host would not have the significance that may be attached to the association of an old species to an old host. A few species belonging to the tribe Lachnini, it is true, are not monophagous but there is nothing suggestive of a formal migration from one host species to another. The species which are not monophagous develop equally well in all their stages upon two or three hosts which are hardly ever more distantly related than specifically.

A species which confines its feeding to species belonging to a single host genus, or at most to species belonging to a family would appear to represent a very primitive polyphagous condition. This is precisely the condition that is commonly met with in many of the tribes belonging to the family and is particularly true of the tribes closely associated to the Lachnea. Polyphagous aphids must not be regarded as omnivorous in any sense of the word, for species in which the polyphagous habit has reached its

highest development are still highly restricted in their choice of food plants when compared with more generalized polyphagous insects. The polyphagous habit appears not to be well developed or established in the sexual forms which still confine their feeding and oviposition to a very narrow range of hosts if they show any tendency towards a polyphagous habit at all. The tendency of the sexual forms to be monophagous suggests again the original feeding habit.

If one accepts the theory that aphids first reproduced wholly by sexual means, further evidence that aphids were originally monophagous may be brought forth which is even more direct and convincing than the evidence furnished by the tribe Lachnini. The evidence is quite conclusive that an aphid species is either monophagous in the sense that it does not migrate from a primary host to a host distantly related to it, or that the primary host upon which the sexual forms are produced is older than the secondary host. For an aphid species to have been originally polyphagous, the secondary and primary hosts would have had to exist at the same time and to have had the same range. Such a condition is not met with by the plants which aphids having a formal migration have chosen for hosts, for usually a wide gap exists between the relationship of the primary and the secondary host plants. This can only be explained by their having originated at different times. However, there are exceptions to the rule that the secondary host is always younger than the primary; these exceptions may, however, for the most part be ruled out, for the secondary hosts in such cases are grasses upon which the complete cycle of generations can not occur, due to the fact that the eggs can not pass the winter on the roots.

The fact that some aphid species migrate from an overwintering primary host to a secondary summer host and back is an extremely interesting phenomenon, and one which immediately challenges the curiosity of the naturalist. The factors responsible for the production of alate individuals have been the object of a great deal of research, but the fact remains that the factors thought to be responsible for the production of wings (without which there could be no migration), do not explain why it is necessary for a species having a formal migration to migrate from its primary host to an entirely unrelated secondary host. The development of wings in species having a formal migration must, therefore, be looked upon as a taxic response to food, a response not directly associated with the function of distribution, as is the case with the development of wings in non-migrating species. It may be suggested that perhaps the sap of the primary host undergoes some change in its osmotic concentration or in its chemical nature which is unfavorable to the aphids which feed upon it. This reason will not explain why species, perhaps belonging to the same genus, and having similar feeding habits may remain upon such a host throughout the year; nor will it explain why such a migrating species may occasionally be collected throughout the year upon the primary host; neither will it explain why a species may feed upon the same host in the fall from which it was caused to migrate in the spring without any harmful effects. Perhaps the continued feeding upon a given host for a few generations has an

accumulative effect upon certain species of aphids so that the sap of that particular host becomes toxic to them and a migration to an unrelated host necessary. Such a condition as that just referred to could not arise until the family had developed the capacity to pass through a number of generations a year, and would not arise in a species capable of counteracting the toxic effect. This hypothesis is not without its objections, but in the absence of experimental evidence contrary to it and the preceding hypothesis, it would appear to be better to delay judgment until such evidence as may be gathered is at hand.

Wings are perhaps the most characteristic structures insects have, and have always been so. The absence of wings is a derived condition which aphids have gone a long way to establish. The factor responsible for bringing about the apterous condition in aphids has undoubtedly been their parasitic habit. It is easy to see that such small delicate insects as the Aphididae, at the mercy of every gust of wind and highly restricted in regard to hosts, would be greatly benefited by any condition tending to lessen the danger of becoming lost from suitable food sources. The wings of the oviparous females (where they are a positive detriment and add only to the possibility of them becoming lost from a suitable host for the young, which are to hatch from their eggs) have all but disappeared, there being but few species where they have been retained, indicating a very primitive condition. The males of many species are apterous (a derived condition) other species have both apterous and alate males (an intermediate condition) while still other species have all of the males alate (a primitive condition). In regard to wings, species belonging to the tribes *Callipterini* and *Calaphidini* are decidedly more primitive than the Lachnini, for in these tribes the summer generations invariably acquire wings before reproducing.

The close continuous relationship that aphids have established with their hosts is not without its phylogenetic significance and in the future this relationship is bound to receive careful consideration from the aphid taxonomist. The narrow range of plants that almost all groups of aphids have selected as hosts, furnishes convincing evidence that aphids have kept up with the evolutionary pace set by their hosts—the plants. Such evidence as this when carefully considered may indicate the approximate time that certain groups of aphids originated. Such evidence, however, must either be based upon monophagous aphids or upon the primary hosts which the species as a group have selected. The position of the secondary host in its botanical classification is not without its special significance, for the relative position of the secondary host in relation to the position of the primary host should indicate the approximate time in which the species became polyphagous. The divisions already made between the *Chaitophorini* and the *Callipterini* and between the Aphidini and Macrosiphini on morphological grounds are substantiated biologically by the hosts which they as groups have selected for food. The host relationships may in the future suggest the association of the tribe Hormaphidini with the tribes Calaphidini and Callapterini in the subfamily Aphidinae.