Some notes on morph determination in Aphids

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LEES' (1959) paper on *Megoura viciae* Buckton seems to make it desirable to coordinate some published and unpublished data on determination of aphid morphs.

LEES has confirmed the findings by UICHANCO and MORGAN that in aphids already in embryones egg-cells are developing. So a viviparous mother-to-be is at the same time an expecting grandmother. A male egg generally develops from a female diploid egg by the latter loosing at its first division half its X-chromosomes. SHIBATA found no difference in chromosome numbers in body cells between the sexes in the far from primitive *Myzocallis* with which he worked, but it is likely that also in that species the genetic sex determination takes place before there are a number of nuclei in the egg. Therefore one may conclude that the determination of sex in Aphididae takes place at the first division of the egg-cell, i.e., at least partly inside the grandmother. The sex of the first few offspring will be determined in the grandmother and this probably explains why in LEES' experiments the birth of male larvae was preceded by the birth of females, as he did experiments only on mothers. Submitting expecting aphid viviparae to various external conditions might certainly also influence the male production in their direct offspring by suppression of male embryos, as LEES supposes, but it need not completely influence sex determination.

A female diploid parthenogenetic egg can develop either into an oviparous female, or into a viviparous female. LEES' beautiful experimental work makes it clear that this switching mechanism works only via the mother in this sense, that at a certain temperature a short photoperiod continually acting from first instar larva on will make her produce only oviparous females, a long photoperiod will make an offspring of only viviparous females. This agrees with the findings of earlier workers. LEES further finds that change in photoperiod during the further development of a larva will turn a part of her progeny into morphs corresponding to that changed photoperiod. Unfortunately he does not quote DE FLUITER (1950) in this context, who to my knowledge was the first to demonstrate that switching takes place in the mother by making gynoparae (= producers of oviparous females) of *Aphis fabae* Scop. finally produce 20% of viviparae after changing (when they were teneral) the temperature to which they were exposed before.

From the above it is clear that at least in Aphididae determination of males, and the determination of oviparous females are two independent processes, the sex determination occurring before the other. The parthenogenetic eggs have first a choice between remaining female or becoming male eggs, partly during prenatal development of the mother. If they remain female it is decided later, during postnatal development of the mother, whether they will develop into an oviparous female or a viviparous female.

LEES has indeed found that different conditions are responsible for male production or oviparous female production in his species, and it is clear that when

he writes on p. 95 "that the mechanisms of female and male determination must be entirely different" he means oviparous female determination and male determination.

In *Megoura viciae* Buckton this is confirmed in nature. In the last 6 years I found that in nature the species regularly produced a certain number of males in midsummer, from the last week of June till the end of July, but no oviparous females before the end of September, when males are once more produced, now in larger numbers.

In the existing literature one finds that in Aphididae the eggs produced by oviparous females have to be fertilized for development and then develop into females. The mechanism is said to be, that the male produces only haploid functional sperm with half the X-chromosomes, the oviparous female only haploid eggs with half the X-chromosomes and the fertilized eggs have therefore two sets of X-chromosomes and consequently are female. However, among mature and immature fundatrices of *Glyphina schrankiana* Börner, collected on *Alnus incana* near Innsbruck, I found a nearly adult male larva. It would seem therefore that a hibernated egg produces occasionally a male. Whether in such a case the diploid egg could loose an X-chromosome at its first division, or had after fertilization only one X-chromosome to begin with, is not clear. Morphological characters intermediate between those of oviparous females and viviparous females in specimens developing from hibernating eggs are know from several species and one could imagine that switching mechanisms can work also in the winter eggs, after they have become diploid.

In aphids sex determination in the generation preceding the mother generation is not a new discovery. MORGAN (1909, p. 272) had already found in some Phylloxeridae on *Carya*, that males are produced by females that are often differently built than those producing females. In such cases there are different androparae and gynoparae. In Aphididae androparae were first found by myself in species which have greenish females, but red males, e.g., in *Metopolophium dirhodum* Wlk. The females that produce exclusively males can be easily recognized because the pink embryones are visible through the integumentum. Specimens with mixed pink and green embryones have not yet been found in nature. Sex determination clearly took place a generation before: simultaneously one finds apterous viviparous females of the same age with only green embryones inside.

It is well known, that not in all species the production of different aphid morphs is restricted to different mothers. This is clear also from LEES' work. One viviparous female of *Aphis farinosa* Gmelin can produce oviparous females, males, apterous viviparous females and alate viviparous females, as has been known since long.

However, in the Eriosomatidae males and oviperous females are always produced by the same mother which does never produce viviparous females and which therefore is termed a sexupara. Here the determination of the male egg would seem to be induced by the same factors as, and simultaneously with the determination of the female eggs to future oviparous females.

LEES, after finding that the feeding of aphids on senescent host plants has no influence on the production of oviparae writes, that nutrition had no effect on

the production of oviparae. If this statement is taken in its widest sense, and therefore nutrition translated as ingested plant sap, this statement is not proven. For we still do not know whether photoperiod acts on the aphid directly or via the plant. The very regular transfer of the aphids to food previously submitted to another photoperiod would seem to make this subject accessible, but recent research on the photoperiodic responses in plants has demonstrated that an irrevocable response can be caused after 24 hours, and besides that an agent is produced which is transported with about the same speed as carbohydrates. This makes the problem of the action of photoperiod, direct or via the plant, practically insolvable unless one succeeds in rearing aphids on artificial media that have no photoperiodic response. On the other hand there is ample proof that action via the plant occurs. In subterraneous aphids the production of sexual or presexual forms follow the same line as that on superterraneous parts of the plants. The influence of photoperiod on the aphids in a direct way is excluded and it is even doubtful whether temperature plays a role in some species living at a depth of ½—2 meters in the soil. In cases like these one would assume that nutrition determines the production of the sexual forms.

From the available literature one might conclude that production of the sexuals in all aphids is governed by day-length and/or temperature. There certainly are exceptions known. In the tropics near and on the equator some aphids periodically produce sexuals, about which only scanty data are available. In this case both day-length and temperature are rather constant, but periodic changes in humidity occur. The few European Aphididae that form their sexuals normally in early summer (*Aphis farinosa* Gmelin, *Dysaphis devecta* Wlk., *Lachniella costata* Zett., *Mindarus abietinus* Wlk. and *M. obliquus* Chol.) have not yet been closer investigated but the production of sexuals takes place at long day-length. I have pointed out elsewhere that most Greenland aphids produce their sexual or presexual forms at 24 hours of day light and near the local maximum of temperature. A species like *Dactynotus obscurus* Koch produces near Stockholm its sexuals in early August, but in the Netherlands in late September. In fact, one should be very careful not to generalize the findings on a few aphid species to aphids in general.

Though, as we have seen, photoperiod in subterraneously living aphids presumably acts via the plant, we cannot exclude the possibility that in aphids living above ground it acts directly on the aphids. In this context it may be of interest that work by TODD and his collaborators (1948) has shown the presence in some quantity in many aphid species of a curious substance which they call protoaphin, and which through enzymic action is converted into a series of pigments which in many respects are related to hypericin, also in their photodynamic action. Hypericin is a colouring matter from *Hypericum perforatum* which makes a. o. white sheep oversensitive to direct sunlight, but which does not affect black sheep. Perhaps aphids are in this respect white sheep.

References

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Men kan zich afvragen of er in Frankrijk behoefte bestond aan een nieuwe Curculionidenmonografie, nu het bekende werk van HUSTACHE nauwelijks ouder is dan ongeveer 30 jaar en aan veler verlangens voldoet. HOFFMANN voert o.m. aan, dat het werk van HUSTACHE in vele tijdschriftjaargangen verschenen is (meer dan 10), waardoor het voor determinatiedoeleinden bijzonder onpraktisch is, terwijl het ook bijna niet meer compleet te krijgen is. Vergelijkt men de nieuwe monografie met die van HUSTACHE, dan blijkt echter duidelijk, dat HOFFMANN een prestatie geleverd heeft die ver uitsteekt boven het werk van zijn voorganger. Het enorme aantal zeer goede tekeningen, de uitvoerige tabellen en de veel meer gedetailleerde beschrijvingen steken wel zeer gunstig af bij alle vroegere bewerkingen van deze uitgebreide familie.

Na de uitvoerige beschrijvingen, waarbij aan de variabiliteit zeer veel aandacht wordt besteed, volgen steeds, indien bekend, de voedselplanten van larven en adulti. Daarna volgen van elke soort de uit Frankrijk bekende vindplaatsen, meestal beperkt tot de departementen, en tenslotte de globale verspreiding buiten Frankrijk. Het derde deel bevat o.a. een flink aantal goede tekeningen van door snuitkeverlarven veroorzaakte beschadigingen aan allerlei plantedelen, o.m. gallen en bladmijnen. Behalve de reeds bekende gallenverwekkers blijken er toch nog vele soorten te zijn waarvan deze bijzonderheid nog niet bekend was, zodat dit werk ook voor de Cecidologen nieuwe gezichtspunten kan openen.

Overgaande tot kritiek op enkele ondergeschikte punten, valt het in de eerste plaats op, dat *Otiorrhynchus veterator* Uyttenb. door HOFFMANN gedegradeerd wordt tot een subspecies („une grande race géographique") van de uitsluitend in de Pyreneeën voorkomende *O. impressiventris* Fairm. Een opvatting, die mij gezien in het licht der verspreiding, willekeurig en onhoudbaar voorkomt. Merkwaardig doet het ook aan, dat onze welbekende halobionte *Polydrosus chrysomela* Oliv. door de Fransen hardnekkig aan het genus *Eusomus* Germ. wordt toebedeeld. De meeste exemplaren van deze soort hebben inderdaad afgeronde schouders, zodat met de Franse tabellen op *Eusomus* uitkomt. Er bestaan echter wel degelijk exemplaren, o.a. in mijn eigen collectie, die precies zulke hoekige schouders hebben als alle *Polydrosus*-soorten en die dus met de Franse werken ondetermineerbaar zouden zijn. Misschien zijn deze in Frankrijk niet bekend, HOFFMANN noemt deze soort „assez rare". De auteur heeft de vanouds bekende speciesnaam *chrysomela* Oliv. vervangen door *salcicola* Fairm., waardoor de verwarring nog groter is geworden.

De ervaring heeft geleerd, dat men met Franse faunistische gegevens wat voorzichtig dient te zijn. Teveel leest men in hun werken, ook in het thans besprokene: „presque toute la France", hetgeen toch voor verschillende soorten en zeker in dit grote land onmogelijk juist kan zijn.

De eindconclusie is: een prachtig uitgevoerde monografie, waaraan slechts zeer weinig tekortkomingen kleven. In ieder geval de meest moderne snuitkeverbewerking van de laatste tijd en ook voor onze eigen fauna van groot belang. De prijs van dit werk geeft minder reden tot verheuging. Als de tendens tot steeds duurder wordende wetenschappelijke werken zich nog wat voortzet, zal het niet lang meer duren of deze zijn alleen nog maar te vinden in de bibliotheken van universiteiten en grote instellingen. Om de eenvoudige reden, dat de particulier ze niet meer betalen kan. — P. J. BRAKMAN.