

OCCURRENCE OF ABNORMAL PHENOTYPES IN A HOST-ALTERNATING APHID AND THEIR IMPLICATIONS FOR GENOME ORGANIZATION AND EVOLUTION.

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ABSTRACT: Aphids of the Eriosomatinae alternate hostplants cyclically and show conspicuous polymorphism within a parthenogenetic line. This leads to the supposition that the genome consists of gene sets each producing phenotypes of one morph and of regulatory systems controlling the sequence of their activity. This supposition was corroborated by the appearance of abnormal larvae, which express features that should appear in another morph. The sudden appearance may be explicable by a mutation in a regulatory system rather than substitutions of structural genes. Such mutations are assumed to be responsible for the origins of the soldier caste in certain aphids and of radical changes of life cycle. In this hypothesis mutants can escape from the adaptive gap which exists in an evolutionarily intermediate state. Another implication of the appearance of abnormal larvae is the role of atavism in evolution. Besides features of the mimicked morph, they show a wholly novel feature, which is however found among ancestral eriosomatine genera. The regulatory mutation may have incidentally induced the appearance of the latent structure held in common by the members of the subfamily. It is suggested that the genome of a species maintains potentialities for phenotypic expression at various levels.

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Introduction

In the attempt to incorporate developmental biology in the evolutionary synthesis, some attention has been directed towards the phenomenon that different morphologies are alternatively manifested from the same genomic system through small changes in the internal environment (Goldschmidt, 1938; Raff and Kaufman, 1983). Well-known examples of the phenomenon are polymorphism in locusts and hemipterous insects, seasonal polyphenism in butterflies, occasional occurrence of neoteny in some salamanders, sexual dimorphism, and caste differentiation in social insects (e.g. Shapiro, 1976; Lüscher, 1976; Matsuda, 1982). As a particular example, homoeotic mutations in *Drosophila* have served as a clue to clarify the developmental mechanism of phenotypic differentiation (Garcia-Bellido, 1977; Lewis, 1978). In aphids a number of experimental studies have been concerned with physiological mechanisms producing alternative appearance of the alate and the apterous form or of the viviparous and the oviparous female. The studies show that morph determination is influenced by various ecological factors such as crowding, photoperiodism, nutritional condition, etc. (Bonnemaison, 1949; Lees, 1961, 1966; Hille Ris Lambers, 1966; Mittler, 1973; Blackman, 1975). These studies have traditionally been centred on the Aphididae (sensu Heie, 1980) which are suitable for experimental treatments. However, far more remarkable instances of aphid polymorphism are found in the Pemphigidae and Hormaphididae (Hille Ris Lambers, 1966), but there have been few attempts to incorporate such polymorphism into evolutionary theory, or to identify the causal factors.

Most of the Pemphigidae have life cycles involving alternation of hostplants, utilizing two extremely different environments; they live in leaf-galls on some deciduous trees (called primary hostplants) in spring to early summer and on the roots of various other plants (secondary hostplants) from summer to autumn. In my ecological study on the gall generations of a pemphigid species, among many

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individuals mounted on slides I found some larvae showing abnormal features. Comparisons of the abnormal larvae with normal ones on the galls and the secondary host-plants permitted some inferences concerning genetic basis of the phenetic manifestation. In this paper I discuss the genetic basis for the remarkable polymorphism within the conceptual framework of genomic hierarchy and gene regulation. It is suggested that diverse modes of evolution can occur in aphids having peculiar polymorphic forms coupled with cyclical parthenogenesis.

Aphids of the Pemphigidae

The apterous forms of the Pemphigidae comprise three major morph classes--1) gall generations including stem mothers, which initiate the galls, and the succeeding generation, 2) root generations occurring on the secondary host, 3) sexual generation, or sexuales (males and oviparous females) which are deposited on the trunk of the primary host by alates matured on the secondary host. Sexuales are extremely dwarfish in the adult stage, with no postnatal development. The oviparous female has only one egg which occupies almost the whole mother body. There are two different alate morphs; the spring alates which fly from the galls on the primary host to the secondary host, and autumn alates which undertake the return migration and produce the sexuales. This life cycle scheme is complicated by some variations between species, and a typical case is shown in Fig. 1. In spite of the fact that these generations are connected as a continuous clonal series, they are morphologically so distinct that the primary and secondary host forms of a species were occasionally classified into different genera.

The following discussion is concerned with one subfamily of the Pemphigidae, the Eriosomatinae. Aphids of this subfamily are associated with trees of Ulmus or Zelkova as the primary host and there form leaf-galls of various types (Akimoto, 1983, 1985). The Eriosomatinae are in my opinion (1983) composed of 12 genera, including two known only from the secondary hostplants. Hemipodaphis persimilis is an eriosomatine species with very large differences between the gall generations and root generations, especially in the first instar (Fig. 2). This apparently corresponds to a behavioural difference; in the gall the first instar larvae show an active defence behaviour against predators (Aoki, 1978), while they probably pass a sessile life on the secondary hostplant. The defence behaviour is carried out by monomorphic first instar larvae which complete larval development. No sterile soldiers appear in the gall of this species. The secondary hostplant of H. persimilis is unknown at present, but the features of the root generations can be readily seen in the spring alate's embryos, which have features substantially like those of the root generation larvae into which they develop.

Material and method

During my ecological investigation of H. persimilis, a total of 4764 larvae collected from 26 galls from June to October in Sapporo were mounted on slides. All the samples were heated in 10% KOH and then in chloral-phenol (Eastop and Van Emden, 1972) each at 65° C, and mounted by gum-chloral. Five larvae showing abnormal phenotypes were found in one gall collected on 10 September, 1977. This gall, when collected, held a total of 371 aphids, of which 176 were first instar larvae and 37 were adults. Of the 5 abnormal larvae found, 4 were in the first instar and 1 was probably a third instar. I compared them for some qualitative and quantitative characters with normal first instar larvae occurring on the same gall, and with those borne by spring alates collected on a gall in 1983.

Result

A) Morphology of abnormal larvae

Although the 4 abnormal first instar larvae hardly differ from first instar larvae occurring in galls in terms of body size, all the appendages show statistically significant decreases in size (Fig. 3, and Table 1). General changes are described as follows. "The body is more elliptical in shape. Stylet far longer than rostrum, reaching or exceeding the posterior end of the body. Legs shortened and thickened. Tarsus spinulose, tapering, with thick spine-like hairs. Claws slenderer, with long empodial hairs (lacking in normal larvae). Antenna with a few apical segments fused into one, thicker, intensively spinulose (smooth in normal larvae), with long hairs (absent in normal larvae). Body hairs capitate at the tip instead of smooth." These characters are ones which can also found in the first instar larvae deposited by spring alates. That is, the abnormal larvae express the characters that should appear originally in the root generations. The degree of expression of these characters differs among the larvae. Two larvae, denoted by M1 and M2, show a slight morphological change, with the character state of the gall generation larvae remaining in siphunculi and wax plates. In the one abnormal larva (M5) which attained to the third instar, the change is especially slight and virtually limited to wax plates (Fig. 5C). On the other hand, the larvae of M3 and M4 closely agree with the larvae on the secondary host over all features except for the difference in wax plates and size. The arrangement and structure of wax plates found in them (Fig. 3 and Fig. 5B), however, can be detected nowhere through all the morphs of this species.

It is possible that these 5 abnormal larvae were derived from 1 adult. By a careful inspection of embryos within the abdomen of adults, I detected only one which contained at least 2 embryos showing the same phenotypes as found in the abnormal

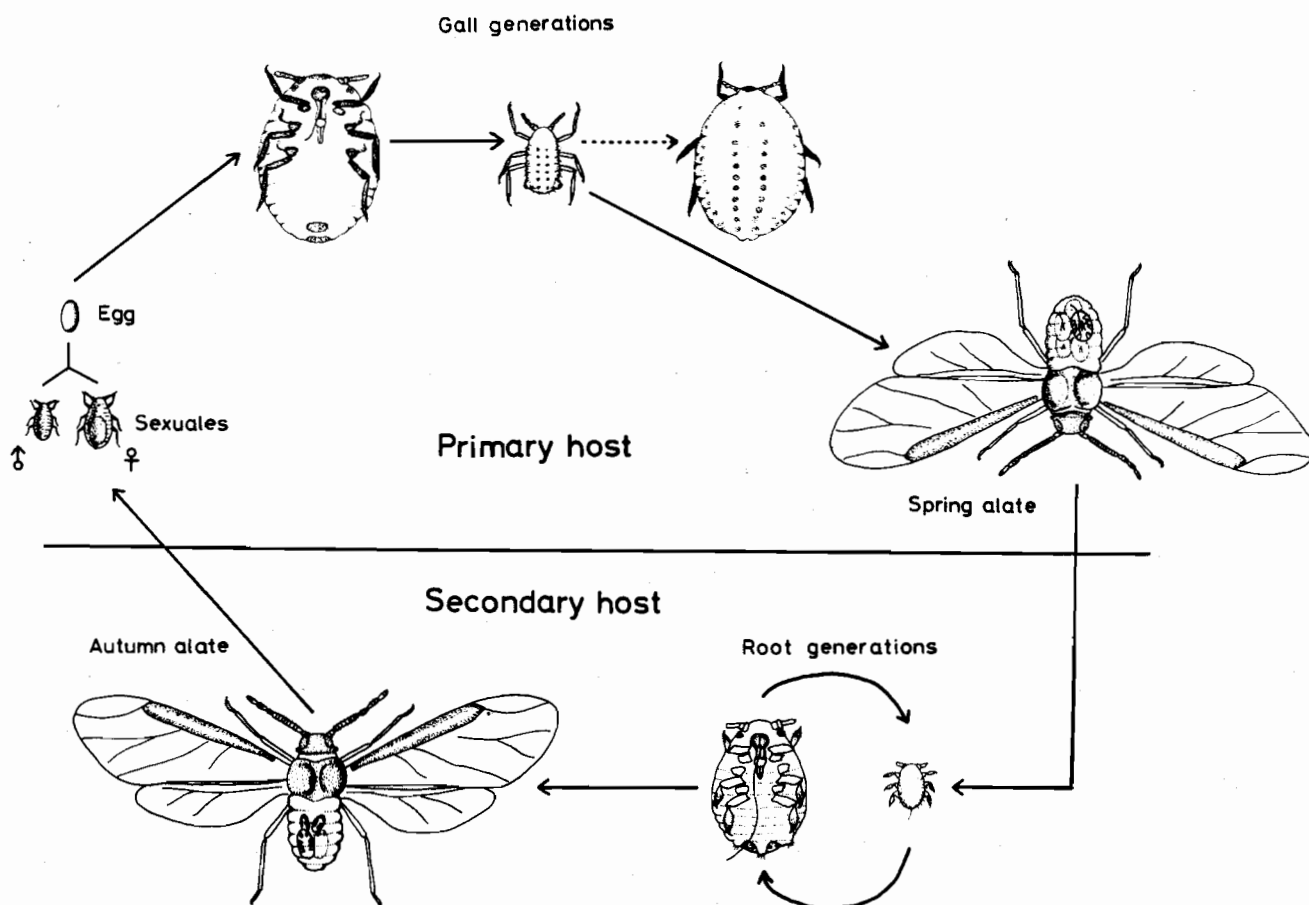


Fig. 1. A typical life cycle of pemphigid aphids. In some species, including *Hemipodaphis persimilis*, a part of larvae in the galls grow into apterous adults.

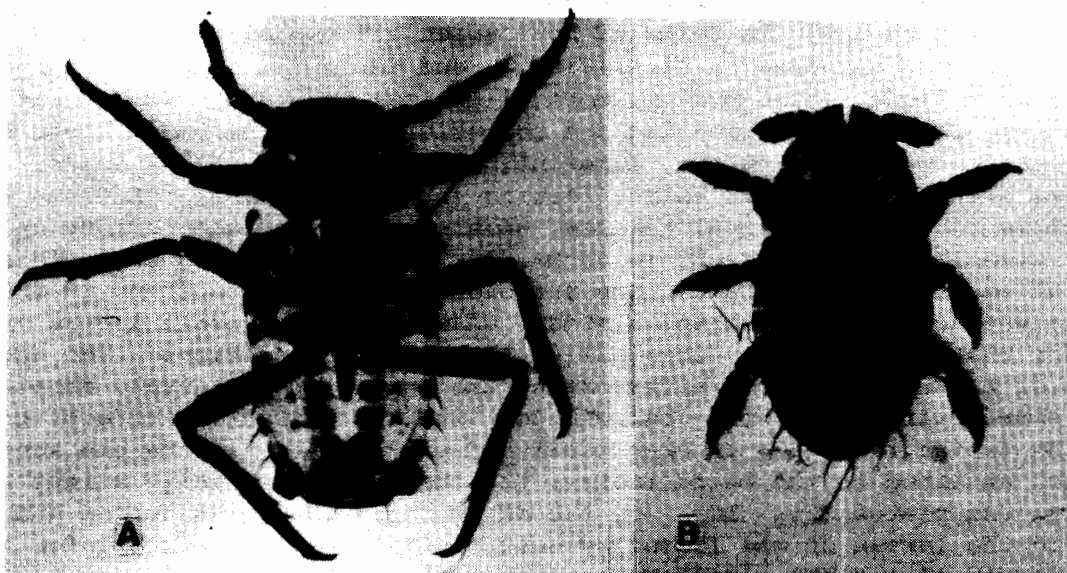


Fig. 2. *Hemipodaphis persimilis* first instar larvae. A, from the gall; B, deposited by the spring alate (the root generation). Equal in magnification.

larvae. The adult was morphologically compared with the other ones in the same gall. They showed neither outstanding differences nor statistical significance in some quantitative characters (Table 2).

B) Wax plates occurring in abnormal larvae

Wax plates in the root generation are conspicuous features appearing on the dorsal surface. Waxy secretion from them generally covers the body. The feature is stable through all developmental stages and therefore taxonomically important. In normal larvae of the root generations, wax plates are present at lateral positions of every segment and additionally there are vestigial ones at spinal positions of thoracic segments. Each wax plate is circular as a whole, consisting of 1 bright central circle and rather dusky cells which surround the former in a single layer. On abdominal segment VII they are much larger, including more numerous cells among which several bright circles are interspersed (Fig. 5A). A remarkable difference is found in abnormal larvae (M3-M5), whose wax plates are enlarged and appear also at positions which are normally unoccupied: they are all identical in size and arranged in 6 longitudinal rows at spinal, pleural, and lateral positions over the central part of body (mesothorax-abdominal segment IV) (Fig. 3). In M3 and M4, which have them best developed, each wax plate includes 4-7 bright circles in the central part of body and is rather similar to the plates of abdominal segment VII in normal root generation larvae.

Discussion

A) The structure of genomes

The first synthetic hypothesis for the morph determination of aphids was proposed by Johnson and Birks (1960), who postulated that the developmental pathway is initially programmed to lead to the manifestation of the phylogenetically primitive state. Through subsequent endocrine control the development proceeding along that course is, at some point of time, suppressed and reoriented to another pathway for a phylogenetically derived phenotype. In this scheme they thought that the development at first proceeds along the pathway to the alate male or alate oviparous female, which apparently mimic the ancestral characters as Hille Ris Lambers (1966) suggests. If daylength and other external stimuli prevent the development from proceeding along the sexual course, it is switched over to the parthenogenetic

course, where the pathway first set is one for the alate which is morphologically more primitive than the aptera. Finally the pathway to the apterous morph is opened according to crowding, nutritional conditions and the maternal effect. This hypothesis has generally been accepted as a model compatible with the results of experimental studies (Hille Ris Lambers, 1966; Lees, 1966). Moreover, the essential proposition of this hypothesis may be corroborated by the application of a genetic and developmental analysis of homoeotic mutations in *Drosophila*. For example, the imaginal disc of the *Drosophila* metathorax is programmed to develop along the pathway for the formation of a mesothorax-like structure, but at some point of time the function of a gene set makes the development deviate towards the completion of another structure. Mutation occurring at any of such genes (selector genes) leads to the loss of the function, consequently transforming the original metathoracic feature into the mesothoracic one (Garcia-Bellido, 1977). The analysis of this bithorax mutation implies that a derived structure is induced by converting the developmental pathway for the primitive structure into another.

Johnson and Birks' model, however, needs to be altered when applied to the Pemphigidae which show remarkable polymorphism. In the Aphididae, despite conspicuous differences between alates and apterae, morphological differences among generations are not so large when only apterae or alates are considered, and, further, functional differentiation among generations is often not decisive. For instance, some apteriform characters are readily produced by smearing juvenile hormone-like substance on the surface of alatiform larvae, although the effect is restricted to particular structures owing to the prenatal control by the mother (Lees, 1961, 1966). This shows that the alternative of alates and apterae is determined under a rather simple genetic basis. Moreover, if a changed condition of temperature is applied to alates that produce only oviparae of *Aphis fabae* immediately after the

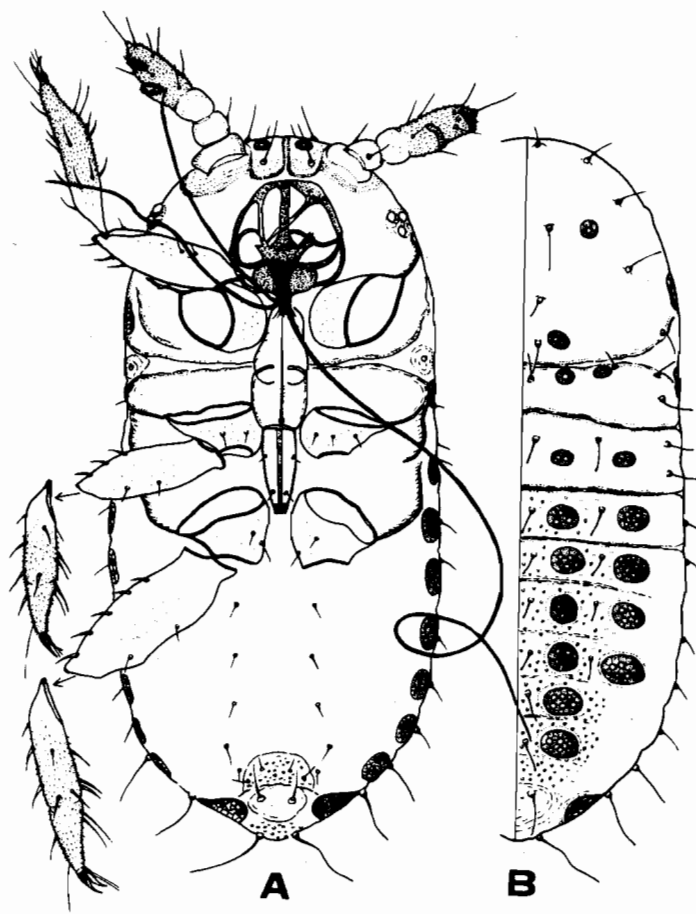


Fig. 3. Abnormal larva (M4). A, ventral view; B, dorsal view.

last molt, they change their own function from the oviparae-producer to the viviparae-producer (De Fluiter, 1950). The functional change in the same individuals is verified in other aphids (Lees, 1959; Blackman, 1971). In the Pemphigidae, especially Eriosomatinae, the gall and root generations are morphologically discrete entities, with differences not limited to particular structures. The alternative of alates and apterae is determined not only in the gall generations but also independently in the root generations, suggesting that the polymorphism of the Eriosomatinae is not brought out from one underlying genetic basis through a series of choices of the developmental pathways. The sexual generation is, moreover, most specialized and undoubtedly deviates developmentally furthest from the basic structure. For the genetic organization of the Eriosomatinae, therefore, it is postulated that in the genome major gene sets coexist which give rise to the phenotypic expression of the gall, root, and sexual generations. Wing dimorphism occurring

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Table 1. Comparisons of some characters between abnormal (M1-M4) and normal (L1) first instar larvae. Measurement in mm (mean \pm SD).

	L1 on gall [N=70]	L1 on root [N=28]	M1	M2	M3	M4
Body length	0.616 \pm 0.0232	0.511 \pm 0.0137	0.636 (P*=0.38)	0.611 (P=0.83)	0.667 (P=0.03)	0.636 (P=0.38)
Ultimate rostral segment	0.114 \pm 0.0035	0.060 \pm 0.0018	0.089 (P=0)	0.094 (P=0)	0.084 (P=0)	0.083 (P=0)
Hind femoro-trochanter	0.212 \pm 0.0080	0.124 \pm 0.0033	0.192 (P=0.01)	0.192 (P=0.01)	0.180 (P=0)	0.177 (P=0)
Antenna	0.216 \pm 0.0083	0.107 \pm 0.0034	0.167 (P=0)	0.162 (P=0)	0.149 (P=0)	0.141 (P=0)
Rostrum	0.259 \pm 0.0067	0.141 \pm 0.0037	0.197 (P=0)	0.210 (P=0)	0.190 (P=0)	0.187 (P=0)
No. of antennal segment	5	3	4	4	3	3
Stylet	as long as rostrum	far exceeding body end	almost reaching body end	reaching body end	a little exceeding body end	reaching body end
Tarsus	smooth, straight	intensely spinulose, conoid	slightly spinulose, straight	slightly spinulose, straight	intensely spinulose, conoid	intensely spinulose, conoid
Siphunculus	large	absent	small	small	absent	absent
Dorsum	without nodules	with nodules	without nodules	without nodules	with nodules	with nodules
Types of wax plate	A	B, BB	A, B, BB	A, B, BB	B, BB	B, BB

P*: probability that a larva on the gall shows a more deviant value from the mean than the value of each abnormal larva.

A----assemblage of dusky cells.

B----one bright circle and dusky cells.

BB---some bright circles and dusky cells.

Table 2. Comparisons between the apterous adult which deposited the abnormal larvae and the other apterous adults on the same gall.
Measurement in mm.

	Hind femoro- trochanter	Hind tibia	Ultimate rostral segment	Antenna	Body size
Adult which deposited abnormal larvae (AA)	0.321 (P*=0.79)	0.247 (P=0.12)	0.152 (P=0.87)	0.293 (P=0.35)	1.620 (P=0.49)
Other adults					
Mean \pm SD	0.317	0.281	0.150	0.317	1.552
[N=36]	\pm 0.0141	\pm 0.0214	\pm 0.0106	\pm 0.0255	\pm 0.0988

P*: probability that an adult derived randomly from the gall population shows a more deviant value from the mean than the value of AA.

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in both gall and root generations may be due to a secondary mechanism which switches over to the other state according to a change of the titre of, say, juvenile hormone within the framework of each major gene set. In this scheme, therefore, the gall generation maintains the phenotypic potential for the morphologies of the root and sexual generations. In the Eriosomatinae the morph determination is wholly independent of external stimuli except in the production of autumn alates; in most species the stem mother is necessarily followed by the spring alate, and the latter by the root generations. Moreover, aphid embryos generally start to develop before their mothers are born (Blackman, 1981). This suggests that the developmental destiny of an aphid had been more or less programmed within the grandmother. These implications inevitably require regulatory systems under which all the major sets of genes are rigorously controlled to be activated in a certain sequence throughout the life cycle.

The models proposed for gene regulation in eukaryotes by Britten and Davidson (1969, 1971) and Davidson and Britten (1971), though not verified by positive evidence yet, are quite applicable to the morphogenesis of this group. In the Eriosomatinae it is probable that a major set of structural genes, a battery of genes in the terminology of Britten and Davidson, is under the control of a series of regulatory genes led by a master sensor gene. Through an enormously long history of adaptation, the generations on the primary and secondary hostplants must have accumulated structural genes producing the phenotypes adaptive to each environment, and these genes may have been organized into a proper regulatory system. According to Britten and Davidson models, we can suppose that the genes constituting a battery are interspersed throughout the genome rather than clustered in a specific portion of a chromosome, and are only regulated to be transcribed in concert during an ontogenetic process. In such a hierarchically organized genome, a point mutation occurring in a regulatory system might result in the transcription of a certain group of genes which is suppressed in the normal developmental process. In particular, a change in sensibility of a sensor gene for the products of other integrative sets might activate structural genes. If these assumptions for the gene organization are true for the Eriosomatinae, mutation of a regulatory gene would result in the replacement of some or all features of a morph class by the corresponding features of another morph class. This hypothesis is supported by the abnormal larvae, in which some characters of the gall generation larva are converted to those which

normally should appear in the root generations, with different degrees of expressivity among them. Variable expressivity often accompanies the expression of mutant genes having weak effect, as found in some bithorax mutations of *Drosophila* (Garcia-Bellido, 1977). The mutation responsible for the abnormal larvae seems to have occurred in one apterous female in the gall, because if it had come down to the generation of the female from the stem mother or the preceding generations, more apterae would have given birth to many more abnormal larvae.

In aphids, intermediate forms are not rare between the successive morphs, and the embryos in the abdomen of an intermediate form often also show an intermediate state (Hille Ris Lambers, 1966). Therefore, if the abnormal larvae had been borne by an intermediate between the apterous form in the gall and the spring alate, they could be regarded as abnormalities resulting from a disorder of endocrine control. This possibility can, however, be ruled out, because their mother is morphologically normal as an apterous female, showing no significance in the comparison of some measurements (Table 2). So far no intermediates have been found in *H. persimilis*. However, there still remains the possibility that the abnormal larvae were produced not by a regulatory mutation in their own developmental process but by a mutation in the endocrine system of the morphologically normal mother. Steel (1976) showed that the cerebral neurosecretion of an aphid directly manipulates the programming of the embryos' endocrine system. From this fact, it is obvious that through endocrine control a larva destined to be an aptera in the gall must develop its embryos to the gall generation, while a larva destined to an alate must develop its embryos to the root generation. However, the mother of the abnormal larvae may have released a hormone which is normally present in the alate mother. In the hierarchically organized genome, indeed, an abrupt alteration in the endocrine control by a mother can lead to the same result as expected from a regulatory mutation occurring in its embryos themselves by disturbing the sequence of activation of the embryos' gene groups. Therefore, in this case and the following instances an abrupt phenotypic change in an aphid with polymorphic forms is explicable by assuming an alteration in any of the following two phases: in the developmental process of an embryo and in the endocrine system of the mother.

B) Evolutionary implication of structured genomes

The mutants shown here are apparently inadapative. Above all, their altered mouthparts must make it impossible for them to feed in the gall. One mutant which attained to the third instar stage shows very weak expressivity, having virtually the same mouthparts as in normal larvae. In general there is no doubt that mutations which impose a large-scale alteration on body structure will be selected out. However, suppose that as a rare case, the morphological and the physiological characters of a generation on one hostplant are also adaptive on the other hostplant. Then, the mutation which expresses some of such phenotypes of a different morph may increase its gene frequency by selection until fixation. Once fixed in a population, the substituted phenotype will accumulate gradual modification to improve the adaptation to the newly encountered environment. One expected result of this assumption may be the appearance of two morph classes in one generation. This could explain the remarkable differentiation of the soldier caste found by Aoki (1977a, 1977b, 1983) in the secondary host generations of an eriosomatine genus, *Colophina*. The soldiers are borne together with normal larvae by a female and stay in the larval state. At present it is wholly unknown how the remarkable morphological gap between the soldier and the normal larva originated. They differ especially in the length of the mouthparts. The normal larva has long mouthparts reaching the posterior end of the body, and this is necessary for the larva to absorb sap from the sieve tubes in the stem of the secondary hostplant. On the other hand, the soldier has very short mouthparts reaching half of the body and uses them for piercing predators. Such short mouthparts are unusable for feeding at least from sieve tubes. Did intermediate forms between the normal larva and the soldier have any adaptive function in the early evolution of the soldier caste, if we assume gradual transformation? The caste differentiation in *Colophina* aphids seems to

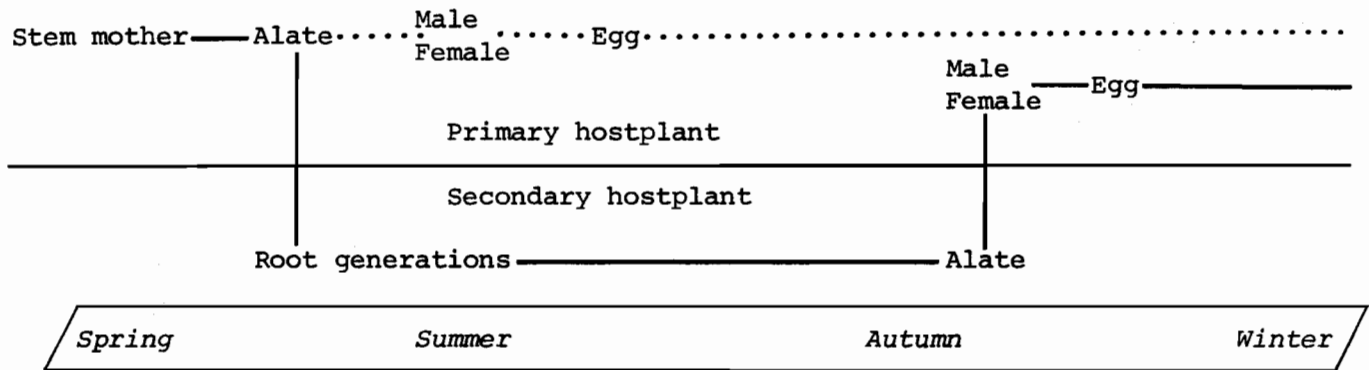


Fig. 4. Differentiation of a sedentary life cycle (.....) from a heteroecious life cycle (———).

differ from that of ants and termites (Wilson, 1971) in that the incipient form is probably inviable and useless because of the inability to take in food.

It is noteworthy that the larvae in *Colophina* galls are monomorphic, but rather specialized to attack predators and morphologically similar to the soldiers occurring on the secondary hostplants (Aoki, 1980). For the evolution of the soldier it could be an important step that larvae having the structures of gall generation larvae appear as mutants in the colony on the secondary hostplants. Since such abnormal larvae are most likely to have short mouthparts suitable for attack, they could have been effective in defending the colony against insect predators and thereby have contributed to increase the inclusive fitness of the colony. Moreover, they would not always need to accomplish a sophisticated adaptation to the hostplants because they, as soldiers, do not develop and molt at all after birth. What I am suggesting is not the appearance of crude phenotypes of the gall generation larva on the secondary hostplants but the genetic potential as material basis in producing the soldier. Undoubtedly, its morphological evolution relates also to other factors such as allometric transformation in the prenatal developmental process, as well known in the caste differentiation in ants (Huxley, 1932; Wilson, 1953).

The foregoing possibility was concerned with partial replacement of the phenotypes in a morph. However, a mutation occurring in major regulatory genes might result in the whole replacement of one generation by another. In the Pemphigidae generally the embryos of an autumn alate develop to both males and oviparous females and the possibility of frequent sib mating is suggested (Dixon, 1985). Suppose that the gene set responsible for the sexual generation is activated by alteration of a regulatory gene in a foregoing generation, for example, during the embryogenesis in the spring alate. Then the sexuales born to this alate may mate between siblings and leave fertilized eggs. By chance this inbred population may continue to last beyond an incipient bottleneck. Such a large-scale alteration is generally an unpromising challenge. Nevertheless, once this deviant population had succeeded in establishing itself in a favourable environment, it would have accomplished reproductive isolation from the ancestral population sympatric with it and established a sedentary mode of life on the primary hostplant (Fig. 4).

There is an example explicable under this scheme. *Kaltenbachiella japonica* has a sedentary life cycle on the Japanese elm, *Ulmus davidiana* var. *japonica* (Hille Ris Lambers, 1967; Akimoto, 1985). The alates emerging from a closed gall on an elm leaf bear the sexuales on the branch in mid summer. The sexuales copulate and leave the eggs, which remain in diapause from summer to the next spring. Recently another *Kaltenbachiella* species, *K. spinosa*, was found to form galls similar to those of *K. japonica*. It is distinguished from *K. japonica* on the basis of the karyotype and some external characters and shows a geographical range which overlaps

with the range of *K. japonica*. Morphological comparisons of the gall generations, karyotypes and galls suggest that they are more closely related to each other than to other *Kaltenbachia* species (Akimoto, 1985, unpub.). In *K. spinosa*, however, the alates maturing in the gall contain the embryos which are to grow on the roots of the secondary host, the species thereby differing from *K. japonica* in the mating season. The speciation process between the two species can be explained by supposing alteration in the regulatory system. Otherwise, we must assume that the altered life cycle has gradually evolved through successive short steps. It is, however, difficult to imagine that a gradual change of the embryo of the root generation into the sexuales embryo or vice versa is selectively favoured, because the embryos at an intermediate state demonstrate no adaptive function. An evolutionary transformation between the two embryonic forms, as a logical consequence, must be a saltational process, explicable by alteration in the timing of activation of major gene sets, rather than by gradual substitutions of structural genes.

In terms of the underlying genetic change the partial or whole transference of an aphid morph to a different generation may correspond to heterochronical transformation in metamorphic ontogeny. It has repeatedly been proposed that changes in the timing of an early developmental event have profound effect by altering many subsequent ontogenetic steps, consequently creating various evolutionary novelties (Goldschmidt, 1938, 1940; Alberch et al., 1979; Gould, 1982). Matsuda (1979) paid attention to abnormal metamorphosis in insects, and regarded an enormous phenotypic potentiality of genomes as a material basis of macroevolution. The aphids of the Eriosomatinae most clearly illustrate an ample potentiality of the genome for phenotypic expression in respect that they show sequential polymorphism connected by a single clonal series. In this group, like heterochrony in ontogeny, changes in the sequence of the activation of major gene sets may have produced not only the remarkably deviated life cycles but also discrete forms in a single generation.

C) Atavism and its implication in phylogeny

Another problem presented by the abnormal larvae of *Hemipodaphis* concerns their wax plates. The abruptly manifested character in their wax plates, however, cannot be regarded as novel, because some similar arrangements and structures occur in the phylogeny of the Eriosomatinae.

The primitive state of the arrangement of wax plates may be inferred by considering the Adelgidae, which are utterly oviparous and maintain many putatively primitive characters, and some fossil aphids found in Baltic amber (Heie, 1967). These primitive aphids have distinct and rather uniform wax plates arranged in 6 longitudinal rows in the central part of body. In this respect the root generations of the Eriosomatinae show large interspecific variability, having 2, 4, or 6 rows according to species. The variability occurs even in a single genus, e.g. the genus *Eriosoma* (Akimoto, 1983). Through the Eriosomatinae the potential for inducing a wax plate at a particular portion seems to be governed according to certain tendencies. The species having 2 rows of wax plates always show them at lateral positions, and the species having 4 rows at spinal and lateral positions (the lateral wax plates are generally larger than the spinal ones on the same segment). Pleural wax plates often appear rudimentarily. That is, the potential decreases in the following sequence--lateral, spinal, pleural rows. Within a single row a wax plate becomes larger towards certain posterior segments (usually segment VII), and thus the potential may increase towards the same direction. Considering these tendencies and the features found in primitive aphids, it is certain that all the species of the Eriosomatinae maintain the ability to express 6 rows of wax plates.

Similar wax plate structures to that shown by the abnormal larvae can be found among some other eriosomatines, especially in *Schizoneurella* (Fig. 6). Other similar structures consisting of more than 1 bright circle and circumferential cells exist in *Schizoneurata* and *Aphidunguis*. *Paracolopha* and *Colopha* represent a further modified structure with 1 bright circle. These patterns suggest that the basic developmental pathway for the formation of individual wax plates is common through the Eriosomatinae, and that their expression depends on the degree of the

concentration of an inducing substance. In the ancestral Eriosomatinae, the substance may have abundantly and almost equally been assigned to every developmental pathway, and induced wax plates may have appeared as a multicellular structure including some bright circles. However, given partial suppression during development, wax plates may become smaller and bright circles may reduce to a single one surrounded by cells (e.g. the wax plates on tergite VI of *H. persimilis*). As further suppression is added, the bright circle will disappear, leaving an assemblage of cells, and in the ultimate case all will be repressed. These assumptions are illustrated in Fig. 7, where difference in the potential (or the degree of the concentration of inducer) and the position of a threshold are proposed as main factors giving rise to the differentiation of patterns among positions. Probably, distribution of the inducer concentration has changed during the phylogenetic evolution and this resulted in interspecific differentiation of the expression. The wax plates derived from partially suppressed potentialities are found in *Eriosoma*, *Kaltenbachiella* and *Tetraneura*. The first two genera mostly have 1 large central field and circumferential cells. The central field apparently has the same origin as the bright circle, but does not differ in brightness from circumferential cells. *Tetraneura* has much altered wax plates, which have no apparent structural correspondence to those of

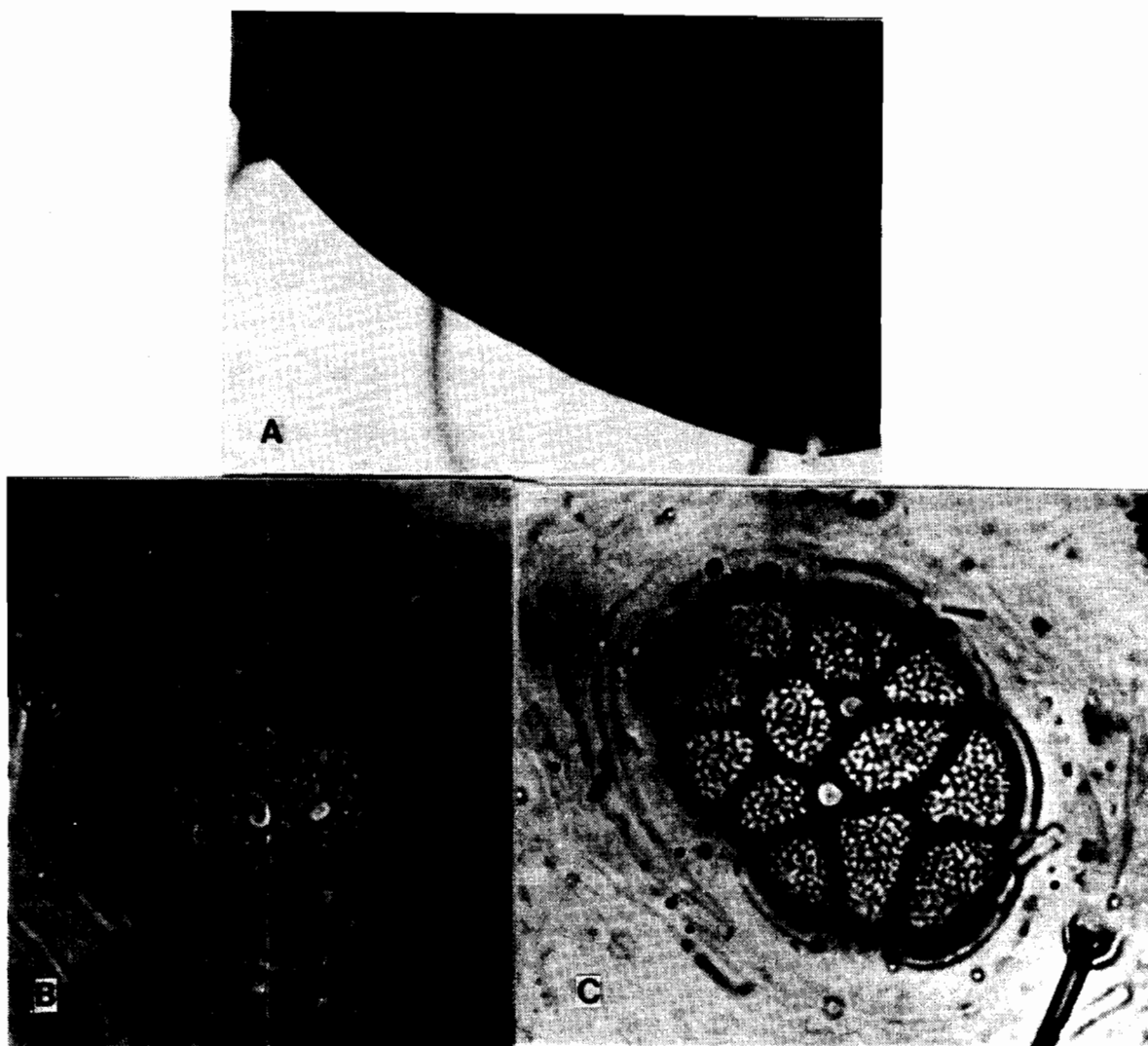


Fig. 5. Wax plates. A, from a larva deposited by the spring alate (showing a large wax plate on segment VII and a smaller one on segment VI); B, from abnormal first instar larva (M4); C, from abnormal third instar larva (M5).

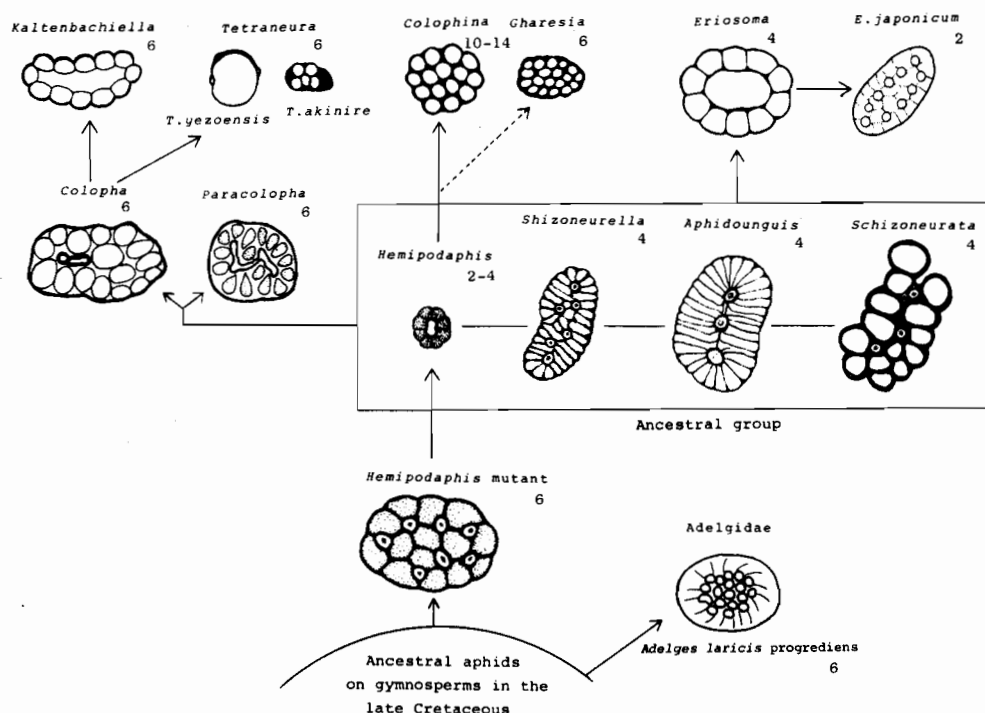


Fig. 6. Changes in the expression of the wax plate through the phylogeny of the Eriosomatinae. Figures under the generic or specific names show the number of the rows of wax plates. Wax plates of *Adelges laricis*, *Schizoneurella*, *Schizoneurata* and *Gharesia* are redrawn from Inoue (1945), Hille Ris Lambers (1973a, b) and Stroyan (1963), respectively.

other genera and vary largely in structure among species. In *Colophina* and *Gharesia*, wax plates are strongly represented as multicellular structure in 6 rows (or more in *Colophina*), but lose the bright circle, consisting of uniform cells.

There is a certain instance which shows that a species having a derived structure in the wax plates maintains the potentiality for the basic structure. In *Eriosoma* whose members mostly have 4 rows of wax plates, only *E. japonicum* shows 2 rows. Its individual wax plates are large and similar to those of the abnormal larvae (Fig. 6), and there is no apparent intermediate connecting the structure in *E. japonicum* with that in other *Eriosoma* species. In other characters *E. japonicum* quite agrees with other *Eriosoma* species. It is probable that in this species the inducer was concentrated at lateral positions, where the potential increased to induce the basic structure. In conclusion, the novel features shown by the abnormal larvae M3 and M4--multicellular wax plates arranged in 6 rows--agree with the supposed primitive state and may have appeared because the basic pattern was released from suppression in connection with the systemic mutation which induced some features of the root generation. In this sense, the appearance of the novel feature can be regarded as atavistic. This state is normally suppressed, but not lost potentially in *H. persimilis*.

There is in the Eriosomatinae some correspondence between the state of expression of the wax plates and the phylogeny. *Schizoneurella*, *Schizoneurata*, *Aphidounguis* and *Hemipodaphis* which contain more than 1 bright circle in each wax plate are all small groups comprising 1 or 2 species and, except *Schizoneurata* whose hostplant is unknown, associated with primitive groups of the Ulmaceae. These plant groups are supposed to have originated as early as the Early Tertiary on the basis of fossil records (the genus *Zelkova*, the host of *Hemipodaphis*, and the section *Microptelea* of *Ulmus*, the host of *Aphidounguis*) (Tanai, 1961; Endo, 1968), or of the analysis of the chemical components (*Ulmus villosa*, the host of *Schizoneurella*) (Bate-Smith and Richens, 1973). At present these hostplant groups show disjunctive

geographical ranges restricted to warm-temperate regions between or within continents (Elias, 1970; Bate-Smith and Richens, 1973; Akitomo, 1985), and thus can be regarded as relicts of the Early Tertiary flora. On the basis of comparisons of gall generations in the Eriosomatinae, Akimoto (1983) inferred that Hemipodaphis and Aphidounguis maintain some primitive characteristics in their life cycles. Evidence from these different sources indicates that these 4 genera are remnants of groups which flourished in the Early Tertiary, and thus can be called ancestral groups in the sense of Van Valen (1978). On the other hand, the groups having modified wax plates, Eriosoma, Kaltenbachiella and Tetraneura, are associated with an Ulmus section which has prospered with the progress of arid and cool climates since the Miocene (Akimoto, 1985). The host group (the section Ulmus) shows a continuous and extensive geographic range in the Holarctic region in the present. Eriosoma and Tetraneura are each composed of about 30 species and Kaltenbachiella has 8. On the basis of biogeographical data, Akimoto (1985) proposed the view that Colopha, now including 3 species, represents the ancestral stock from which Kaltenbachiella and Tetraneura were derived, and has not deviated much from the basic pattern. In this connection it is notable that Colopha has the wax plates approximating to the basic pattern. Through these lines of evidence, the modified pattern is thought to be associated with derived groups, although the relationship is not simple. It seems that the genomes of the ancestral taxa have continued to provide the material basis for evolutionary changes. The supposed huge potentialities of the genome in evolution are also a logical consequence of the hierarchical system of the genome.

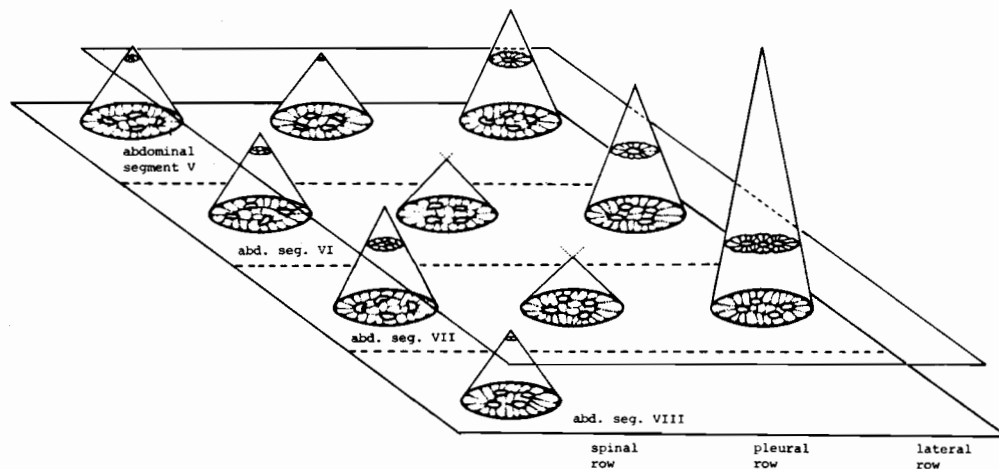


Fig. 7. A model for the expression of wax plates. The strength of inducing a potentiality at each position is shown as the height of a cone. Each wax plate is supposed to be manifested when the amount of an inducing substance exceeds a threshold. During the evolution not only the distribution of inducer concentration but also the position of the threshold may change. In the lowest position of the threshold each wax plate would manifest the basic structure common to all the species of the Eriosomatinae. The pattern on the upper threshold is found in Eriosoma harunire (Akimoto, 1983).

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