

AN INTERPRETATION OF SECOND INSTAR MALE CHARACTERS IN
THE SYSTEMATICS OF THE DIASPIDIDAE*

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ABSTRACT

Sexual dimorphism in the diaspidid 2nd instar larvae considerably varies in the degree of differentiation and also in the type of difference. There are some cases where the 2nd instar males are strikingly different among species which are obviously closely related so far as based on the adult female characters. These phenomena in the 2nd instar male characters may be explained by supposing the existence of more or less stable "prepatterns". The phenotypic suppression or manifestation of prepatterns must occur more or less suddenly, with no process of direct adaptive selection for itself, and entail parallelism and/or atavism. If this view is correct, the degree of resemblance among the 2nd instar males does not necessarily indicate the degree of phylogenetic relationship.

1. Our study of the second instar males of the Diaspididae is still in its infancy, and the more examples we know, the more complicated the classificatory problem of this stage appears to be. I would like to focus on the phenomenon that some of the second instar males greatly differ in external characters among species which are obviously closely related so far as based on female characters. Needless to say, this evokes grave doubts as to the validity of the current classificatory system, which is primarily based on female characters. The published cases of this phenomenon are still few, but I believe that they will afford clues to proceed with the problem of the second instar males in the systematics of the Diaspididae.

2. Before going further, I would like to discuss morphocline analysis. A morphocline, or a transformation series of homologues, is a logical arrangement of characters and is expected to be an approximation to an evolutionary series of changing characters.

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This expectation is based on the supposition that a morphocline has originated from a chronocline, in which it has corresponding parts (Maslin 1952). When most or all morphoclines constructed for a set of organisms are concordant, that is, when they agree in the order of the organisms, the series formed by the organisms may represent an approximation to the ancestral-descendant lineage which has brought these organisms into existence. Varying characters in such a series of organisms may suggest what happened in the course of the organisms' evolution.

3. Three species of the genus *Florinia* Targioni-Tozzetti, namely *F. hymenanthis* Takagi, *F. odaiensis* Takagi and *F. nachiensis* Takahashi, all occurring on rhododendrons in Japan, appear to be closely related in the characters of the second instar and adult females. Concordant morphoclines were constructed for most of the varying characters of the females in the mentioned order of the species, of which *F. hymenanthis* is deemed, based on ex-group comparisons of characters, to be the primitive extreme (Takagi 1975, 1979). Examples of the characters changing among the three species are given in Fig. 1, which shows the numbers of two kinds of external secre-

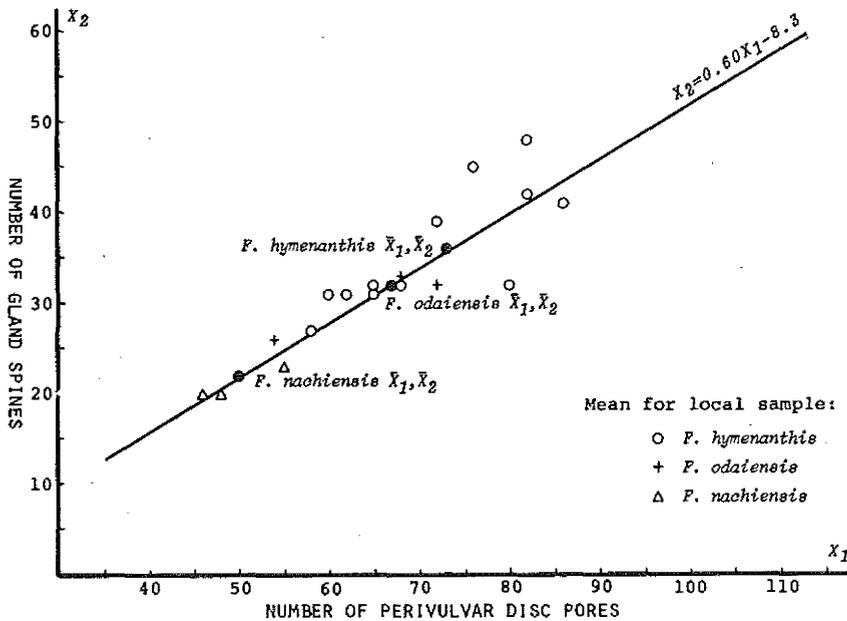


Fig. 1. *Florinia hymenanthis*, *F. odaiensis* and *F. nachiensis*, adult females. Mean number of gland spines against mean number of perivulvar disc pores. (From Takagi 1979.)

ories and their association. Here the numbers change gradually and continuously, and their association seems to hold a uniform tendency throughout. Other characters of the females are also changing more or less continuously, although one shows a statistical gap, thus making it possible to distinguish between *F. hymenanthis* and *F. odaiensis*. On the other hand, the second instar males show no differences between *F. hymenan-*

this and *F. odaiensis*, while they abruptly change from what I call "glandular" type in *F. odaiensis* to the "non-glandular" type in *F. nachiensis*. These differences involve certain remarkable features which occur in the glandular type, but are completely lacking in the non-glandular type.

The majority of *Fiorinia* species possibly belong to the glandular type, whereas only four species, including *F. nachiensis*, are known to have non-glandular second instar males (Fig. 2). However, this division does not always hold in the characters of

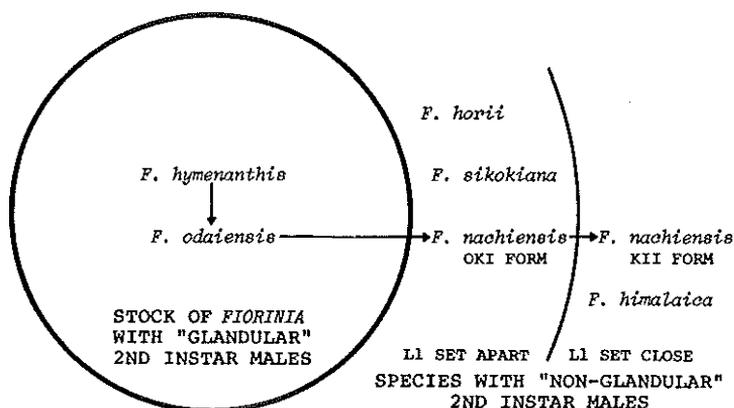


Fig. 2. Occurrence of "glandular" and "non-glandular" second instar males in *Fiorinia* species. The view here adopted is as follows: part of *F. hymenanthis* approximates the form ancestral to *F. odaiensis*; the Oki form of *F. nachiensis* approximately represents the transition from *F. odaiensis* to the Kii form of *F. nachiensis*; the glandular type as against the non-glandular one is primitive in *Fiorinia*; the four species belonging to the non-glandular type could have been derived separately from the stock of *Fiorinia* with glandular second instar males. (From Takagi 1979.)

the females. The four species belonging to the non-glandular type are not particularly closely related to each other, based on the analysis of female characters. (The above four species, together with *F. hymenanthis* and *F. odaiensis*, occur on the underside of rhododendron leaves and are characterized by a common tendency in the female median lobes, but the exhibition of this tendency must involve parallelism, or even convergence, and may be associated with the female habit of mining under the indumentum of the host leaves.) Nevertheless, the resemblance in the second instar males is very close between *F. nachiensis* and another non-glandular species, *F. himalaica* from the Himalayas. These two species are also characterized by being in a most derived form and *F. nachiensis* comes next.

From the above observations the following inferences may be drawn: 1) in the evolutionary course of *F. hymenanthis*, *F. odaiensis* and *F. nachiensis* the phenotypic characters of the females changed more or less gradually and continuously; 2) the phenotypic characters of the second instar males changed abruptly between *F. odaiensis* and *F. nachiensis* and this change has strongly affected the structure of the body; 3) the same phenotypic change that occurred in the second instar male of *F. nachiensis*

took place in the evolution of *F. himalaica*, which belongs to another evolutionary lineage.

It may be inferred that gradual and abrupt changes concurred in one and the same evolving lineage and that substantially the same abrupt change was repeated in a different lineage. This suggests that a sort of saltationism should occur in some relation with gradualism and that there should be some common base among related organisms for the abrupt manifestation of the same or similar phenotypic characters.

4. Reasoning adopted in constructing and analysing morphoclines, though in accord with some basic evolutionary generalizations, is purely logical, and inferences based exclusively on morphocline analysis remain within the bounds of logical probability. The construction of concordant morphoclines may involve inadequate interpretations of characters, or the concordance may be a mere coincidence. *F. nachiensis* may be closely related not to *F. hymenanthus* and *F. odaiensis* but to *F. himalaica* and other species with non-glandular second instar males. Furthermore, the genus *Fiornia*, as currently understood, may be an artifact, containing two distinct groups, one with glandular and the other with non-glandular second instar males. On the other hand, the abrupt change from the glandular type to the non-glandular type may be a mere chance. It may simply be due to the extinction of intermediate forms, and, if so, the gap which should be present in the female characters between *F. odaiensis* and *F. nachiensis* may have been obscured by secondary or local variations. The main objection to this possibility is in explaining why *F. nachiensis* and *F. himalaica* are so similar in the second instar males in spite of their discordance in the female characters. All this forces us to proceed further, beyond the bounds of formal comparisons.

5. Morphoclines may represent hypotheses, but hypotheses must be tested. As pointed out by Bock (1977), tests here may involve secondary hypotheses about particular features, further hypotheses about the mechanisms of evolutionary change, and so on.

My inferences given above postulate some threshold effect on the manifestation of second instar male characters. Threshold hypotheses are known in biology. For example, Goldschmidt (1946) in his experimental studies on drosophilid flies presented a threshold model to explain the phenotypic manifestation of a homeotic mutation. He further maintained that a model of the same structure as that for the homeotic mutation might be applied to explain a certain supposed evolutionary phenomenon — saltationism. His idea of “hopeful monsters”, a hypothesis of saltationism, was obviously based on his threshold hypothesis in phenogenetics.

But supposing a threshold effect alone is not sufficient for our problem. We need a hypothesis which can explain the association of gradual change with abrupt change in phenotypic characters in an evolving lineage and also the parallel manifestations of more or less similar abrupt changes in different but related lineages.

There are many experimental studies concerning the manifestation of structural patterns. Among them Sondhi's (1962) study appears to be relevant to the problem that faces us. In his experiments with drosophilid flies he found that continuous selection on certain structures produced new structures at places not predicted. The “neomorphs” thus produced are normally absent in the family Drosophilidae but are present in a few other closely related families. He explained the origin of the neomorphs in terms of an unvarying “prepattern” which determines the positions of these

structures, and of a varying "precursor" which must be present in the required amount if the structures are to be formed. The term "prepattern" as originally conceived in developmental biology denotes the physical and/or chemical conditions preceding the formation of a visible pattern. It may be adopted as "a convenient name for what is determined at any stage before the last" (Van Valen 1970). A gradual phenotypic change may be associated with a gradual change of the amount of a precursor until this amount attains the threshold of a structural manifestation. Prepatterns should also change. But, because the prepatterns are supposed to be relatively stable, closely related organisms are expected to have more or less similar prepatterns. Thus, the model presented by Sondhi (1962) only implies the concurrence of gradual and abrupt phenotypic changes in a group of organisms, and also the possible occurrence of more or less similar abrupt changes in different but related groups of organisms. In other words, the model implies that gradualism and a sort of saltationism are not unrelated phenomena, and that the latter will be accompanied with parallelism. What the prepattern-precursor model means is that a change induced by direct adaptive selection, while it is necessarily gradual, may give rise as its inevitable result to a discontinuous change, which primarily has no adaptive significance by itself.

6. The evolutionary inferences I have drawn from the morphoclineal study of the rhododendron-feeding species of *Fiorinia* fulfill what the prepattern-precursor model implies on the level of phenotypic characters. To proceed further with testing them we must clarify what is the adaptation which induced the gradual change and then the abrupt change. This involves the question why the abrupt change occurred in the second instar male and not in other stages. We may also have to show that the changing phenotypic characters of the second instar males involve neutrality or redundancy from the viewpoint of adaptation. I do not think that all this is easy to approach. But I think that we can proceed with a test on the level of routine external characters, using further material of the organisms in question and new organisms more or less related to them. We can also extend our quest over various groups of the Diaspididae. The North American species of *Quernaspis* may afford another case of the concurrence of gradual and abrupt changes of phenotypic characters (Takagi and Howell 1977). As long as the result of morphoclineal analysis on them fulfills the implications of the prepattern-precursor model, we need not give up the application of the model to the phenomena under study.

If we can adopt the idea of prepattern, we need not regard the series composed of *F. hymenanthis*, *F. odaiensis* and *F. nachiensis* as a mere coincidence of female characters, nor need we divide the genus *Fiorinia* as understood in the current concept into two unrelated genera. Thus we may now explain the close similarity between *F. himalaica* and *F. nachiensis* in the second instar males. We do this by accepting the development of similar prepatterns in the epigenesis of the second instar males among members of the same genus, as well as a common effect of the much derived condition of the adult females on the phenotypic characters of the second instar males (because males and females share the same genetic base).

All this, I believe, shows that we can select among possible classificatory schemes on a biological background. Finally, I would like to point out that our studies will in turn strengthen the prepattern-precursor model itself. And this should at least be a beginning, from our side, towards the integration of biological sciences.

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