

# PLANT REPRODUCTIVE ORGANS AND THE ORIGIN OF TERRESTRIAL INSECTS

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## INTRODUCTION

It is widely believed that plants facilitated the evolution of terrestrial insects (Southwood 1973). However, the mechanisms by which this evolution occurred are not yet fully understood. I therefore propose a hypothesis about one possible mode of formation of terrestrial insects and fauna. The soil, warm shallow lagoons, tidal zones, and accumulations of detritus are assumed by many authors to be the "bridges" for the transition of aquatic organisms to terrestrial existence.

The linkage of insects to plants has been offered as an explanation for the evolution of complete metamorphosis and the ability to fly. It has been suggested that holometabolism occurred in narrow cavities of the substrate, which might be represented by the cavities and ducts in the plant reproductive organs. It is assumed that wings and the ability to fly evolved owing to its advantages in finding food and escaping from enemies.

### The Transit to Land

The aquatic fauna is known to be extremely diverse; ancestors of the present arthropods were highly differentiated in the aquatic environment. In the transient water-land zones, the proto-insect's migration onto the land seemed inevitable, although this transit took a long time. Thus it could not have been simultaneous for various insect groups, although some groups evolved concurrently. Each group probably had its own bridge. Let us imagine those conditions which contributed to an obligatory and inevitable transition of aquatic organisms to land. The earth at that time (the Lower Silurian-Upper Devonian) was represented mostly by rocky, dry desert with scanty vegetation, oxygen deficiency, and unlimited amounts of severe ultraviolet radiation.

Organisms living in water were shielded from UVR and from drying and over-heating. They could easily move in a water environment which provided them with necessary support. Those organisms which moved onto land faced formidable ecological difficulties, the most serious being the lower viscosity and density of the air as compared to those of the water. Their bodies actually lost support and their free movement became impaired. For such groups of ancestral arthropods, soil might have been the bridge to terrestrial life. The land was almost devoid of organic life, having drastic changes of temperature, humidity, and illumination. The chance to survive and have progeny was probably very small. The vegetation (the plant protocommunities) had not yet contributed to the process apart from accumulations of detritus and remnants of aquatic plants which served as screens.

Another, later evolutionary branch of aquatic arthropods was associated with the transition of plants to terrestrial existence. This happened as a result of differentiation of the plant life cycle into

sexual (gametophyte) and asexual (sporophyte) generations which was accompanied by the formation of a special reproductive organ "strobilus," which may be regarded as an analogue of modern cones.

Primary-terrestrial plant protocommunities were prostrate creeping plants partly yet connected with water, and served as optimal habitat for Arthropoda ancestors to be temporarily found outside the water. The reproductive organs rose above the water surface. If we take into account the fact that plants in a water environment could have been used as food and shelter by insects, then endophyte mode of life could be optimal. Plant fibers on land contained moisture and oxygen, and perhaps the reproductive structures provided for the best isolation from external hostile conditions. Moreover, they were food substrates rich in nutrients.

Within this hypothesis it is impossible to imagine other more ecologically optimal habitats for the insect's ancestors. Thus we can postulate the existence of two likely "bridges" for the transition onto the land of aquatic ancestors; they moved via the soil and via plant reproductive structures. This by no means excludes other ways and means. We should emphasize that these two bridges established the two further directions of evolution of terrestrial Arthropoda. The soil bridge Arthropoda actually "stopped" their evolution, e.g. the modern Apterygota, Myriapodes, and Arachnoides. Their environments excluded both the possibility and the necessity of complete metamorphosis and flying ability. The second group has undergone substantial evolution and has transformed into the modern Holometabola. We should postulate on the basis of the above that the aquatic ancestors of modern insects have not experienced any metamorphosis; this conclusion is recognized by many authors.

### The Origin of Flight

We can suggest that flight and metamorphosis are inherent features of higher insects and have a common origin. They appeared because the association with plants predisposed their evolution. Peculiar features of plant reproductive organs, as habitats for endophytes, are their ephemeral, patchy existence in comparison with the constant character of the plant proper. They formed on the ends of the branches, being unevenly and irregularly distributed depending on dynamic weather and soil conditions. In other words, the habitats and food resources of this branch of terrestrial insects originally appeared to be discrete in space. Evolution in insects could have proceeded in the following way: a certain group of terrestrial insects under certain favorable conditions could make locally a morphological and physiological "jump" which can be regarded as aeromorphosis.

Living conditions in strobilus (or other reproductive organs) were such that an insect as a rule could not complete its ontogenesis in one strobilus, it had to move to another one situated nearby, on a neighboring branch, or a neighboring plant, the time for migration being extremely limited. Similar migrations were performed by adult insects to lay eggs and to provide the food for its progeny. Crawling would not have been optimal. A jump would be more advantageous, but jumping makes it necessary to overcome gravity and to move large distances. Insects with elongated bodies would be favored. The necessity for organs to appear, which would make the insects able to fly first in a passive mode and then in an active mode, would be accompanied by re-structuring of muscles and formation of a wing.

Let us now examine a hypothetical fate of an insect grown in the primary plant reproductive organ. Its life time was determined by the fulfillment of its own reproduction and was quite short, though this does not mean that the whole period of plant reproduction was so short: strobila (or other organs) could exist in the tree crowns quite long, new strobilae substituting for old ones. Those insects which could deposit their eggs faster had a higher probability to survive and have progeny, laying their eggs in the neighboring reproductive organs or in those which died later. Larvae hatched from these eggs, that is embryonation of post-embryonal development occurred as postulated by Iezhikov-Berleze theory. Under such conditions larvae had to live through unfavorable nutrition and development periods (cooling periods, droughts, absence of food and habitats). The development under these unfavorable conditions became retarded, but it should have been compensated for by faster rates

of physiological metabolism (hystolysis, histogenesis) in the period of transition from a wingless, sexless larva to the winged and sexually mature "imago."

The development within the living plant tissues did not require the development of morphological and physiological adaptation. Exactly the same advantages are available to primary wingless insects which occur (and still occur) in strongly moisturized soil cavities. (See Gilyarov 1970.) However, the temporal discreteness of plant organs and tissues forced the insect to exist outside plants during a certain period of their ontogenesis, which resulted in the forming of new adaptations. The development of an isolated pupa (where these processes take place), not affected by the environment, appeared to be an optimal evolutionary trend. In a number of cases the developed ability of retarding or stopping the development without morphological reconstructions was fixed, i.e. diapause.

On the other hand, those insects who primarily or secondarily were related to non-discrete plant organs (leaves, branches) and have created not only the chewing feeding mode but also a sucking one as well (Orthoptera, Heteroptera, Homoptera) did not develop the pupal stage, they are known as Hemimetabola.

The above presents the main concepts of a theory which is by no means complete. It should be considered as a preliminary assumption for a future hypothesis.