

THE SIGNIFICANCE OF THE GENITALIA TO TAXONOMIC STUDIES OF THE LEPIDOPTERA

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Morphological characters, of which the reproductive organs are but one feature in most organisms, are the basis of any taxonomic system. Early man recognized different kinds of plants and animals by their external appearance. With the development of modern biology through the late 19th century kinds or species were still defined by their gross anatomical features. Relationships were inferred by similarities and relative dissimilarities of appearance. Today, practical taxonomy, and all considerations of phylogeny, still rests on the weighting of morphological characters.

Contemporaneous with the basic work of KARL JORDAN in the development of the *Rassenkreis* principle around the turn on this century, and the beginning of the "species problem", entomologists started seriously using characteristics of the male genitalia to distinguish closely related species. In some groups, such as many Coleoptera, studies could be simply made on pinned specimens. The Lepidoptera proved more difficult, but the problem was by no means insurmountable. Lepidopterists widely accepted this practice to separate species which were complicated by a high degree of geographic variation and overlap. The logic behind the sudden emphasis on this organ was that of the "lock and key" principle, whereby the highly complex male and female genitalia were believed a major barrier to interspecific mating. Direct functional significance was read into these variations, a view which has persisted to some extent to the present time. It was presumed that the structures were so specific that only the same type of male and female parts would fit. In the case of the male valvae this was believed particularly true, since these appear to be structures that clasp the two sexes together during mating; and which also showed the highest correlated variance between well defined species. In the following I will discuss some research on this subject, and summarize the general significance of studies of the genitalia to taxonomic problems of the Lepidoptera.

A classic attempt to evaluate the importance of the insect genitalia as an interspecific reproductive barrier was made by KERKIS (1931) in the hemipteran, *Eurygaster integriceps*. He found that in this species the genitalia were as variable as any other external character. Workers in other groups provided equivocal evidence, although crosses between widely different entities (genera) were sometimes mechanically impossible. We shall presently review a most important paper by LORKOVIC (1953), who investigated the role of the various genitalic structures of some butterflies during copulation. First, however, let us enumerate the major functional components of the genitalia. In the male the 8th and 9th abdominal segments are for the support of the armatures only. The 10th segment is modified into the *uncus*, *subuncus*, and/or *gnathos*. The *valvae* attach to the base of the 9th segment and appear

to be the major clasping organ. The *aedeagus* and its supports are the directors of the actual intromittant organ. In the female, the *ostium bursae* is the major component of its external genitalia, functioning to direct the male intromittant organ properly. The *papillae anales* are concerned strictly with oviposition.

As mentioned above, the *valvae* have long intrigued lepidopterists as they are usually characterized by many spines, bulbs, and hairs, which may be quite specific. LORKOVIC was concerned primarily with these in his work. The technique which he employed was recently discussed by CLARKE and SHEPPARD (1955) in this journal, and reference shows that its advantage lies in the ease of observation of the genital structures during the entire period of copulation. The remarkable conclusions of these observations were that the *valvae* of the species he tested appeared to have a minor importance in either orienting the male to the female or in actually holding the two together. In *Erebia* the *valvae* didn't even touch the female. If this is true in groups beyond the representative sample of LORKOVIC, the role of the *valvae* are negligible indeed.

LORKOVIC found that the *uncus* and *subuncus* are very important functional organs in the forms which possess them. During copulation in such forms the male *uncus* was observed to be reflexed into a pouch above the female ovipore, holding the two closely together. In cases where the *uncus* was artificially removed, the males were unable to closely grasp the females and insemination was usually unsuccessful. He points out, however, that in some genera the *uncus* of large numbers of species remains relatively unmodified while the *valvae* undergo enormous interspecific variation.

The specific role of the *aedeagus* appears minor, since it does not penetrate the female ostium during copulation. By extrapolation this female organ may likewise not be specific in reference to mating barriers.

An interesting hypothesis may be advanced concerning the selective significance of the *valvae*. This was partially suggested by LORKOVIC in his paper, and stems almost entirely from his findings. It appears that since the *valvae* have little functional significance in assuring either the survival of the individual, or its offspring, they are not subject to direct selection. However, they do apparently reflect some adapted quality as the result of pleiotropic gene effects for other characteristics. This would also account for their variation. It may be further argued that their presence, in lieu of direct importance in some forms, is the result of genetic linkage to essential characters, or to their necessity as part of an integrated genic system. The essential components such as the *aedeagus*, 8th, 9th, and 10th segments may display the variance they show for similar reasons, although they are obviously necessary to persistence. Further experimental attacks and observations on this subject would be highly interesting, as is needless to say.

On the basis of these data it seems reasonable to conclude that except for possible specialized cases, or differences of very large magnitude, the highly complex genital apparatus of the Lepidoptera has limited significance as a specific reproductive barrier.

Nonetheless, the basis of taxonomy must rest practically on morphological differences between entities, quite apart from the adaptive qualities they imply. Morphological differentiation unquestionably reflects genetic gaps. Regarded simply in this manner, the study of genitalia is a most important tool for the taxonomist. The ultimate decision of specific gaps should not rest on these parts themselves, however, as we know that they may vary considerably within a species. They should not be assigned higher weight than other characters due to heretofore mystical properties. The complex independent variance of the many male and female genitalic traits may nevertheless be most excellent criteria of phylogenetic relationship, particularly in clarifying cases where mosaics of superficial external variation exists. This is particularly true at the generic level.

Another usefulness of the genitalia is in the perception of cryptic or sibling species. Where sympatric populations of two vaguely different forms are found, consistent genitalic differences may provide the simplest clue to the situation. Thus early in my own work with *Philotes*, I mistook several series as either *P. battoides* or *P. enoptes* being entirely one species or the other by determination of a single male. Later more detailed examination showed that all was not right, and two more or less different types were present in these series. After separating these approximately and running slides on the lot, I found that in fact both species were present together. It is now necessarily routine for me to do this with material from several areas, for when the two species fly together, they cannot be easily told apart superficially. The critical characters in this case are the *valva* of the male, and the *ostium bursae* of the female. Similar instances must be widespread in the Lepidoptera. Suspect cases may be first and most easily tested by genitalic study. I understand there exists a somewhat parallel example between *Mitoura gryneus* and *M. hesseli* (RAWSON and ZIEGLER, 1950).

In concluding, I would like to say that one must be well oriented to the particular group being worked upon finally to evaluate genitalic characters. Small differences in some groups may be relatively more important than large ones in others, and under any circumstances an attempt to study variance should be made, which has been rare to date.

References Cited

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