Some remarks on function as a base for classification and its relationship to form

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(Presented by O. H. Swezey at the meeting of February 2, 1928)*

In the classification of living organisms the primary divisions can be stated in terms of function as well as in terms of form. Plants and animals; vertebrates and invertebrates; cold and warm blooded animals; mammals and non-mammals; fishes and birds; all these can be differentiated in terms of function as well as, or, in some cases, better than, in terms of form or morphology. As we descend to the secondary and lower divisions form becomes apparently of more and function of less account, mostly because of our ignorance.

When we take a group of animals like the insects we find the same conditions. The higher divisions can be stated in terms of function but the lower divisions can not.

In the early days of entomology, when the foundations of our present classification were being laid, systematists were morphologists, or they used what knowledge of morphology was then available, and morphologists studied function as well as form. Thus they noted whether insects could fly or not, whether by one pair or wings or two, whether one pair functioned for some other purpose than flight such as covers or "balancers." The mouthparts were recognized as functioning for gnawing or sucking, and the various ways of sucking were considered. Thus function was just as important as form and the classification thereon erected has proved to be very workable, and, on the whole, quite natural.

With the increased facilities for travel and the increased interest in natural history, systematists were swamped with material. Their task of classifying, naming and describing their collections was enormous and under the pressure they cut down their morphology to the least possible compatible with their object, and they stereotyped their terminology. Morphology, being divorced from systematics, also found itself overloaded with material. Morphologists

* This paper was intended for the meeting of December 1, 1927, but there was a delay in receiving it from Mr. Muir, in England at the time. [EDITOR.]

Proc. Haw. Ent. Soc., VII, No. 1, June, 1928.

forgot function and settled down to compare sclerites through long series. Neither systematists nor morphologists can be blamed, it was the result of circumstances which were impossible or hard to avoid.

While exceptions can be found to the above statements, as they can to most generalizations, yet the above represents the tendency in insect systematics and morphology over a considerable period and the results can be traced in much of our systematic work today.

If we wish to improve our classification, especially the subordinate divisions. I believe that we must broaden the morphology used in systematic work and associate it with function. Towards this end the organs composing the genitalia, especially in the male, will prove to be of much greater value than has been generally recognized. In saying this I do not belittle the good work already done along this line, but I wish to insist that considerably more can be done.

Our knowledge of the morphology of the genitalia of insects is still very slight but our ignorance as to their functions is nearly complete. It is therefore impossible to draw any generalizations on a broad basis. My own knowledge of these matters is chiefly confined to the Coleoptera and the Hemiptera so I must deal chiefly with those orders. Fortunately they represent two types which in many respects offer striking differences in form and function.

In the Hemiptera we have an arrangement of genitalia which we can call "exposed." The tenth and eleventh abdominal segments are small, the ninth (perhaps in conjunction with other units) forms a large ring segment (pygofer). From the membrane between the eighth or ninth segment and the tenth arises a median aedeagus and a pair of genital styles (claspers or parameres). These three organs, while internally arranged for coordinated movement, are never consolidated into a single structure. While the genital styles are often large and cover the opening of the pygofer, and while in some Homoptera structures from the ventral margin of the pygofer (genital plates) more or less cover the genital styles as well as the opening of the pygofer, the genitalia are never withdrawn into an invagination and enclosed therein while at rest. It is unfortunate that some Homopterists have referred to the aedeagus and genital styles as internal because they are covered by the genital plates. This type of genitalia is found in Lepidoptera and Trichoptera, but it is possible that further study of the development will show that the details of the structure are not homologous in all cases.

In the Homoptera the pygofer is fastened to the eighth segment by a very short membrane, and, in some cases, the eighth segment, especially the sternite, is amalgamated with the pygofer, preventing it from twisting. The genital styles, often in conjunction with the anal segments (10 and 11), form clasping organs which prevent the male from twisting round on the aedeagus. In copulation the male rides the female; when the ovipositor is large the base of the oviposter and the gonopore are some distance from the apex of the body and the male has to pass his abdomen down the side of the female (false male vertical pose), but when the ovipostor is short or rudimentary (as in the majority of Fulgoroidea) the abdomen of the male passes over the apex of the abdomen of the female (male vertical pose). Owing to the absence of any provision for a twist the male cannot leave the female and take up an end to end position, but simply remains holding the female with his claspers while his body takes up a position at an angle of between 50 to 150 degrees to the female. The aedeagus in Homoptera is of two types. In one it is tubular, in some cases being divided into a basal and an apical portion; in the other type (certain Fulgoroidea) the basal portion is large and the apical portion is drawn within it. In the tubular type there is generally a modified portion of the ejaculatory duct which can be everted by blood pressure, and forms the chief intromittent organ. If we understood the functioning of these two types, we might be in a better position to explain the causes which led to the modifications. That the tubular type is the more primitive is demonstrated by several lines of evidence. While there is some evidence to indicate that there may be a correlated differnce in the female, our knowledge of the ovipositors is too limited to allow of a generalization.

Turning to the Heteroptera we find the same fundamental type as in the Homoptera, but with certain distinct specialisations. Here we find the pygofer (9th abdominal segment) to be comparatively small, the eighth abdominal segment is also small and attached to the pygofer and to the seventh abdominal segment, by large membranes which allow a twist of the pygofer through 180 degrees. So far as I am aware the Heteroptera always take up a male vertical pose and later the male lets go of the female and takes up an end to end position with an inverted pygofer. While this is common to the vast majority of the Heteroptera there may be exceptions especially among the water bugs, and a study of these may indicate the line of evolution of this specialisation. That the Homopterous form is the more primitive is evident from several lines of evidence. In those cases among the water bugs where the male takes up a position alongside the female it is probable that they both take part in progression, a thing they cannot both do in an end to end position.

In a comparatively few Heteroptera the aedeagus is small and tubular and the internal sac is very little differentiated; in the majority the aedeagus is large, and the internal sac is large and complex, often with a large flagellum. The large, complex internal sac acts as a clasper and where it is found the external clasping appendages are never very large or very complex, and the time occupied in copulation is generally long. Thus in the Heteroptera the genital styles or claspers are never as large as in most Fulgoroidea and the time occupied in copulation is longer. The end to end position with the inverted pygofer may be an adaptation due to the longer period of copulation. This again may be related to a more complete and direct connection between the testes and the spermatheca, and so be a saving of material to the species, and be bound up with the physiology and metabolism of the insect. Another important point is that once copulation has started the insect should be able to fly, hop or crawl away from danger without uncoupling. In the Homoptera the paired couple hop away and alight nearby still attached together; if there was no adequate means of clasping externally as by genital styles and anal segment, then the jerk caused by the sudden springing away would place a severe strain upon the aedeagus. In the Heteroptera the slower movement involved in flight or crawling would not cause such a sudden jerk, but would cause a more continuous strain, and the development of the internal sac, the end to end position, and the twist of the pygofer may be adaptations to meet these conditions.

In Orthoptera where the formation of the individual spermatophore takes some considerable time, the time occupied by copulation is also very lengthy. There is no internal sac and the clasping organs are very poorly developed. Since the spermatophores are formed and passed one by one into the female there is no need for a continuous conduit from testes to spermatheca. Thus it can be said that the actual copulation—the passing of the spermatophore from male to female—is repeated many times and so the pose (usually male vertical or false male vertical) is retained all the time. Under these conditions complex clasping organs are not necessary for should the pairing insects have to move away it is not of great importance if the act of copulation is discontinued for a short time.

It must always be borne in mind that adaptations for "pose" may have no relationship to "position" and when dead insects in copula are studied they are nearly always in "position." When copulation takes but a very short time, as with many Hymenoptera, then there is a pose, generally the male vertical or false male vertical, but no position. Position is an adaptation to a lengthy copulation and the nature of the position is one of convenience, adaptation to habitat, etc.[1]

One is tempted to go into further details, such as the absence of genital styles in all the Cicadidae except one genus, and its probable relationship to function, but until more data are accumulated it is better to refrain.

Turning to the Coleoptera we find a totally different condition, in which the genitalia, when at rest, can be described as "hidden." The apical segments of the abdomen, the eighth or ninth, tenth and eleventh are withdrawn into a cavity, a pseudocloaca, the apex of the abdomen being formed by the meeting together of the hind margins of the eighth or seventh tergites and sternites. The genital styles (lateral lobes, parameres) are dissociated from the abdominal sternite and are in intimate association with the median lobe (penis). In most forms there is a development of a large sclerite (basal plate) to which the lateral lobes are often articulated. The whole makes a very compact aedeagus which is attached to the body wall by a large membrane. The invaginated abdominal segments are greatly reduced and dechitinized. The withdrawal of the male genitalia into a pseudocloaca is also found among the

[1]Many mammals have a male vertical pose and an end to end position.

Orthopteroid forms, and in those forms having reduced ovipositors the females also have a similar arrangement (ie. e. Blattidae).

In the exposed forms mentioned above the well-developed ring-like pygofer, the large genital styles and the genital plates form ample protection to the primary organ of copulation, the aedeagus in the free, exposed lives they lead. It is interesting to note that in the Coccidae where the abdomen is considerably flattened horizontally, the ring-like pygofer has disappeared and the aedeagus is more or less protected by being partly withdrawn into the abdomen. It is possible that hidden genitalia were originally associated with a cryptic habit of the insect, hiding under bark, in dirt, etc., where exposed genitalia would be a disadvantage. It leads to complete protection.

Coleoptera take up the male vertical pose, often followed by the end to end position, with a twist of 180 degrees at the base of the aedeagus, which is made possible by the large membranous connection between the aedeagus and the body wall. When the aedeagus is curved, either dorsally or ventrally, it must lie on its side when at rest. In some cases (i. e. Dytiscidae, Scarabaeidae) while it lies on its side during repose it does not return to the normal position during use, but continues the twist through 180 degrees.

So far as we know at present the three families, Dytiscidae, Haliplidae and Pelobiidae, differ from all other Coleoptera in the form of the median lobe which is funnel shape. It was suggested that they must function differently to others, and it has been shown that this is so in Dytiscidae. In this family the funnel shape lobe serves to hold the large spermatophore while the sperm is transferred to the female through a hole in the spermatophore. As the structure of the median lobe is the same in the three families it is highly probable that they all function in a similar manner. In the vast majority of Coleoptera the median lobe is tubular or a development from the tubular, and there is an internal sac which is evaginated during copulation. In the majority this sac is large and complex, and the lateral lobes seldom, if ever, serve as claspers but only as guides or organs of touch.

In the Carabidae we find the basal piece absent; in the Cicindelidae it is represented by a small sclerite. It appears probable that the former is the more primitive condition. In the Scarabaeidae we can follow the reduction of the median lobe to a mere membrane and the development of an enormous and complex internal sac, along with a reduction of the lateral lobes and a great development of the basal plate. This latter serves as a protection to, and a foundation for, an elaborate muscular bulb for the evagination of the internal sac. In the Staphylinidae we can follow the tubular median lobe with fairly well developed lateral lobes and small internal sac, through gradate series to a wonderfully constructed bulb for the evagination of a complex sac, and the reduction of the lateral lobes. In the Phytophaga and Rhynchophora we have a ring shape tegmen with lateral lobes attached to it; the median lobe is tubular, long, attached to the ring shape tegmen by a long membrane which allows considerable movement of the median lobe through the ring tegmen. In these groups we find gradate series showing the loss of the lateral lobes and the reduction of the ring to a Y shaped piece and even to a mere rod. The internal sac is well-developed. These gradate series give joy to the evolutionist as much as they give sorrow to the systematist.

The Odonata form one of the most isolated orders among insects. They can be recognized by almost any part of their structure, not only in the adult but also in the young. In nothing do they differ more from other insects than in the form of the male genitalia and their method of copulating. The normal male genitalia are reduced to mere rudiments or are even absent and an intromittent organ, unique among insects, has arisen upon the ventral surface of the second abdominal segment. As the male gonopore is situated in the normal position at the end of the abdomen it is necessary for the insect to curve its abdomen under and charge this intromittent organ with sperm. The male then seizes the female by the back of the head or by the pronotum by means of claspers at the apex of his abdomen and carries her about in "tandem." This position allows both individuals the full use of their wings and offers less resistance. It is then necessary for the male and female to curve their abdomens ventrally so as to bring the end of the female abdomen in contact with the male intromittent organ, making a complete circle. In cases which I have watched where this is done while the male rests upon a suitable surface, the pendent female is swung backward and forward till she curves up her abdomen in the desired method. If a slight wind is blowing it is often impossible for copulation to take place as the long thin female hanging from the long thin male gets carried slightly sideways and she misses the mark each attempt.

How such a unique structure arose or how such a strange departure of function took place we can only guess, as we have no data upon which we can build a probable theory.

These insects are true children of the air and no other insects have such a complete command of flight, or turn and twist on the wing so quickly. They are the swallows of the insect world. This is necessary for the capture of their prey. Their whole structure is to this end—the large wings supported by numerous veins, the large thorax and battery of muscles, the large eyes and jaws, the long slender abdomen. If they assumed the male vertical pose they would have to do so while at rest, and even then it would most likely be necessary to assume the false male vertical pose, as with such a long slender abdomen it would be difficult for the male to curve it over the tip of the female's. But this would necessitate rest, which, to such children of the air, is not congenial. Any of the usual poses and positions would have hampered their flight. They have solved their problem along a unique path, but from the point of view of evolution we are totally in the dark as to the stages by which they attained their end. It is possible that at first a spermatophore was deposited in a groove on the second abdominal segment, such as is found in some ant lions, but the stages along which the unique intromittent organ developed are unknown. So far neither comparative morphology nor development has thrown light on this subject.

In the Diptera we have some very interesting conditions which have been described by several workers. Unfortunately we do not know as much about the comparative morphology and mechanics of the male genitalia of Diptera as we do about those of Coleoptera and Hemiptera. Among them we find a number of cases in which the genital segments, and often some of the others, take up a twist of 180 or 360 degrees as soon as they leave the pupa, thus we have a prearranged condition connected with the act of copulation. Interesting as are these cases of a pre-copular twist they are not more so than any other structure for certain end. The modification of the eighth abdominal segment in Heteroptera and its attachment to the preceding and succeeding segments is equally a pre-copular arrangement for similar ends. The genitalia are all developed before they are used, like all other organs.[1]

The false male vertical pose seems to be common among these flies and the inverse and circumverse genital segments may be an an adaptation for that pose, and the whole may be bound up with the length and slenderness of the abdomen. In insects with a wide, flat abdomen, such as in most beetles and in the Blattidae, the pose is the male vertical, whereas in many cases where the abdomen is long and comparatively slender, as in many Acridiidae, etc., it is the false male vertical.

In the wingless Diptera (i. e., Nycteribiidae) and in some Diptera which pair while at rest, the clasping organs are small or absent, whereas those with active flight which pair on the wing the claspers are generally large and complex. So far no case of a complex, large internal sac has been reported in Diptera and copulation generally takes but a comparatively short time.

A review of all the orders of insects, even in the above cursory manner, would be a large task, even with our present limited knowledge. The above I hope will be enough for the thesis in view, viz., that a better knowledge of the form and function of the genitalia of insects will enable us to understand much better their evolution, relationship to one another, and therefore enable us to rest their classification upon a more scientific basis than at present is possible in many groups.

It is impossible to leave the subject without touching upon certain speculations. Is the great diversity found in the genitalia among many allied species "many keys to open a single lock" or is there always some correlated female difference? This requires much more evidence than we possess at present before it can be answered with any certainty, but in cases studied by myself there are such correlated differences. The genitalia are as important for the race as the mouth parts are for the individual; whatever changes have taken place all down the ages in their form we can be sure no break has ever occurred in their function. Large mutations are therefore unlikely to have been preserved in one sex without co-ordinate mutations in the other. Wherever we find several distinct types in an order, functioning along distinct me-

[1] This phenomenon is bound up with the Biogenetic law where characters are pushed back to earlier stages.

chanical principles, we can be sure that they arose, and were developed to perfection, in response to urgent mechanical necessities. They were not sudden, large morphological mutations which the organism had to make the best use of that it could. Equally improbable does it appear to me that a long series of small mutations, every one of which must be co-ordinated to the others, arose through the shuffling of the genes, quite irrespective of the biology of the insect or of its necessities. This leads to the question as to which came first, function or form, a question which we can debate about it and about, and come out at the same door as we went in.

Environment, in its widest sense, is the great potter's thumb which has shaped the organism; function or the urge to function, is the motive power that drives the wheel. The forest-loving, slow moving five-toed animal evolved into the prairie-loving, quick-moving one-toed animal parallel with geological changes from forest to open country. If the original five-toed animal had not been forced by its environment to move quickly over hard ground, or to feed on grass instead of on leaves, would its form have been modified? The same can be asked of the different animals, unrelated to one another, that have taken to desert life and assumed similar form. The camel's foot could never have arisen if its ancestor had lived on wet, hard land; it had to take to the sandy lands before the foot could be adapted to it. In all these cases the animal had to begin to function before the change of morphology could take place. This is quite irrespective of whatever views we hold as to the causes of the morphological changes.

In discussing insects on small islands it has been put forward that an increase of the size of the wings would be of advantage and therefore any small increase would be conserved by natural selection. Such an increase would be of little use unless it was accompanied by an increase of muscular power to work the wings; this would require a larger thorax and apodemes, a different proportion in the size of the thoracic sclerites, and an alteration of the nerves working these muscles. If this process was carried far it would necessitate an alteration of the position of the coxae, and, if carried still further, might involve an alteration of the shape of the abdomen on account of weight. It is difficult to say how many factors would have to be altered in the shuffling of the genes to bring all this about, or what are the odds that such changes would all appear in due sequence and co-ordinated. In the case of the reduction of the size of the wings a parallel set of changes in the reverse direction would be necessary, and here again co-ordinated changes in right sequence would be just as necessary. More complex cases can easily be conceived. To me some co-ordinated mechanism of growth is necessary, which must have some relation to use and disuse; no blind shuffling of the genes at maturation and fertilization, quite irresponsive of the activities of the animal, can satisfy the needs of the situation.

The factors causing and guiding changes in organisms are numerous, and those responsible for the main lines of evolution, for the co-ordination of the various parts, and for the wonderful adaptations of the organism to its environment, are not likely to be the same as those causing most of the speciation. Personally, I have often thought that had Darwin called his great work "Evolution by natural selection," and not placed stress upon speciation by natural selection, it would have presented a better balanced picture.

While some of the minor differences found in the genitalia of closely allied species may be merely speciations, the more fundamental differences, often based upon different mechanical principles, appear to me to be adaptations in response to functions due to differences in habits, form, environment and, in some cases even to psychology.