

SEXUAL DIMORPHISM IN THE ACANTHO-
CEPHALA¹

H. J. VAN CLEAVE, UNIVERSITY OF ILLINOIS

Frequently, animals differing widely in appearance belong to the same species. Polymorphism, as this condition is called, occurs in various groups throughout the animal kingdom and is especially prominent in insect states and in the colonies of some of the coelenterates, especially among the Siphonophora. Under these conditions individuals representing each of the different forms carry on restricted, specialized functions for the colony or state. The causes of such diversity of form within the members of the same species are not understood thoroughly. There are those who contend that polymorphism has arisen as a result of a division of labor among the individuals while others adhere just as strongly to the view that because the individuals are different they are thereby fitted for only one kind of special work and consequently each does the work for which bodily structure fits it. The type of bodily difference accompanying restricted function most frequently encountered in the animal kingdom is that associated with the differentiation of the sexes.

Sexual dimorphism, as somatic differences between males and females is termed, is of frequent occurrence throughout the animal series. However, most of the published accounts dealing with this phenomenon have been concerned with the most conspicuous instances such as those in which male and female differ so profoundly in superficial characters that they might well be taken as representatives of entirely distinct species. Technically, any somatic difference, however slight, which enables one to differentiate males from females without an examination of the gonads, may be considered as sexual dimorphism. In many species certain restricted organs or parts of the body, not directly associated with the reproductive process, display distinctive differences in the two

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sexes. Such characters are termed secondary sexual characters.

Much of the literature concerned with the explanations of dimorphism has placed strong emphasis upon the role of sexual selection as the factor which has originated and emphasized the secondary sexual characters. Most of the popularly cited instances offer no fundamental difficulty for such a possible origin. The development of horns or other organs of offense or defense in the males of mammals would seem to give such individuals greater chance of perpetuating their kind than possessed by other individuals not having such special organs. Similarly, there does not seem to be any fundamental objection to the possibility that females among the birds might show preference for the more highly colored and ornamented males as mates though many authorities question any such show of preference on the part of the female. In all of the most readily available accounts sexual selection and natural selection have been almost exclusively advanced as basis for the explanation of dimorphism. In fact, P. C. Mitchell in the *Encyclopaedia Britannica* (Eleventh Edition, Vol. 24:748) definitely contends in his discussion of Sexual Dimorphism that Darwin's theory of sexual selection is the only comprehensive suggestion capable of explaining why some males and females differ and others resemble each other.

In species having no direct copulation and in all those having no mating of the sexes, obviously sexual selection cannot operate in the development of secondary sexual differences. Frequently ardent advocates of a theory have been so blinded by the implicit belief in the all potent powers of some particular explanation of given phenomena that they have been unable to conceive of the possibility that various factors may act simultaneously to attain the same or similar end results. This seems to have been the attitude of recent writers who have tried to explain all secondary sexual characters on the basis of natural and sexual selection. Charles Darwin, the founder of the theory of sexual selection, has well pointed out that his theory could not be the sole

explanation for the development of dimorphism among the lower sexual animals. In the *Descent of Man* (Chapter 9) he states that among the lower organisms "it is almost certain that these animals have too imperfect senses and much too low mental powers to appreciate each other's beauty or their attractions, or to feel rivalry." It becomes a matter of considerable interest, then, to examine some of the lower bisexual organisms in which mating does occur in order to see if it is possible to offer any explanation of the factors causing dimorphism under such conditions.

In the course of work upon the Acanthocephala, I have come across a number of instances of sexual dimorphism which, because of the conditions under which they occur, seem to offer some interesting obstacles to the operation of sexual selection or of natural selection in their development. Before discussing the specific instances, a few facts regarding these organisms should be enumerated. The Acanthocephala are worms of uncertain phylogenetic relationships which, through complete adaption to the parasitic habit, have arrived at a state where they no longer possess a free living stage at any point in their life cycle. In the reduction of organs characteristic of free life the Acanthocephala represent the extreme condition of complete absence of any structures for locomotion in any stage of their development, and total elimination of all special organs dealing with the processes of metabolism. Similarly there has been an entire loss of all organs of special sense. The whole central nervous system consists of a small mass of ganglion cells from which a few fibers are distributed to the body wall and to the muscles which control the operations of the proboscis and of the anterior region of the body. In spite of the fact that these organisms are reduced to essentially little more than a sac for containing the developing reproductive elements and a special organ, the proboscis, for attachment to the host, yet they display rather marked differences between the sexes in many species. Many of these differences are apparently of no advantage to the individuals possessing them and

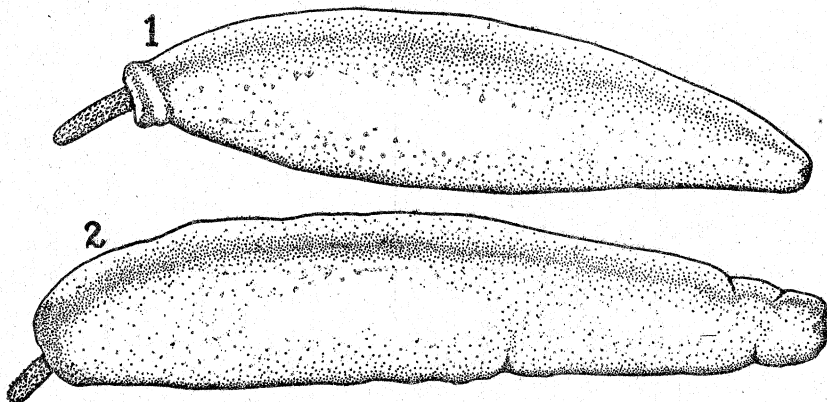
in some instances appear after the single necessary copulation so they can have no very essential relation to the perpetuation of the species. All evidence seems to point to the fact that the Acanthocephala are, as a group, too far removed from any free living ancestors to make it possible that dimorphism could have been carried over as an inheritance from free living ancestral forms. It then becomes a matter of some interest to examine these instances of sexual dimorphism in the hopes of finding some of the factors responsible for their development.

The somatic differences between the sexes encountered in these parasites constitute two fairly natural classes (a) differences in form and size, and (b) presence in one sex of structures entirely wanting in the other. Under the first of these are included all the differences in body form, in body size, and in proportions of the body or of any of its individual structures while the second, of much rarer occurrence, is possibly based upon incomplete and faulty observations. Frequently structures such as body spines, apparently wanting in one sex, have, upon closer examination, been found greatly reduced in size or obscured by other structures.

Almost invariably the mature female acanthocephalan is larger than the male of the same species. In some instances, however, the difference is so slight that among fully mature specimens some males are as large as the smaller females and in a few instances there is practically no external means of differentiating the sexes. This last mentioned condition is best exemplified in *Plagiorhynchus formosus* VanC. as shown in figures 1 and 2.

Extreme differences in size are to be noted in *Gigantorhynchus hirudinaceus* (Pall.) from the hog. The female of this species may reach a length of 65 cm. while the male rarely attains a length of more than 10 cm. In average, mature, individuals the male is about 4 mm. in diameter while the female measures about 6 mm. Thus in this species the difference in length is much more conspicuous than the difference in diameter. Simple sexual difference in length appears rather late in the development of the individuals of most species that have been

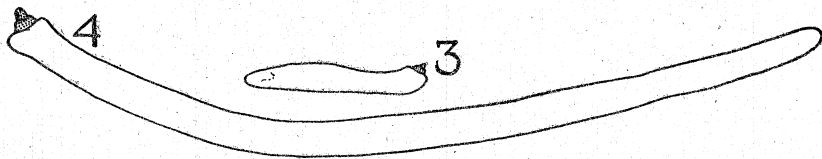
observed. In immature specimens it is impossible to distinguish the sexes without observation of the essential organs of reproduction.



Plagiorhynchus formosus VanC.

Fig. 1. Male. Fig. 2. Female. Both figures drawn to same scale.

Another extreme example of difference in length is found in *Heteroplus grandis* (VanC.), the female of which is approximately five times as long as the male (see figures 3 and 4) but only about one-third greater in diameter of the body.



Heteroplus grandis (VanC.)

Fig. 3. Male. Fig. 4. Female. Both figures drawn to same scale.

No one has ever demonstrated the presence of cell division in other than germ cells in the body of an acanthocephalan after it has entered its definitive host. In addition to this the writer has shown that in members of the family Neoechinorhynchidae the number of cellular elements is fixed and in structures common to both sexes is

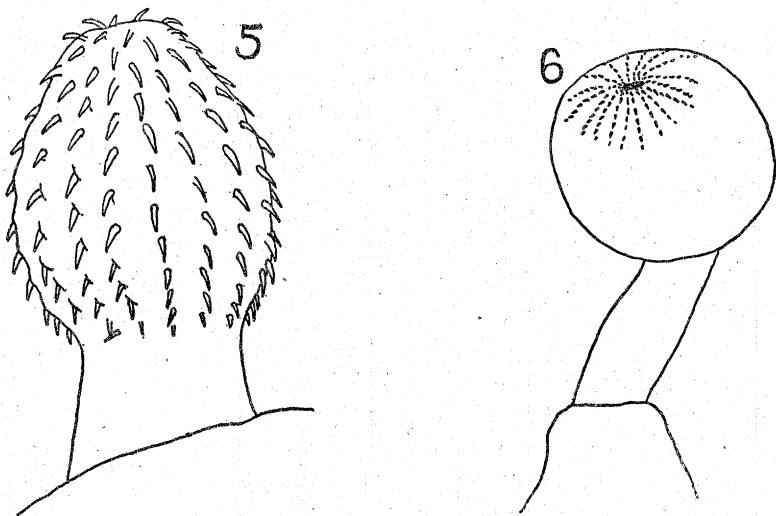
constant in all individuals. Consequently any difference in body size, in members of this family at least, could result only from differences in physiological processes which would permit simple increase in bulk without any corresponding increase in number of cells. Since the start of this differentiation in bulk of the members of the opposite sexes occurs at about the same time that the germ cells start to form it seems possible that simple difference in size of the two sexes may be directly correlated with differences in physiological conditions accompanying the development of the sex cells.

General body form frequently shows marked contrast in the two sexes other than the relative size discussed above. In *Arhythmorhynchus pumilirostris* Van C. the writer has shown that the male has the posterior region of the body distinctly attenuated while the gravid female displays no distinctive difference in diameter of anterior and posterior regions of the body. In this species the musculature of the body wall is also apparently more highly developed in female than in male. In preserved specimens the females present a distinctly wrinkled appearance due to the contraction of the muscles in the body wall, while the males present a perfectly smooth surface on the exterior of the body.

Frequently a portion of the body of a gravid female becomes distorted from the form characteristic of the young female and of the male. Localized distended areas have frequently been attributed to the mechanical effect of the myriads of developing embryos which fill the entire body cavity of the gravid female. Thus in *Neoechinorhynchus cylindratus* (VanC.) and in *N. agilis* (Rud.) the middle third of the body of the female usually shows a distinct enlargement. In some instances the entire body becomes greatly distended, forming a capacious sac for the retention of the embryos as the writer has described in the females of *Filicollis botulus* VanC.

Difference in size and form are not restricted to the body proper. A radical difference in form of the proboscis has been described for the female of *Filicollis*

anatis (Schr.). In this species the proboscis of the male and of very young females is of an ordinary type with rows of hooks extending from the extremity to near the base (fig. 5). In contrast with this the proboscis of the female is an inflated spherical organ which bears a star-like crown of hooks (fig. 6), limited in distribution to the anterior face of the structure.



Filicollis anatis (Schrank)

Fig. 5. Proboscis of male magnified about 120 diameters. From Lühe 1911, fig. 44.

Fig. 6. Proboscis of female magnified about 30 diameters. Modified from Lühe 1911, fig. 39.

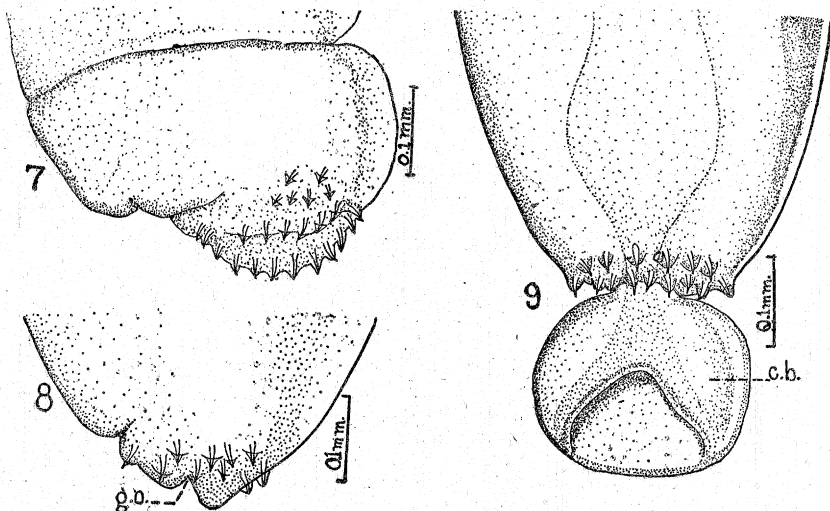
Cuticular spines appear on the body proper of species belonging to certain genera of Acanthocephala. These spines display dimorphism in some instances through dissimilarity in size and in others through difference in distribution. In one species of *Rhadinorhynchus* the body spines of the female range from 60 to 70 μ in length while those from the same region of the male are only about 28 μ long. In this instance the female shows greater size of spines in just the same manner as greater body size is associated with the females in the Acanthocephala. On the other hand the writer has described two

North American species belonging to the genus *Filicollis* in which the males bear conspicuous body spines while those of the females are very inconspicuous.

In the genus *Corynosoma* the cuticular spines cover the anterior region of the body in both sexes. According to Lühe (1911:37) the males of *C. strumosum* (Rud.) and of *C. semerme* (Fors.) possess numerous strong cuticular spines surrounding the genital orifice at the posterior extremity in addition to these on the anterior extremity of the body, but the genital spines are entirely wanting in the females of the same species. This stands as the only instance in literature of the presence of structures in the body of one sex among acanthocephalans entirely absent in the other sex. But since in *C. semerme* the spines around the genital opening of the male are directly continuous with those distributed on the remainder of the body even this instance become an example of relative distribution of body spines rather than separation of genital spines and body spines. In the original description of *Corynosoma constrictum* VanC., the writer failed to discover any cuticular spines around the genital orifice of the females. An abundance of specimens belonging to this species, recently received from Mr. L. B. Dickey, has made it possible to re-examine this question and has thrown considerable light upon the nature of the dimorphic condition of the spines in at least the North American species, *C. constrictum*.

In the new collection mentioned above, I have discovered that young females (Fig. 10) possess genital spines closely resembling those of the male, (Figs. 7 to 9) except slightly smaller in size. In later development, and especially after copulation has taken place these spines become less conspicuous in the female. In some instances I have been able to observe that spines have been apparently forcibly removed from the body as evidenced by the frayed nature of the cuticula in the region of the genital aperture. In this species, as in many other acanthocephalans, a cap-like structure (Fig. 11) covers the posterior extremity of the female following the act of copulation. This structure, for which I propose the name

copulatory cap, is formed by the hardened secretions of the cement gland of the male during the act of copulation. Not all fertilized females carry this copulatory cap for after a time it is apparently rather readily discarded. It seems evident that the spines surrounding the genital orifice of the female aid in holding this copulatory cap in position since they become embedded in the substance



Corynosoma constrictum VanC.

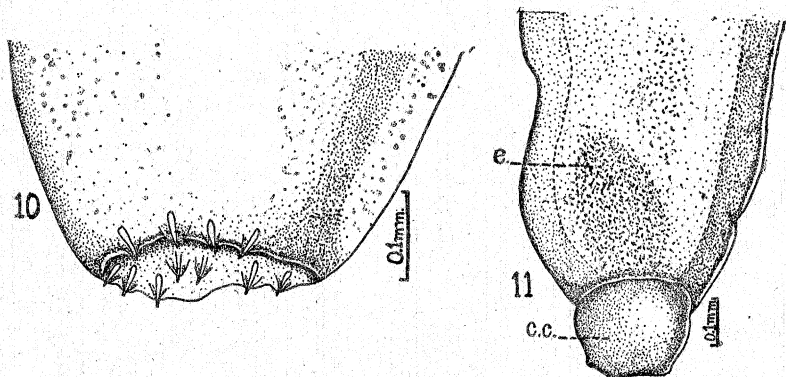
Fig. 7. Posterior region of male with copulatory apparatus fully retracted within body.

Fig. 8. Posterior region of male showing position of genital spines when posterior extremity is slightly protruded.

Fig. 9. Posterior region of male with copulatory bursa fully extruded.

of the cap. With the final loss of the cap, probably due to the movements of the parasite, it is readily believable that the spines might adhere more firmly to the cap in which they are embedded than to the cuticula where they had their origin and thereby become lost. If copulation occurs more than a single time each successive deposition and removal of a copulatory cap would reduce the number of genital spines until in the older females no spines would remain. In such an instance sexual dimorphism would result from mutilation of the body of one sex to render it unlike that of the other sex.

There has been a general acceptance of the view that the spines surrounding the orifice of the male function during copulation, probably as a means of attaching the male to the female. Advocates of this view have failed to recall the fact that the copulatory apparatus of the



Corynosoma constrictum VanC.

Fig. 10. Young female showing spines around genital orifice.

Fig. 11. Gravid female showing copulatory cap which is attached at time of copulation.

male acanthocephalan must be everted from a position far within the body before it can be brought into position for use. When the copulatory bursa containing the cirrus is extruded during copulation the genital spines could not serve for attachment to the female (Fig. 9) because they lie behind the bursa and are completely covered by it.

CONCLUSIONS

Many theories have been advanced to explain the origin and development of sexual dimorphism. Of these natural selection and sexual selection have probably been most prominently advocated. J. T. Cunningham (1900) has advanced a modified form of inheritance of acquired characteristics as explanation. According to his view organs or structures used directly or indirectly in the reproductive process become modified through function. Thus a tendency toward modification in such structures is passed from generation to gener-

ation. As with most hypotheses regarding secondary sexual characters his evidence is taken largely from higher animals.

Numerous investigations have shown that the development of secondary sexual characters is directly associated with the development of the gonads. In many instances males deprived of the testes have failed to develop characters peculiar to the male sex. Similarly, it has been shown that old individuals after the close of reproductive activity tend to acquire characters intermediate between those characteristic of the two sexes. Unfortunately, because of their endoparasitic habit, the *Acanthocephala* do not lend themselves to experimental investigations such as those of castration mentioned above. However, in as much as all of the instances of dimorphism cited among the *Acanthocephala* are restricted to differences in development or relative size of similar structures in the opposite sexes, it seems probable that the physiological conditions accompanying the development of the gonads are directly correlated with the differences in general metabolic processes which control general body growth.

Child (1915:350) has shown that fully formed eggs have a relatively low rate of metabolism. Among the *Acanthocephala* egg production is not a continuous process. In the individual female the period of development of the eggs is restricted to a single cycle for the gonad becomes entirely used up in the production of the eggs. Consequently the mature female grows considerably in size after the period of egg formation has ceased. This is probably due to the fact that food material during the period of egg formation is largely utilized in that process and at the close of that cycle becomes more generally available for body growth.

In contrast with this the male *acanthocephalan* continues to produce spermatozoa through an indefinite period of functional activity of the persistent gonads. It seems probable that the continued development of gametes utilizes available elaborated food at the expense of the farther growth of the body. Upon this

basis may be explained why the females continue to increase in size long after maturity is attained while fully mature males of any given species differ but little in size.

While the foregoing attempts to explain the physiological basis for differences in relative development of the body or of restricted regions of the body in the two sexes, no hypothesis can be advanced to explain why the modification of physiological processes regulating growth becomes expressed in such widely varying manners. It is not clear why stimulation to farther growth should in one instance involve the entire body uniformly, in another be confined chiefly to length, and at still other times cause excessive enlargement of restricted areas or of individual structures.

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