Hormones in Arthropods

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The endocrines of vertebrates have been extensively investigated but those of invertebrates have been relatively neglected. In the last few years several books and articles dealing with invertebrate hormones have appeared (a few are: Scharrer (1941), Koller, "Hormone Bei Wirbellosen Tieren", and Hanström, "Hormones in Invertebrates"), but a perusal of these works impresses one with the sketchiness of our knowledge. Most of the hormonal research on invertebrates have used the higher forms, namely the arthropods, as the experimental animals. Not all of the arthropod groups but principally members of the classes Xiphisura, Crustacea, and Insecta have been used. Following this order, let us first consider the investigations dealing with the horseshoe crab, *Limulus*, of the class Xiphisura.

No long search through the literature is necessary, since to the best of my knowledge, the only two papers offering positive evidence of hormones in *Limulus* appeared in the Biological Bulletin issued in August of this year. One of these was by Dr. Scharrer describing some secretory cells that occur in the central nervous system, to the greatest number in the posterior portion of the nerve ring. These cells are also found in the ganglia of the nerve cord. There is considerable variation in the number of cells in different animals. By counting the cells in serial sections, a not infallible method since the same cell may be counted in more than one section, but of sufficient accuracy to give a quantitative approximation, she found that some individuals had only one or two cells in the entire central nervous system while others had up to 2494. There seems to be a direct correlation between the number of cells and the size of the animal. Small animals of 5.8 cm. carapace width had none, but adult animals always had them. Larger adults had more than smaller adults. Only one type of cell was found and it had the following characteristics. Each cell was enclosed in a capsule and the interior of the cell was filled with a mass of colloid-like material resembling the colloid of thyroid cells. The second paper dealing with *Limulus*, by F. A. Brown and Cunningham, gives excellent physiological support to the histological work of Scharrer. They made extracts of sections of the central nervous system at different levels and tested their chromatophorotropic action. It was found that there was a principle in the extracts that caused the concentration of the black chromatophores of *Uca*, the fiddler crab, and the white chromatophores of *Cambarus*. The region from which the most potent extract was obtained was the posterior third of the nerve ring. This extract was active at a dilution of 1 to 5000. However, *Limulus* has no chromatophore system and therefore the significance of the secretion to *Limulus* has not been discovered.

Most of the work on the class Crustacea has dealt with hormonal effects on chromatophores. The color bearing units of Crustacea may be monochromatic or polychromatic and may be unicellular or syncytial. Their color may be red, yellow, blue, white, or black. By the degree of expansion or contraction of these units the animal is capable of making color adaptations to its environment. In 1928 Perkins and Koller independently showed that a substance was present in the eyestalks of crustacea that could bring about changes in the dispersion of chromatophores. The extracts they used were made from the whole eyestalk since the gland involved was unknown. Hanström (1935), a Swedish scientist and outstanding worker on crustacean nervous systems, indicated that a blood or sinus gland probably was the organ involved. Subsequent work by Brown (1940) and others have shown this contention to be correct. The sinus gland is generally small, tear-drop shaped, and bluish-white in color. The action of an extract of this gland on the black chromatophores of *Uca* is very similar to the action of intermedin on the melanophores of lower vertebrates, i.e., both cause expansion. The eye stimulated by light seems to act as a check on the release of both of these secretions and, apparently, it is the lower half of the retina or the lower half of the compound eye that has this function. Thus if the eye is covered the animal will darken because the check on the release of the secretion is no longer operative. Abramowitz (1938) has used intermedin injections into eyestalkless crustacea and eyestalk extract injections into hypophysectomized lower vertebrates with, in general, normal expansion of the melanophores in both. The work of Brown and Scudamore (1940) indicates that more than one hormone may be secreted by the sinus gland. They obtained an alcoholic extract of the eyestalks of several crustacea that effected primarily the red chromatophores and a non-alcoholic extract that primarily effected the black chromatophores. Brown and Ederstrom (1940) showed that some chromatophores were under dual control. In *Crago,* a marine shrimp, the telson and uropods contain many melanophores that are contracted by sinus gland extract and expanded by an extract of the circum-esophageal commissures.

In addition to the effect of eyestalk extracts on chromatophores several other functions have been demonstrated. Kleinholtz (1934, 1936) found that an eyestalk extract, particularly from light adapted animals, injected into dark adapted *Palaemonetes,* another shrimp, caused the eye pigments to migrate to the light adapted position. Koller (1930) stated that the normal deposition of calcium did not take place in the skeletons of animals without eyestalks. Abramowitz and Abramowitz (1939), Brown and Cunningham (1939), and Smith (1940) have shown that eyestalkless animals molt more rapidly than normal individuals. The more rapid molting is apparently the result of shortening the intermolt period. Brown (1938) and Abramowitz and Abramowitz (1939) have shown that animals without their eyestalks do not live as long as the normal controls.

There is some indication in crustacea that secondary sex characters and certain reproductive phenomena are under the control of gonadial hormones. Yonge (1938) has shown that the oviduct epithelium of *Homarus* and other decapods exhibits rhythmical changes associated with ovarian activity. The effect of parasitic castration in modifying secondary sex characters, particularly in the male toward the female type, has been noted by many authors since the original work by Girard in 1887. Callan (1940) used X-rays to destroy the gonads of prawns with the result that breeding characters did not develop.

Now let us consider the insecta. Kopec (1922) was the first to indicate that there was something present in the heads of certain lepidoptera *(Lymantria)* that was necessary for the inception of pupation. By tying off the posterior from the anterior body region he was able to show that only the part of the body anterior to the constriction would pupate. Fraenkel (1935) repeated and substantiated Kopec's work using the blowfly, *Calliphora erythrocephala.* Closely associated with the brains of insects are two glands called the corpus cardiacum and the corpus allatum that might be involved. The corpus cardiacum is generally on or around the wall of the anterior end of the aorta. The corpus allatum is generally located in close proximity to the dorsal side of the esophagus in the hind part of the head but it may be located in the neck or anterior part of the thorax. This gland may appear singly as in the hemipteran, *Rhodnius*, or doubly as in the cockroach, *Periplaneta americana.* In certain dipterous larvae it seems that both of these glands may be combined into a circular structure surrounding the aorta. Weismann (1864) first described this so-called ring gland although he thought that it acted as a support for the dorsal blood vessel. Hadorn (1937) and Scharrer and Hadorn (1938) described large and small cells making up the ring gland of *Drosophila* larvae. The larger cells form the outer part of the ring and apparently are homologous to the corpus allatum of other insects while the smaller cells directly around the dorsal blood vessel may be homologous to the corpus cardiacum. Working with the Drosophila mutation, "lethal giant", in which pupation is greatly retarded from the normal or does not occur at all, Scharrer and Hadorn (1938) found that the ring gland was not as well developed as in normal larvae and that the implanting of ring glands from normal larvae would induce and accelerate pupation. Acceleration of pupation was brought about also in normal larvae following the implantation of ring glands. Wigglesworth (1940) using *Rhodnius prolixus* indicated that two hormones are involved in moulting and pupation. One of these has been called an "inhibiting" hormone because it prevents the appearance of adult or imaginal characteristics. It is present in the first four nymphal stages but decreases in amount from the first to the fourth nymphal stage. It is secreted by the corpus allatum. Wigglesworth suggests that possibly "nymphal" or "juvenile" would be better names than inhibiting since it does not oppose the action of the moulting hormone but tends to keep the insect in the nymphal condition. The moulting hormone, which as its name implies induces moulting, seems to be secreted by large cells in the dorsal region of the protocerebrum that stain deeply with acid fuchsin.

The work of Wigglesworth (1936, 1940) on *Rhodnius* indicates that the secretion of the corpus allatum is necessary for egg production in females and for the secretion of the accessory glands in the male. If the corpus allatum is removed from the female, egg production stops and the eggs already produced disintegrate. Supplying corpus allatum secretion from either sex brings about normal egg production. Also, the secretion from females will bring about the normal secretion of the accessory glands in the male. Thus it appears that the hormone is the same in both sexes. The work of Weed (1936) showed that in the grasshopper, corpora allata were necessary for the normal development of eggs and the normal secretion by glandular portions of the oviduct. Iwanoff and Mestscherskaja (1935) studied the permiability of the oocytes in the immature and mature ovaries of insects and concluded that the essential change at maturity is an increased permeability. They believe that this change in permeability is normally brought about by a hormone from the fat body and that the reverse change, the arrest of egg growth due to diminished permeability is brought about by a secretion from the so-called "corpus luteum" present as a yellow lipoid in old follicles.

The corpus cardiacum has been relatively neglected perhaps because it did not exhibit the rhythmical changes that are shown by the corpus allatum. However, Brown and Meglitsch (1940) have shown that an extract of the corpus cardiacum of *Periplaneta americana* could concentrate the red chromatophores of the crayfish, *Cambarus immunis,* and in fact had six times the potency of the sinus gland per unit volume. Although some insects are capable of making adaptive color changes, the control of this action is unknown. The effect of corpus cardiacum extract on the crayfish erythrophores may indicate the gland involved in color change in insects.

The central nervous system is another region of secretion in insects. Scharrer (1941) found secretory cells in the suboesophageal ganglion and in the pars intercerebralis of the protocerebrum of three different genera of cockroaches. The suboesophageal ganglion seemed to be the primary secretory region. The function of this secretion is unknown.

In conclusion, it can be said that the field of invertebrate hormones is in its infancy and consequently offers great possibilities for research. Much of the work already done should be verified and many inviting problems remain unexplored.

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