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George Howard Parker
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Chapter I

INTRODUCTION

A. Preliminary Survey of Animal Colour Changes

ALTHOUGH colour changes in animals were known to classical antiquity and received attention from such an authority as Aristotle, they did not claim the serious consideration of naturalists till a little over a century ago. They were then taken up in such work as that of Cuvier (1817) on the cephalopods and of Stark (1830) on fishes, but it was the monographic treatment of the colour changes in the African chameleon by Brücke (1852) that put the subject on a thoroughgoing scientific basis. Brücke raised and discussed some of the most important questions in the physiology of animal chromatic responses and laid the foundations for much of the work that has been carried out in this field during the last three-quarters of a century.

The results of the work on animal colour changes have been ably summarized in two extended reviews: one by the European physiologist, van Rynberk (1906), and the other by the zoologist, Fuchs (1914). In these surveys, the contributions to this subject from ancient times to the dates of publication of the two compilations have been brought together. The present account covers in the main papers that have been published between 1910 and 1943. The initial date, 1910, overlaps the time of appearance of Fuchs' compilation by some four years. Hence the review of the subject herein contained continues without serious break the accounts given by van Rynberk and by Fuchs. The recent growth of the subject has been very considerable and may be inferred from the fact that in the bibliographical lists included in Fuchs' monograph, which are remarkably full and complete, there are in all some five hundred items. In the present survey, covering as it does only the period from 1910 to 1943, an interval of thirty-three years, there are in the bibliographical lists more than 1200 items, over twice the number given by Fuchs for the whole period to 1914.

The bibliographical titles brought together in the present survey are assembled at the end of the volume under three heads: first, surveys covering the general field of colour changes and chromatophores; next, important historical references from the time prior to 1910; and lastly, the large body of references from the period proper to this review, 1910 to 1943. An attempt has been made to give as

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complete a list for this period as possible. It is to be regretted that this list on scrutiny will undoubtedly show deficiencies. These are in part to be explained by the disappearance of many of the scientific bibliographical agencies as a result of the disturbed conditions of the times and in part to the limitations of the author for which he offers his apologies. It is nevertheless hoped that the lists, even with their imperfections, may be of service to scholars in this field of inquiry.

B. Chromatophores as Activated Effectors

The innumerable activities by which animals respond to the environmental changes about them are carried out by their effectors, of which there are some seven classes variously distributed throughout the animal kingdom. Glands and muscles are of universal occurrence. Cilia, the delicate means to motion, are more restricted, for, though they are found from protozoans to vertebrates, they are strangely absent from nematodes and arthropods. Nettling organs, highly efficient offensive and defensive weapons, are characteristically limited to the coelenterates. Electric organs, modified parts of the muscular system, occur only in fishes; and luminous organs, though found in many creatures of the sea and the air, are absent from fresh-water forms. Chromatophores, by which the marvellous colour changes of certain creatures are accomplished, appear mainly among the higher animals. A few sporadic instances are to be met with in what may be called the lower half of the animal kingdom, but well differentiated and extensive chromatophoral systems are found only among the cephalopods, the crustaceans, and the cold-blooded vertebrates.

The word chromatophore, though often used to indicate any animal pigment-cell, is more appropriately employed for those bodies in which colouring matter may be dispersed or concentrated in order that the possessor may change its tint. This restricted usage of the term will be the one employed in the present survey. It conforms well with the name as originally proposed, for it was first used in the Italian form *cromoforo* by Sangiovanni in 1819 for the very active chromatic bodies responsible for the colour changes in the cephalopods.

Chromatophores are of several kinds and are usually classified in accordance with the character of the colouring matter within them. The most usual colour-cells contain dark brown or black pigment and are called melanophores. Such a designation must not be taken to indicate a class whose representatives are necessarily uniform either morphologically or physiologically. Although it is often intimated that the pigment in these cells is melanin, it is by no means certain

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that this is always true. Furthermore, it is well known that melanophores may react very differently to the same agent. Thus to the extract from the eye-stalks of a crustacean the melanophores in the shrimp *Crangon* concentrate their pigment and those in the crab *Uca* disperse it. In lower vertebrates, such as frogs, an injection of adrenaline calls forth a concentration of the pigment in the integumentary melanophores and a dispersion of it in those of the retina. In the skin of a number of animals, some of the melanophores are characteristically large and others small, and in consequence they have been designated as macromelanophores and micromelanophores respectively (Gordon, 1927). Thus melanophores are chromatophores that in several important respects may differ from one another.

Chromatophores that contain red or yellow pigment soluble in alcohol, ether, or other like reagents, are designated collectively as lipophores. They are assumed to possess carotenoid colouring matter. When their pigment is reddish in colour, the cells are called erythrophores and when yellow, xanthophores. Ballowitz (1913*e*) has pointed out a class of chromatophores in which the pigment, though red or reddish brown in tint, is not soluble in alcohol. For these he has proposed the name of allophores.

Chromatophores that contain guanine or guanine-like substances have been termed guanophores. When the guanine is in the form of fine granules and subject to change of position within the cell, the colour-element has been called a leucophore. When the guanine has the form of relatively large, plate-like crystals, the containing cells may be called iridophores. These are the colour cells to which Pouchet gave the name of iridocytes because of their iridescence, but in conformity with modern terminology they may well be designated iridophores.

All the classes of chromatophores thus far noted are represented by single cells containing a single chromatic substance characteristic for a given class. Such colour elements have been called monochromatic chromatophores. These unicellular elements may be contrasted with coloured bodies composed of groups of unicellular chromatophores so closely united as to constitute a single colour-unit. All the cells in such a unit may contain the same kind of colouring matter, the unit in consequence being of one tint, but more usually the cells contain some one colour and others another thus producing a parti-coloured effect. Such combinations have been called polychromatic chromatophores or, if more detailed descriptive terms are required, dichromatic, trichromatic, tetrachromatic chromatophores, etc., depending upon the number of colours present (Brown and Wulff, 1940). Such compound chromatophores are to be found in the crustaceans, in the amphibians, and in some fishes. Thus in the shrimp *Crangon*, in addition to monochromatic chromatophores, there are dichromatic (black and red), trichromatic (black, red, and yellow) and tetrachromatic (black, white, red, and yellow) elements (Brown and Wulff, 1941*a*, 1941*c*). For these compound chromatophores, the name chromatosome has been proposed by Ballowitz (1914*d*, 1931), a term which may well be retained, notwithstanding the fact that Sumner (1933*b*) has suggested it for the mass of pigment within a single chromatophore.

By an appropriate combination of terms, chromatosomes may be named and their compositions indicated. Thus a melaniridosome is a combination of a melanophore and an iridophore, a not unusual occurrence in many teleost fishes. A melanoxantholeucosome would be a combination of melanophores, xanthophores and leucophores, as is to be met with in some crustaceans.

Although chromatosomes may consist of two or more different kinds of colour-cells, they can scarcely be called organs, for they are not composed of different classes of tissues. In the cephalopods, however, a chromatophore is made up of a colour-cell and a circlet of muscle-fibres and thus involves at least two sets of histological elements. These chromatophores are therefore truly diminutive organs. In this respect they are the most complex of all chromatophores and are the only ones that have reached such a structural dignity. All other chromatophores are either groups of colour-cells, chromatosomes, or single colour-cells, chromatophores in the restricted sense.

Chromatophores and chromatosomes are the essential elements in the colour changes of animals. Such changes range over not only the common spectral colours and their mixtures, but also over white, grey, and black. In fact, in some animals the change in tint is limited to white through grey to black and back again. Such ranges might well be said to be colourless, but the term colour has been used to include blacks, greys and whites as well as the spectral tints, and will be so employed in this review.

Two other terms call for a word of explanation. In the past it has been common for writers on animal chromatophores to designate the dot-like condition of the colour-cell as its contracted state and the fully branched one as its expanded state. The designations contracted and expanded as applied to chromatophores are unfortunate terms, for they imply an activity of the colour-cell that may not take place. These terms are usually employed by writers after a word of apology and are generally understood not to imply necessarily any change in the form of the cell. But opposition to these terms has been raised recently and the subject has been thrown open more or less to discussion (Sumner, 1933*b*, 1934*a*; Mast, 1933, 1934; Parker, 1934*c*). Sumner, on the assumption that it was the mass of pigment in the chromatophore that contracted and expanded, proposed to designate this mass as the chromatosome and to describe it as contracting or expanding. This view was rejected by Mast, who suggested for the two processes the terms aggregation and distribution of pigment granules. Parker proposed that no mention at all should be made of the condition of the chromatophore, but that the pigment should be described as concentrated or dispersed, in doing which he unwittingly revived the identical terms that had been proposed for these states by Hewer in 1923.

In the older literature it was customary to describe chromatophores as open to either direct or indirect stimulation. By indirect stimulation was commonly meant activation through nerves, and by direct stimulation that which resulted from any non-nervous means such, for instance, as the application of chemicals or drugs in the blood to the chromatophores or the impingement of light or of heat from the exterior on these cells. Of recent years, direct stimulation has been limited to such obviously external agents as heat and light, which pass essentially unchanged through the immediate outer covering of the animal to the subjacent chromatophores. In this later usage indirect agents include not only nerves but any other means of chromatophoral stimulation that may arise within the body of the animal such as internal secretions.

Indirect stimuli in this sense are consequently often said to be either nervous or humoral; nervous when the response is due to a nerve terminal in immediate contact with the chromatophore and humoral when the reaction depends upon some substance carried by the blood or lymph to the colour-cell. Nervous stimulation, which in the earlier days was the only form of activation suspected, has been shown by the work of the last few decades to be really subordinate to humoral stimulation. The movement in favour of humoral stimulation began some half a century ago in the discovery by Corona and Moroni (1898) that when adrenaline was injected into the body of a frog the animal blanched. Redfield (1918) substantiated this discovery in his investigation of the colour changes in the lizard *Phrynosoma* and he was led to conclude still further that adrenaline was a normally produced activator in this lizard's own body. Through the researches

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of Adler (1914), P. E. Smith (1916*a*) and Allen (1916), who developed the technique of hypophysectomy in anuran larvae, it was learned that tadpoles, without pituitary glands, were always pale. Krogh (1922) pointed out that the same was true of adult frogs. Meanwhile Hogben and Winton (1922*a*, 1922*b*, 1922*c*), who had been actively engaged in experiments on the relation of nerves and pituitary secretion to colour changes in frogs, reached the important conclusion that nerves played a wholly insignificant part in the colour changes of these animals, if in fact they played any part at all. These investigators showed that such changes were in truth dependent upon humoral substances in the blood. This view gained general acceptance and was extended by Koller (1925) and particularly by Perkins (1928) to the crustaceans, where colour change was shown by Perkins to depend upon material that could be extracted from the eye-stalks of these animals. Notwithstanding this rapid accumulation of evidence in favour of a humoral interpretation of chromatophore activation, the nervous interpretation was believed still to hold for cephalopods, fishes, and lacertilians. The last two of these groups, however, were soon shown to involve with their nervous responses indubitable evidence of humoral effects. Thus a diversity of conditions seemed to prevail in that in certain animals the colour-cells were activated nervously, in others humorally, and in still others both ways. From the standpoint of innervation, chromatophores may be conveniently designated aneuronic when they are without nerves, mononeuronic when they possess a single class of nerves, and dineuronic when supplied with two kinds of nerves (Parker, 1943*b*). So far as activation is concerned, aneuronic chromatophores may with equal propriety be called humoral.

But the distinction between nervous and humoral activation for chromatophores seems to be disappearing. It is becoming evident that the terminals of chromatic nerve-fibres excite their end-organs, the chromatophores, in the same way that many other effector nerve-fibres appear to excite their responding organs, namely, through minute amounts of substance which are passed from the terminal to the effector. Hence, between the nerve terminal and the chromatophores there appears to be the same relation as, for instance, between the adrenal gland and the chromatophore in that a substance produced by one activates the other. The one point of difference between these two instances is that in the case of the nerve terminal the source is very near to the colour-cell and in that of the adrenal gland it is far from this cell. This difference of nearness or remoteness is not, however, in any real sense important; in both instances a specific, secreted substance, a humour, is liberated and on reaching the colour-cell excites it to respond. Such a view is in strong contrast with the older conception of nervous stimulation by a nerve current. In this more recent interpretation of nerve stimulation, the distinction between it and humoral stimulation tends to disappear, for both types of activation rely for their effectiveness on certain liberated substances which from a near or a far source reach and excite a given colour-cell (Parker, 1932*a*).

Substances that are produced in the animal nervous system and its appended glands and that serve as activating agents for other parts of the nervous system or its effectors have been variously called neurohumours (Fredericq, 1927; Parker, 1932*b*), transmitters (Dale, 1935), neurohormones (Huxley, 1935), and chemical mediators (Cannon and Rosenblueth, 1937). Such substances may fairly be regarded as hormones even though their region of origin may be very near that of their effective application. Of the several terms that are used for these substances, those of chemical activator and transmitter do not distinguish them from other hormones such, for instance, as the original pancreatic hormone secretin. The other two terms relate them distinctly to nervous activities, and of these the former, neurohumour, is perhaps to be preferred because of its greater flexibility. It was first proposed for this general purpose by Fredericq (1927) and will be the term commonly used in this survey.

A neurohumour may be defined provisionally as a hormone produced by any type of nerve-cell (receptor cell or neurone) or by a gland controlled by neurones, and effective as an activator or inhibitor for other nerve-cells or for effectors. From this standpoint, neurohumours are substances that mediate all intercellular relations in the nervous system and its appended receptors and effectors. Whether or not neurohumours will be found to have such a wide application as is implied in this definition is still to be ascertained, but at the moment there appears to be no evidence for the denial of such a possible application. As the present survey will show, neurohumours include a considerable number of substances such as adrenaline, intermedine, acetylcholine, sympathine, other products from chromatophoral nerve-terminals, and whatever of an activating nature occurs in the extract from the eye-stalks or other secretory centres in crustaceans.

Neurohumours are for the most part soluble in water and are consequently open to transportation by blood and lymph. In this

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way, adrenaline, intermedine, and other like neurohumours are conveyed from place to place. Such water-soluble neurohumours have been called hydrohumours (Parker, 1934*h*, 1935*b*). Other neurohumours, such as those that emanate from the nerve terminals in the skins of a number of fishes, appear not to be carried by the blood or lymph, but to diffuse slowly in the skin itself and by means that are not aqueous. They are believed to be soluble in the fat-like materials of the cells, their lipoid constituents, and to diffuse slowly through these from one part of the skin to another. Such neurohumours, which in consequence of their peculiar solubilities are much more limited in range of action than hydrohumours, have been termed lipohumours (Parker, 1934*h*, 1935*b*) and constitute a rather unusual and remarkable class of activators. Acetylcholine appears to be a neurohumour of this kind, though it is also soluble in water and may therefore act either as a hydrohumour or as a lipohumour. Probably further study will bring to light still other kinds of neurohumours. From this standpoint, the nervous activation of chromatophores as a special type of stimulation disappears in that it proves to be a form of humoral activation in which the exciting substance comes from the nerve terminal in close proximity to the colour-cell itself.

C. THE OCCURRENCE OF CHROMATOPHORES AND THEIR ASSOCIATED COLOUR CHANGES AMONG DIFFERENT ANIMALS

The colour changes in the octopus and in the chameleon were known to Aristotle, who mentions them in his treatise on the *History of Animals*. References to the chromatic activities of both these creatures were made by Pliny in his *Natural History*, where an account of the colour changes of one of the teleost fishes, the red mullet, is also given. The chromatic changes of amphibians and of crustaceans do not seem to have attracted the attention of naturalists till comparatively recent times. The first amphibian whose colour changes were recorded was the common European frog whose chromatic activities were described briefly by Vallisnieri in 1715. The colour changes in crustaceans received no real attention till 1842 when Kröyer gave an account of these responses in the shrimp *Hippolyte*. Thus the five chief animal groups, representatives of which commonly possess chromatophores and show colour changes, were recognized: cephalopods, crustaceans, fishes, amphibians, and reptiles especially lacertilians.

These five groups, however, do not include all the animals that change colour by means of chromatophores. In a number of scattered instances through the animal series, individual species or small groups of species are to be found in which both chromatophores and colour changes are known to occur. Some of these instances are well authenticated, but others remain more or less in doubt. It is questionable whether the colour changes ascribed by von Lendenfeld (1883) to certain sponges such as *Aplysilla* and *Dendrilla* actually occur under natural conditions. Von Uexküll's observations (1896) on the change of tints in sea urchins are quite otherwise. The Mediterranean echinoid *Centrostephanus* was found by this investigator to blanch in darkness and to darken in the light (Fig. 1) through appropriate changes in its chromatophores. The same was said by von Uexküll to be true of *Arbacia pustulosa*. This observation has been confirmed by Kleinholz (1938*d*), though Parker (1931*a*) was unable to substantiate it on the allied species *Arbacia punctulata*.

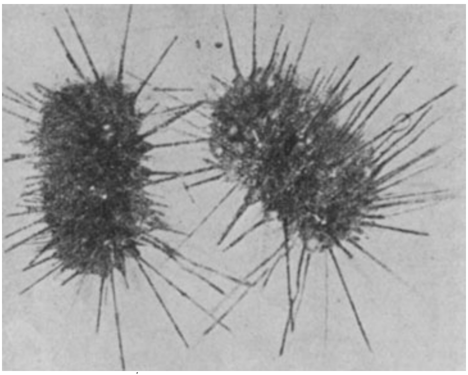

Fig. 1. Photograph of two specimens of *Centrostephanus*, the one to the left after exposure to light, the one to the right after a sojourn in darkness. Von Uexküll, 1896, 327.

Among annelids, the leeches, most of which have brightly coloured skin-patterns, are known to exhibit colour changes. These have been recorded and in some instances studied in detail by Hachlov (1910), Borrel (1914*a*), Stschegolew (1927), Iuga (1931), Wells (1932), Janzen (1932*a*, 1932*b*), and R. I. Smith (1942). In bright light, these animals become dark, and in darkness pale. The change of tint in the body is well illustrated by Jansen's figures from *Glossosiphonia* in which the general state of the chromatophores in darkness and in light can be seen (Fig. 2). Since leeches are negatively phototactic and live generally in shaded situations, it has been suspected that their dark coloration in bright light is a protective measure (Janzen, 1932*b*). Iuga (1931), however, has looked upon the pigmentary cells in *Glossosiphonia* in a very different way and has ascribed to them an excretory function.

Except in cephalopods very little has been done in recent years on the colour changes in molluscs. Weber's study (1923) of the chromatophores in *Limax* show that this slug possesses two types of colour-cells—melanophores and cells containing a reddish brown pigment insoluble in alcohol and hence presumably allophores. *Limax* exhibits a well-marked colour change which persists, though in less degree, after the animal has been blinded. Normal and blinded individuals are said to respond not only to light and to darkness, but also to light of different colours, white, red, and blue. The chromatophores in *Limax* are unicellular and relatively simple. In the pteropods such as *Cymbulia* and *Tiedemannia* the colour organs are sacs with coloured contents and surrounded by a circlet of smooth muscle-fibres much like those in the cephalopods. These remarkable chromatophores justify the separation of the pteropods from the gastropods, as originally maintained by the older naturalists, and the establishment of an independent group for these molluscs between gastropods and cephalopods. No work on the pteropod chromatophores appears to have been done for many years.

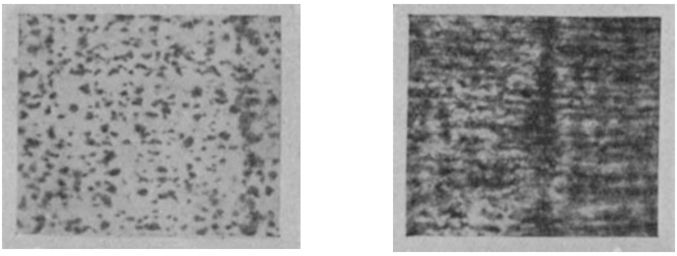

Fig. 2. Photographs of the same spot on the surface of *Glossosiphonia*; left, in darkness; right, in bright illumination. Janzen, 1932*a*, 38.

Very few insects change colour in relation to their environment, and where these changes do take place they are usually slow and relatively permanent. One of the most noted instances of colour change among these animals is that of the phasmid *Dixippus* (*Carausius*) *morosus* which has been studied in recent times by a host of investigators (Schleip, 1910, 1915, 1921; Steche, 1911; von Dobkiewicz, 1912; Zacharias, 1913; Schmitt-Auracher, 1921, 1925; Przibram