THE EFFECT OF LIGHT ON PIGMENTATION

THE dramatic effects of light on the pigments of plants and animals have long been recognized. The yellowish-white pallor assumed by plants containing chlorophyll confined in darkness is well known, while the diatoms of the Lakes of Auvergne, equipped with green chlorophyll and brown diatomin, change colour according to the depth of the water in which they find themselves (Héribaud, 1894) ; but the most dramatic effects are evident in the integumentary pigments of *poikilochromic* [1] animals. The spectacular and rapid changes in colour between black and green seen in the chameleon were noted in the fourth century B.C. by Aristotle, while Pliny described somewhat similar changes in the dying mullet. Since classical times a considerable amount of observation and research has been devoted to the subject and a surprisingly wide range of colour changes has been recorded in a large variety of animals—a euglenoid Protozoon, polychæte worms, leeches, Echinoderms, Cephalopods, Crustaceans, Insects, and among Vertebrates, numerous Fishes, Amphibians and Reptiles.[2]

Biologically these changes may be assumed to serve two purposes, one the antithesis of the other—*cryptic* or protective and *phaneric* or demonstrative. The protective function is the more fundamental and the more common, the demonstrative is a later and more rare acquisition.[3]

The PROTECTIVE FUNCTION is designed in general to allow the animal to adapt itself to its environment and shows three main modifications. In its most primitive form such a variation in pigment probably developed as a *light-absorptive function* to provide protection against deleterious light and heat ; occasionally pigmentary variations are apparently *thermo-regulatory*—an early attempt at thermostasis— as is seen strikingly in some desert lizards in which colour changes may be induced experimentally by changes in temperature alone (Parker, 1906–38 ; Bauer, 1914 ; Krüger and Kern, 1924 ; and others). The most common and dramatic colour variations, however, have evolved as an *adaptive phenomenon* allowing the animal to become as

---

[1] ποικίλος, varied ; χρῶμα, colour.
[2] For extensive reviews see van Rynberk (1906), Fuchs (1914), Hogben (1924), Parker (1930–55) and Brown (1950).
[3] These are examples of a large group of phenomena termed *allæsthetic* by Huxley (1938) which exert their biological effect through the agency of the distance receptors of another individual—sight, hearing or smell.

inconspicuous as possible and obliterate itself in its environment ; and, as we shall see, this faculty of MIMICRY or HOMOCHROMATISM is sometimes carried to almost unbelievable lengths, particularly among teleostean fishes, the animal not only changing its general appearance in light and shade but assuming the pattern of colour—blue, red, yellow, green, black—of its surroundings (Fig. 53).

FIG. 53.—THE EUROPEAN PLAICE, *PLEURONECTES PLATESSA*.
Lying in shallow water on the bed of the sea, to harmonize with which it is able to change its colour within wide limits. The camouflage in the figure is obvious (photograph by Douglas P. Wilson).

Occasionally the opposite type of behaviour is apparent and instead of changing its coat to suit its environment, the animal alters its surroundings to suit its own coloration : thus the silvery young of the Malayan spider, *Cyclosa insulana*, normally rests on a silvery silk platform, but as the animal becomes older and brown in colour, it covers the platform with brown débris (Bristowe, 1941). In other cases a suitable environment is deliberately chosen ; thus the desert lark, *Ammomanes*, will settle with great reluctance on a terrain not of its own colouring such as black lava, red earth, or light sand (Meinertzhagen, 1940), just as bark-like moths will adopt postures that make their disrupted wing-design conform with the configuration of the background (Cott, 1940). In still other cases an artificial camouflage is assumed, such as the beetles or dressing-crabs which drape themselves throughout life with a clothing of leaf-fragments, sticks or weeds suitable to each successive environment, or the geometrid larva of Borneo which similarly adorns itself with flower-buds (Shelford, 1902).

DEMONSTRATIVE COLOUR CHANGES, although less common, may also be striking phenomena. These changes in colour whereby the

Latrodectus

Gasterosteus

Betta

Chlamydosaurus

*Bombinator
in warning
attitude*

animal strives to make itself as conspicuous as possible, may be directed towards several ends. In the first place they may serve the essential biological purpose of *reproduction* whereby, simulating the sexual riot of the flowers, colour displays, sometimes of extraordinary vividness, are associated with courtship and mating behaviour, a phenomenon seen in marked degree in certain cephalopods and fishes (Hadley, 1929 ; Parker and Brower, 1935) ; it is a function analogous to the conspicuousness of many male birds adopted possibly for display and distraction in contrast to the cryptic inconspicuousness of the brooding female. It is interesting that such sexual dimorphism is rarely seen in birds which feel secure, either because of their fighting ability or in their colonial habits, the latter finding safety in a flock (Mottram, 1915). In the second place they may be designed for *aggression*, wherein, as if in defiance of all creation, the animal when sufficiently moved to excitement assumes the most blatant hues possible (as in squids, cuttle-fish, teleostean fishes, spiders and lizards : Kleinholz, 1938 ; and others). Less commonly they may have a more social purpose, serving as signals of warning or recognition between members of the same species or as feeding-releasers between parent and offspring (see Marshall, 1936 ; Huxley, 1914–38 ; Cott, 1940–54 ; Armstrong, 1947 ; and others).

Thus when facing an enemy the venomous Australasian spider, *Latrodectus*, turns a fiery red, and the cornered green chameleon an inky black, opening widely at the same time its brightly coloured mouth. Nowhere, however, in the whole animal kingdom are displays so lavish and theatrical provided as among teleostean fishes in their wild ecstasies of love or fighting ; none so exquisite as the elaborately graceful love-dance of the male European stickleback, *Gasterosteus aculeatus*, when his incandescent blue-green back and transparent red sides glow like neon lighting ; none so awesome as the life-and death war-dance of the ordinarily brownish-grey male Siamese fighting-fish, *Betta pugnax*, as his widespread fins light up in a luminous multi-coloured glory of burning passion which for centuries has whetted the gambling instincts of the Siamese as did cock-fights the English. In these cases the stimulus is purely visual for the stickleback will fight its own image in a mirror with the utmost savagery (Tinbergen, 1951).

In other cases a colour-demonstration is made which, strictly speaking, does not involve a true colour change. The Australian frilled lizard, *Chlamydo-saurus*, for example, carries around its neck a large frill-like fold supported by cartilaginous rods which can be opened like a huge circular umbrella around the head. When scared the frill is closed and the lizard dashes for safety ; when it turns to face its enemy the great greenish-yellow frill splashed with red forms a striking and terrifying picture in contrast to the saffron yellow of its open mouth, before which the enemy usually retires discomfited. Again, the small European fire-bellied toad, *Bombinator igneus*, has its dark under-surface spotted vividly with yellow or red, associated with a poisonous exudate from the skin ; when danger threatens the animal throws itself on its back or arches its body to proclaim its unsuitability as food.

The mechanism of the colour change varies in different species. In the simplest unicellular form, *Euglena*, a red hæmatochrome pigment migrates from a deeper position beneath the green chloroplasts to disperse itself superficially under the influence of light (Johnson, 1939) ; but the most common mechanism is through the activity of special integumentary cells [1] called CHROMATOPHORES ($\chi\rho\hat{\omega}\mu\alpha$, colour ; $\phi\acute{o}\rho os$, a carrier). Occasionally the phenomenon is *morphological* involving a change in the number of functioning chromatophores or an alteration in the quantity of pigment in each. This, a relatively slow mechanism, is well exemplified in the pigmentation that can be induced in the white belly of flounders if normal fish are kept in a black tank or are blinded and are illuminated from below (Osborn, 1940). Sometimes, as in certain insect larvæ and spiders, this is the sole mechanism of colour-change available (Gabritschevsky, 1927) ; it is usually less obvious and impressive than the more common method which is responsible for the dramatically vivid colour changes in poikilochromic Crustaceans, Fishes, Reptiles and Amphibians.[2] This— a *functional* or *physiological* change—involves merely a redistribution of pigment. The change may be effected by a single pigment which at one time is concentrated into tiny spots lost in a pallid background of skin so that it contributes little to the colour of the animal, at another, dispersed so that the animal becomes appropriately tinted. Alternatively a pigment of one colour may stream in front of or retire behind pigments of other colours so that surprising changes of hue may rapidly occur. The two methods, morphological or physiological, are not mutually exclusive, for if the conditions determining the second are maintained for a sufficiently long time, permanent morphological changes tend to occur, a generalization sometimes known as Babák's law (1913).
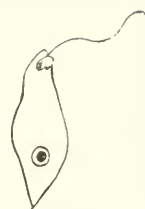
Warm-blooded animals, on the other hand, can only change their colour by the slow and laborious process of renewing their inert feathers or hairs ; to this there are a few exceptions wherein specific stratagems are adopted, such as the antelope-jackrabbit which turns white in its flight by rolling up the skin of its belly on the side towards its pursuer.

Two major types of chromatophores occur. In Molluscs (cuttle-fish and their allies, squid, octopus), the chromatophores are in highly organized groups of cells in which the pigment is redistributed by neuromuscular activity. Each organ consists of a central cell filled with pigment (red, brown or yellow) around which radiate a number of muscle-fibres which, on their simultaneous contraction, pull out the

Euglena

Cuttlefish

---

[1] In certain transparent Fishes part or all of the colour pattern is found in internal organs such as the peritoneum and meninges.

[2] Crustaceans, Keeble and Gamble (1903–5) ; various Vertebrates, Babák (1913), Brown (1934) ; Fishes, Odiorne (1933) ; Amphibians, Sumner (1935).

small pigmented cell-body into a great disc some twenty times the
diameter of the original sphere ; a nerve-fibre supplies each muscular
cell and the resulting changes are rapid (Figs. 54 and 55).[1]   In all
other animals the chromatophores are single cells ; usually they are
specialized cells provided with arborizing processes, arranged singly or
in a syncytium, and by a process of cytoplasmic streaming the pigment
may be concentrated into inconspicuous punctate masses in the centre
of the cell or dispersed throughout the branching structure to give a
diffuse colour to the animal (Figs. 56 to 59).[2]   In Insects, however, the
ordinary epidermal cells fulfil this function ;   normally a dark brown-
black pigment lies beneath an evenly disposed yellow-green pigmented
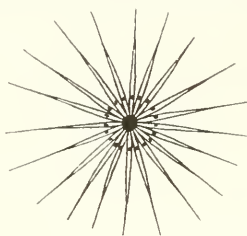
FIGS. 54 AND 55.—A CHROMATOPHORE OF THE CEPHALOPOD.

FIG. 54.   FIG. 55.

FIG. 54.—The appearance of the   FIG. 55.—The extended mass of pig-
chromatophore with the radiating   ment pulled out by contraction of
muscular cells and the small con-   the muscle cells (after Bozler).
centrated clump of central pigment.

layer, and on stimulation the former migrates to the surface and
disperses itself over the lighter layer thus darkening the animal
(Figs. 60 and 61) (Giersberg, 1928–30).

The coloration resulting from the migration of pigment is often
assisted by its new relationship to static pigment.   Under the chromato-
phores of Cephalopods and Crustaceans, for example, there is an
immobile layer of light-reflecting pigment so that considerable varia-
tions in colour are possible depending on the amount of light permitted
to pass to the deeper tissues (Webb *et al.*, 1952).   In Insects, as we have
seen, the variegation is enhanced by the migratory brown or red
pigment covering over or retreating behind the static green and yellow
pigments.   In Amphibians such as the tree-frog, *Hyla arborea*, a colour
change from green through lemon-yellow to grey is attained by varia-
tions in the dispersion of melanin underneath layers of yellow and white

Hyla arborea

[1] See especially—Phisalix (1894), Hertel (1907), Hofmann (1907–10), Fröhlich
(1910), Bozler (1928).
[2] See especially—Spaeth (1913), Perkins (1928), Matthews (1931), Perkins and
Snook (1932), Brown (1935), and others.

FIG. 56.—THREE STAGES IN THE DISPERSION OF PIGMENT IN A MELANOPHORE
OF THE LIZARD, *TARENTOLA* (Hogben).

FIGS. 57 TO 59.—PIGMENT SPOTS IN WEB OF A FROG IN DIFFERENT
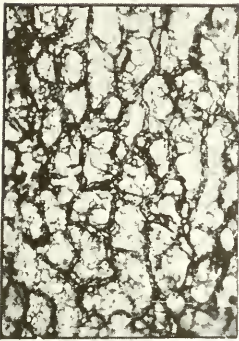CONDITIONS (Hogben).
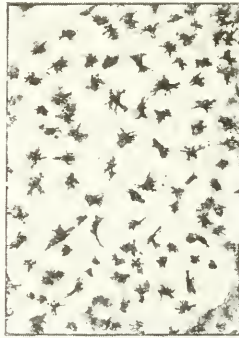

FIG. 57.—Dark animal.
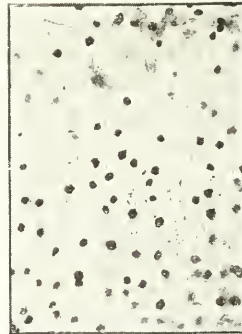
FIG. 58.—Intermediate
condition.

FIG. 59.—Pale animal.

cells and its streaming towards the surface between them (Schmidt, 1920). A comparable arrangement may be seen in Reptiles ; thus in the lizard, *Anolis*, the animal is darkened by the streaming of melanin in the processes of chromatophores to become superficial to an inert whitish layer (v. Geldern, 1921 ; Kleinholz, 1938) (Figs. 62–3), while the proverbial chameleon changes from a dark brown to a light green depending on the degree of dispersion of the melanin which lies in front of a sheet of four different kinds of colour-cells.

The types of pigment also vary, but the intimate chemical nature of many is unknown. The most primitive and universal pigment is melanin [1] of a dark brown colour ; the cells containing it are usually monochromatic and are termed *melanophores*. A second type of pigment—more vivid and varied than the dull brown of melanin—is

Anolis

Chameleon

[1] For a discussion of the chemical nature of melanin, see p. 118.

There are 3 types of pigmentation : (A) the cross-hatching indicates a static layer of yellow-green pigment underneath the cuticle, (B) the fine dots indicate red pigment which may be either aggregated into clumps or dispersed, and (C) coarse dots indicating brown-black pigment which migrates from a deep site underneath the nuclei to a superficial position underneath the cuticle (after Giersberg).
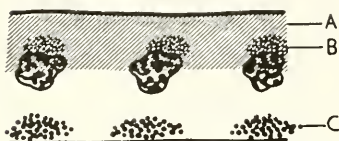
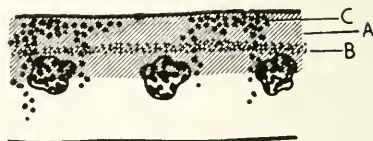FIG. 60.—The epidermis in the light-adapted stage.

FIG. 61.—The epidermis in the dark-adapted stage.

comprised of various fat-soluble carotenoids [1] contained in *lipophores*. In Invertebrates (Crustaceans, Insects) the chromatophores are frequently polychromatic since each may contain a variety of these pigments—blue-green, orange, yellow and red—sometimes each with a separate distribution within the cells.[2] In Vertebrates the chromatophores are usually monochromatic—red (within *erythrophores*), yellow (within *xanthophores*) or green [3]—one animal often having several types of pigment in different integumentary cells (purple astacene and yellow lutein in the brown trout, *Salmo trutta*, Steven, 1948). A third pigmentary factor is found extensively both in Invertebrates and Vertebrates

Salmo trutta

FIGS. 62 AND 63.—COLOUR CHANGES IN THE LIZARD.

FIG. 62.—The deposition of the melanophores in the brown state when the branches of these cells extend into the stratum germinativum.
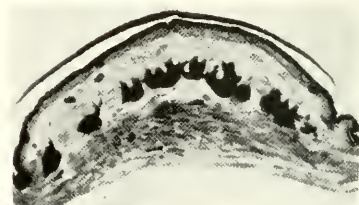
FIG. 63.—The lizard in the green condition when the pigment is concentrated beneath the static pigment in the superficial layers.

The stratum corneum has been displaced from the section (Kleinholz).

[1] The *carotenoid pigments* are of wide distribution and great biological interest, playing a part as sensitizers to the phototropic movements of plants, the phototactic movements of animals, and also participating in visual processes. Their nature will be discussed at a later stage (p. 118).
[2] In Crustaceans—Kühn and Lederer (1933), Fabre and Lederer (1934) ; in Insects—Schleip (1910–15), Giersberg (1928).
[3] See Fox (1947).

—guanine. This may form a white highly reflecting layer, as in Crustaceans, or, as in many Vertebrates, may be contained in white *guanophores* or variegated *iridocytes*, the iridescent colour changes of which are due to the arrangement, form and movements of plate-like crystals of guanine—a form of coloration akin to that due to the diffraction of light by the scales of fish and reptiles or the feathers of birds. The colour changes in these cells are sometimes quite remarkable ; thus in the killifish, *Fundulus*, a single iridocyte may exhibit blue-green, orange, yellow and red phases in successive moments.

Fundulus

The factors causing colour changes in animals include extremes of temperature, humidity, contact stimulation. and psychic stimuli, particularly excitement and fear ; but the most general and much the most important is light.

Light acts upon chromatophores in one of three ways—by a direct, primary effect on the cells themselves, by a secondary reaction through the eye, or by indirect reactions through receptor mechanisms other than the eyes (the central nervous system and the pineal body).

A further response—the endogenous *diurnal variation* in coloration, largely controlled by hormones and nervous centres situated in the mid-brain—we have already discussed.[1]

(a) When light acts directly upon the chromatophores themselves the reaction may be called a PRIMARY RESPONSE. This is the most primitive mechanism and the only one available to unicellular plants (diatoms) or animals (*Euglena*), but it is frequently retained in higher forms, usually as a generalized darkening in the shade and lightening with illumination, a change, however, normally obscured by the more dominant secondary responses through the eyes. The primary response, however, can be observed in young specimens the chromatophores of which have not yet come under the control of the secondary mechanism, in blinded animals (Osborn, 1940), in denervated regions after nerve section and degeneration. and in isolated fragments of the skin when exposed to illumination. a reaction demonstrated in crustaceans (Keeble and Gamble, 1905) and in some sea-urchins (Kleinholz, 1938 ; Millott, 1954–57) (Figs. 64 to 67).

Diatom

The direct motor response of individual ectodermal cells to the stimulus of light survives among the higher animals in the movements of the retinal rods and cones [2] and in the contraction of the pupillary muscles, both of which are ectodermal in origin. In the iris of Cephalopods, Fishes and Amphibia a direct contraction to light commonly occurs,[3] and although the primitive response in the higher Mammals and man has been replaced by a reflex neuro-mechanism,

[1] p. 19.   [2] p. 731.
[3] Brown-Séquard (1847–59), Budge (1855), Müller (1860), Schur (1868), Steinach (1890–92), Magnus (1899). Guth (1901), Marenghi (1902), Hertel (1907), Young (1933), Weale (1956), and others.

Figs. 64 to 67.—Pigmentary Changes with Light Intensity
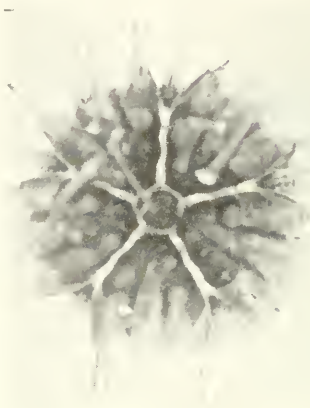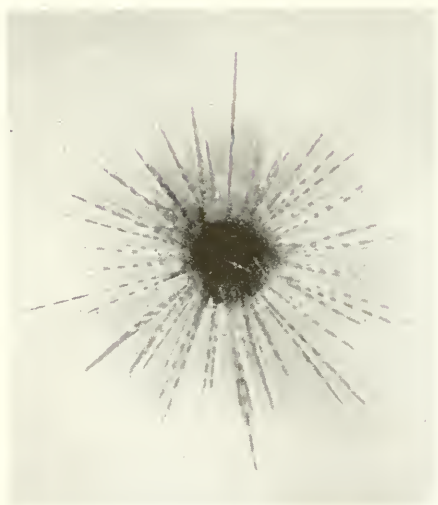in a Sea-urchin.

Fig. 64.

Fig. 65.

Fig. 66.
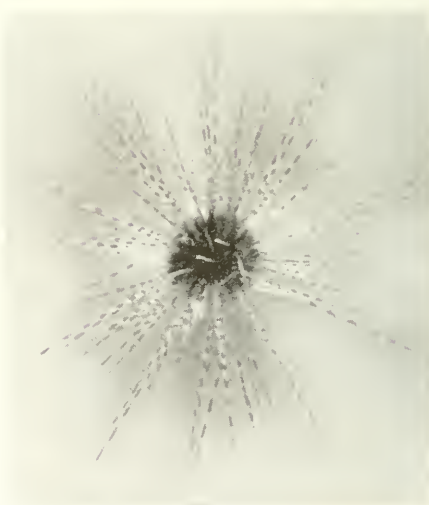
Fig. 67.

To show the variation of pigmentation in a young specimen of *Diadema antillarum*. In the light-adapted phase the animal appears uniformly black owing to the dispersion of melanin pigment (Fig. 64). In the dark-adapted phase the melanin recedes from the aboral surface leaving beautifully defined patterns of white lines and a ring, an effect due to the concentration of pigment (Fig. 65).

In older specimens, the changes are less marked (Figs. 66 and 67) (N. Millott).

it may still be elicited with the more effective stimulus of ultra-violet light after all connections with the central nervous system have been severed.

(*b*) The most dramatic reactions follow stimulation of the eyes (SECONDARY RESPONSES). Hogben and Slome (1931), for example, found that in the case of the clawed toad, *Xenopus*, when the field of vision was occupied by a light-scattering surface the animal became pale, when set in the dark background of a light-absorbing surface the animal suffered generalized darkening of the skin, a response abolished on removal of the eyes. While the primary responses react in general to the total intensity of light, the secondary response is usually based on the ratio of the amount of *incident* light entering the eye directly from above to the amount of *reflected* light from the background, so that on a dark background, when the ratio is large, the animal becomes dark and on a light background, when the ratio is small, it becomes pale ; it is to be noted that these changes occur without regard to the intensity of the total illumination (Sumner, 1911–40 ; Sumner and Keys, 1929 ; Brown, 1936 ; Sumner and Doudoroff, 1937). This influence of the reflectance or *albedo* of the background (to borrow an astronomical term) has been fully established by experiment ; thus the effect of a dark background can be faithfully reproduced by making the lower half of the cornea opaque [1] ; reversal of the fish or of the illumination or the background produces the expected effect ; and Butcher (1938), on rotating the eye of the killifish, *Fundulus*, through 180°, found that it gave its tawny response to a yellow background only when the latter was above the animal.

In his work on teleostean fishes Sumner (1940) established that the reflectance of the substrate had an important effect on morphological colour changes also, for he found that the melanophore count and the total quantity of melanin varied inversely as the logarithm of the reflected light. The mathematical nature of the relationship is interesting and unexpected ; it recalls Fechner's modification of Weber's Law defining the relationship between the intensity of stimuli and their sensory appreciation, and suggests that in assuming control of these colour changes the eye applies the same quantitative standards as govern its sensory activities.

In addition to this general quantitative reaction, a differentiated response to the spectral nature of the light reflected from the background is relatively common so that the animal can assume the colour of its environment, sometimes with remarkable rapidity and accuracy. This apparently extraordinary reaction was first scientifically described in the chameleon prawn, *Hippolyte*, by Keeble and Gamble (1899) and many instances have now received study. The prawn, *Palæmon*, for example, can manipulate its red, yellow and blue pigments, so that with-

Hippolyte

---

[1] In the insect, *Dixippus*—Atzler (1930) ; Priebatsch (1933) ; in shrimps— Hanstrom (1937–38) ; in fishes—Sumner (1940).
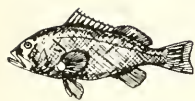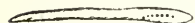
in a few days it can adapt itself to its habitat by becoming red, yellow blue, green, white or black (Brown, 1935), a facility possessed in some degree by several crabs [1] and Cephalopods.[2] Such a change may occur rapidly ; thus the larvæ of butterflies (Brecher, 1922) and salamanders (Kammerer, 1920) when placed under variously coloured glasses readily change their hue ; and not only the tone of the general background but its colour-pattern may be simulated with great fidelity by certain teleostean fishes. The most remarkable changes of this type are seen in the groupers (*Epinephelus*) that swim over the variegated patterns of the coral reefs in tropical waters and within a few minutes may change a livery of bright blues and browns into an equally brilliant costume of yellow and black ; a similar virtuosity is seen in flat-fishes such as the flounder, *Paralichthys albiguttus* (Kuntz, 1916 ; Mast, 1916). It is interesting that adaptation during the early stages of development may play an important part in determining the final pattern of colour in the adult ; thus if the larvæ of the crested newt, *Triturus cristatus*, develop on a dark background the yellow markings of the adult become suppressed, if on a light background, the dark markings suffer a similar fate (Lautz, 1953). It is to be noted that all these reactions are completely dependent on the eyes and have invariably been shown to be lost if the animal is blinded or even if it is dazzled by a blinding light which abolishes the contrast between the dorsal and ventral portions of the retina (octopus, Prince, 1949).

(*c*) Occasionally INDIRECT RESPONSES may follow stimulation of receptor mechanisms other than the eyes—the MID-BRAIN as in some fishes (*Phoxinus*—Scharrer, 1928) or the PINEAL BODY as in lampern larvæ (Young, 1935) or teleostean fishes (Breder and Rasquin, 1950).

The central organization of these pigmentary changes is as varied and complex as the variations in the colours themselves, and in view of the multiplicity of the types of chromatophores and their reactions it is not surprising that our knowledge of their control is by no means complete in spite of much research. Apart from local primary reactions, two methods of coordination are found, hormonal and nervous, the first the more primitive and slower in its development, the second the more elaborate and efficient. Sometimes the one is present alone, as is seen, on the one hand, in the simple hormonal control found in Crustaceans, the more primitive Fishes, frogs and lizards, or, on the other hand, in the simple nervous control found in the leech or the chameleon. More often the two are combined in a dual mechanism of coordination, the hormonal control being sometimes the preponderating influence as in Insects or the eel, but usually being

Epinephelus

Triturus cristatus

Phoxinus

Ammocœte larva of lamprey

---

[1] *Portunus*—Abramowitz (1935) ; *Planes*—Hitchcock (1941).
[2] *Sepia*—Kühn and Heberdey (1929), Kühn (1950).

dominated by the nervous mechanism as in Cephalopods such as the octopus or the more highly developed Teleosteans such as the cat-fish. The hormones (*chromatophorotropins*), of which there may be more than one with mutually antagonistic reactions, are elaborated in Crustaceans in the neuro-secretory cells formed in the eye-stalks and elsewhere in the central nervous system [1] ; in Vertebrates the pituitary-hypothalamic complex [2] is the primary source although the adrenals may provide an antagonistic element. The nerve supply may be simple with one type of fibre which is pigment-concentrating as in the dogfish or the chameleon, or it may be dual comprised of two opposing types of fibre, one resembling adrenalin with a pigment-concentrating (sympathetic) action being antagonized by a second resembling acetyl-choline with a pigment-dispersing (parasympathetic) effect.

Among ANNELIDS, such as some polychæte worms (Hempelmann, 1939) and leeches (Wells, 1932 ; Janzen, 1932 ; Smith, 1942), most of which become pale in darkness and dark when illuminated, the evidence suggests that the control is primarily nervous, correlated most effec-tively through the ocelli at the anterior end but operated less efficiently by widely distributed photoreceptors through segmental reflexes. Thus if a leech is decapitated or stimulated faradically, a pale animal kept in darkness will become pigmented, but if the nerve-cord is truncated the change passes only to the level of trans-section ; while decapitated animals show the same responses as normal animals but respond more sluggishly (Smith, 1942). Among these animals there is no evidence of a response to the background.

In CEPHALOPODS there is a slowly acting hormonal control, probably mediated by substances of the nature of tyramine and betaine ; the former has an adrenalin-like action increasing the tonus of motor centres and producing a dark coloration, while the latter, like acetylcholine, decreases the tone of the chromatophores and lightens the animal. The injection of these substances produces the same colour changes as also does the transference of blood from a dark to a light animal (Sereni, 1928–30). This simple and fundamental chemical action, however, is dominated by nervous activity ; the stimulus is received primarily through the eyes, control being maintained through centres in the cerebral and suboesophageal ganglia, the isolation of which by nerve section stops all colour change in the area affected, and the response is effected probably by a double innervation, both excitatory and inhibitory, to the muscles of the chromatophores (Phisalix, 1892–94 ; Sereni, 1927–28 ; Bozler, 1928–29).

Among INSECTS the control is both hormonal and nervous and the part played by the eyes varies. In this respect the stick-insect, *Dixippus*, has been investigated most extensively (Giersberg, 1928).

[1] p. 552.   [2] p. 556.

Leech
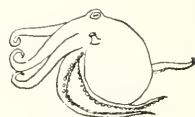
Cephalopod
(*Octopus*)

Dixippus

In it, the eyes are the sole photoreceptors and their occlusion or section of the optic tracts inhibits all normal responses (Atzler, 1930) ; but the fundamental role of hormonal control is seen in the fact that transplanted portions of integument react normally long before nervous connection can be established (Janda, 1936). On the other hand, in the grasshopper, *Acrida turrita*, some colour changes (adaptation to red, orange, yellow and violet) are said to occur after the eyes are totally varnished, while a green colour can be developed only if the eyes are functioning (Ergene, 1952).

Among CRUSTACEANS the vividly dramatic colour changes are

Grasshopper

FIG. 68.—COLOUR CHANGES IN CRUSTACEANS.

The three shrimps (*Crago*) were initially coloured alike, as the specimen on the left. This was used as a control and showed no change after an injection of sea-water. That in the centre was injected with an alcohol-insoluble fraction of the commissures ; that on the right by a total water-soluble fraction of the commissures (Brown and Klotz).

entirely mediated by hormones elaborated in the cephalic neurosecretory system.[1] That a blood-borne agent was the responsible factor was first demonstrated by Koller (1925–30) who found that the colour of a lightly coloured shrimp, *Crago vulgaris*, could be altered by blood transfusion from a darkened specimen. Perkins (1928–32) thereafter discovered in the prawn, *Palæmonetes*, that denervation of a region had no effect on colour responses while occlusion of the blood supply inhibited them ; he also demonstrated that injection of an extract of the sinus gland induced blanching in a blinded animal while removal of the eye-stalks resulted in the assumption of a permanently darkened appearance. These early results have been amply confirmed and it would appear that the intricate control of the chromatophores of Crustaceans is effected by at least two and sometimes three or four

Prawn

[1] See further p. 554.

chromatophorotropins antagonizing and supplementing each other, neither species- nor genus-specific, secreted in various parts of the neuro-secretory system [1] (Fig. 68). In some cases the process is more complex and adaptation to the background is achieved by the production of different hormones when the dorsal or the ventral aspect of the retina is stimulated (the Isopod. *Ligia oceana*—Smith, 1938).

In CYCLOSTOMES and the more primitive fishes such as the SELACHIANS [2] hormones derived from the pituitary seem to be the only active agents in the control of the chromatophores, a pigment-
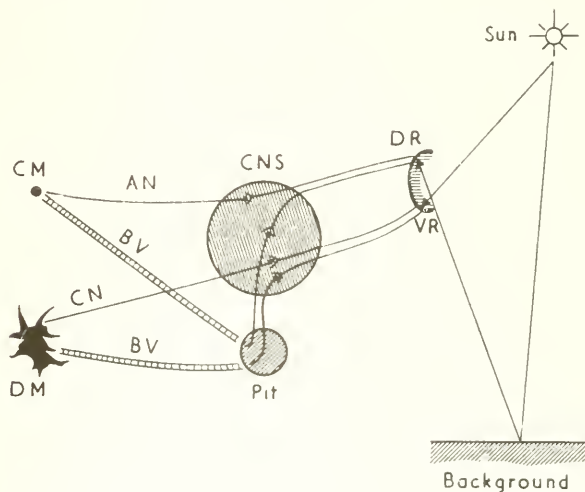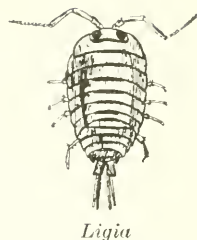
Ligia

Fig. 69.—The Controlling Mechanism of the Melanophores of a Fish (the Eel, *Anguilla*).

The direct light from the sun strikes the ventral portion of the retina, VR, while the light reflected from the background strikes the dorsal portion, DR. From the retina nerve paths lead to the central nervous system, CNS, and thence directly to the chromatophores by adrenergic nerve fibres, AN, and cholinergic nerve fibres, CN. A second relay is made to the pituitary body, Pit, from which hormones are distributed through the blood vessels, BV. CM is a chromatophore with its melanin concentrated ; DM with its melanin dispersed (after Parker).

dispersing agent (intermedin) causing darkening and a pigment-concentrating factor causing blanching ; the colour of the fish is determined by the ratio of these two antagonistic substances in the blood, this ratio being in turn controlled by visual stimuli through the differential effects of dorsal and ventral stimulation of the retina (Zondek and Krohn, 1932 ; Lundstrom and Bard, 1932 ; Young,

[1] The shrimps, *Crago* and *Palamon*, the fiddler crab of the Pacific coast of N. America, *Uca*, the lobster, *Homarus*, etc. (Hanström, 1933–35 ; Brown and his colleagues, 1933–52 ; Webb *et al.*, 1951).
[2] Cyclostomes, such as the lamprey, *Lampetra*—Young (1935) ; Selachians, such as the skate, *Raja*—Parker (1937), and the dog-fish, *Scyllium*—Young (1933).

1935 ; Hogben, 1936). In TELEOSTEAN FISHES, however, which show more elaborate colour changes than any other species, a dual mechanism emerges for a more efficient nervous control has developed, depending on the excitability of specialized retinal areas above and below the level of the optic nerve (Hogben and Landgrebe, 1940) (Fig. 69). In some types, it is true, the hormonal influence remains preponderant ; this is seen in the eel, *Anguilla* (Neill, 1940 ; Waring, 1940), or in the minnow,

Anguilla

FIG. 70.—COLOUR CHANGES IN THE FEMALE GUPPY, *LEBISTES RETICULATUS*

On the left the normal animal ; on the right a fish after 25 μg. per ml. of LSD (D-lysergic diethylamide) had been added to the water of the aquarium (*Sandoz J. Med. Sci.*, 1956).
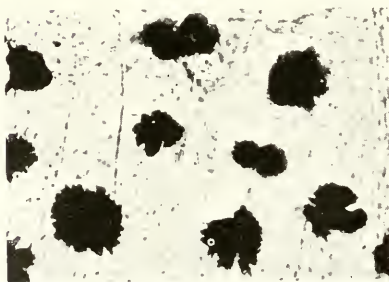
FIGS. 71 AND 72.—THE MELANOPHORES OF THE GUPPY, *LEBISTES RETICULATUS*
(*Sandoz J. Med. Sci.*, 1956).

FIG. 71.—After adaptation to a light environment.

FIG. 72.—After LSD (25 μg. per ml.) had been added to the water of the aquarium.

Phoxinus lævis, in which even section of the spinal cord fails to alter the response to the background (Healey, 1951–54 ; Gray, 1956). In most Teleosteans, however, colour changes are dominated by a nervous control which persists in hypophysectomized animals. That the changes in the chromatophores were determined by chemical mediators liberated at the nerve terminals has been shown in a striking series of experiments by Parker (1940–55), who studied the effects of sectioning the radial nerves of the tail-fin. The chromatophores of Selachians possess a single innervation mediated by an adrenalin-like substance, selachine, which is pigment-concentrating (the dogfishes, *Mustelus* and

Mustelus

Squalus—Parker, 1935–36) ; Teleosteans possess a double innervation with, in addition, pigment-dispersing fibres the action of which is mediated by acetylcholine (the killifish, *Fundulus*—Parker, 1934 ; the catfish, *Ameiurus*—Mills, 1932, Parker, 1940–41 ; and other species). These two types of nerve correspond to the sympathetic and parasympathetic systems of warm-blooded animals since adrenalin blanches and acetylcholine darkens the eserinized animal (Giersberg, 1930 ; Smith, 1931). Similarly, darkening of certain Teleosts (the guppy, *Lebistes reticulatus*) can be brought about by adding D-lysergic acid diethylamide to the water of the aquarium (Cerletti and Berde, 1955) (Figs. 70 to 72). At the same time, however, even in these
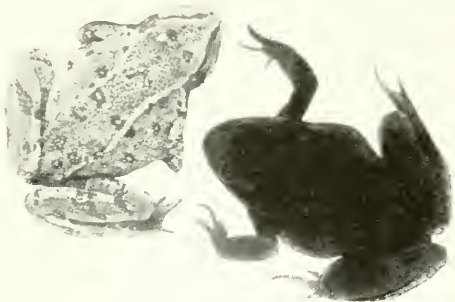

Squalus

Ameiurus

FIG. 73.—THE EFFECT OF THE INJECTION OF PITUITRIN ON A FROG.
The right animal injected six hours previously with pituitary extract from a fœtal ox ; left, control (Hogben).

fishes some hormonal influence remains since pituitary extracts are slowly effective in denervated areas (Matthews, 1933 ; Kleinholz, 1935 ; Abramowitz, 1937).

AMPHIBIANS were the first class of animals in which a humoral control of colour was demonstrated, when P. E. Smith (1916) showed that hypophysectomized tadpoles remain indefinitely pale. Although there is some evidence of a minor nervous influence in some species such as the darkening of the leg of the toad, *Bufo arenarum*, on section of the sciatic nerve and its blanching on peripheral stimulation of the cut nerve (Stoppani, 1942), it may be said in general that amphibian chromatophores are essentially under humoral control. This is maintained by two antagonistic hormones elaborated in the pituitary-hypothalamic system—a melanin-concentrating *W-substance* causing

Bufo

blanching, mediated by the pars tuberalis, and a melanin-dispersing *B-substance* (intermedin) mediated by the posterior or intermediate lobe ; their relative concentration in the blood is determined by environmental stimuli operating through the eyes and their activity is usually abolished when these or the optic nerves are destroyed, although some residual responses remain after removal of both eyes which may be due to the direct action of light on the hypothalamic region (Rowlands, 1952–54). These conclusions have been confirmed by the effects of excision of the whole or parts of the pituitary and by the induction of colour changes by the injection of extracts of the gland both in the frog, *Rana*,[1] and in the African clawed toad, *Xenopus lævis* [2] (Fig. 73). It is also interesting that injection of pineal extract produces a contraction of the melanophores of *Xenopus* (Bors and Ralston, 1951) while pigmentary changes are constantly produced in tadpoles by feeding on pineal tissue (McCord and Allen, 1917).

REPTILES, like Amphibians, show less elaborate responses to light than teleostean Fishes ; the only conspicuous changes occur among lizards and the only active cells are the melanophores which send up pigment into their branches entwined among the variegated chromatophores, thus varying the colour scheme ; the gaiety of their various costumes is due to individual variation in these static cells. The only photic response is to light entering the eye, and the colour of the background is without primary significance. Within these limitations, however, the large family of lizards shows every possible variation in control. On the one hand, the iguanid, *Anolis* (the " Florida chameleon "), shows little evidence of nervous intervention ; it becomes dark brown in bright illumination, pale green in darkness ; a hypophysectomized or a blinded animal becomes light green and thereafter loses all colour responses except a peculiar mottling on electrical stimulation or on the injection of adrenalin ; while denervated areas of the skin respond as do normal areas (Kleinholz, 1938) (Figs. 62 and 63). An intermediate position is occupied by such iguanids as the American horned " toad," *Phrynosoma*. The chromatophores of this animal are under the influence of pigment-concentrating nerve fibres and react to adrenalin ; stimulation or section of these fibres results respectively in blanching or abolition of responses. At the same time the injection of pituitrin or of the blood of a darkened specimen induces darkening, while hypophysectomy or the injection of adrenalin, adrenal extract or of blood from a pale animal induces blanching (Redfield, 1918 ; Parker, 1938). It would seem that the two antagonistic hormones act directly on the chromatophores since they are

Rana

Xenopus

Anolis

Phrynosoma

[1] Hogben and Winton (1922–23), Steggerda and Soderwall (1939), Parker and Scattery (1937).
[2] Hogben and Slome (1931–36), Atwell and Holley (1936).

equally effective in areas denervated by nerve section. On the other hand, in the chameleon the chromatophores show no evidence of hormonal control and appear, apart from the primary response characteristic of this animal, to be influenced solely by one set of pigment-concentrating nerves ; denervation results in darkening, possibly due to the absence of tonic impulses, whereafter there is a complete absence of further responses (Hogben and Mirvish, 1928 ; Zoond and Eyre, 1934 ; Sand. 1935).

Abramowitz. *Proc. nat. Acad. Sci.*, **21**, 677 (1935).
Biol. Bull., **73**, 134 (1937).
Armstrong. *Bird Display and Behaviour*, London (1947).
Atwell and Holley. *J. exp. Zool.*, **73**, 23 (1936).
Atzler. *Z. vergl. Physiol.*, **13**, 505 (1930).
Babák. *Pflügers Arch. ges. Physiol.*, **149**, 462 (1913).
Bauer. *Z. allg. Physiol.*, **16**, 191 (1914).
Bors and Ralston. *Proc. Soc. exp. Biol. Med.*, **77**, 807 (1951).
Bozler. *Z. vergl. Physiol.*, **7**, 379 (1928) ; **8**, 371 (1929).
Brecher. *Arch. EntwMech. Org.*, **50**, 41 (1922).
Breder and Rasquin. *Science*, **111**, 10 (1950).
Bristowe. *The Comity of Spiders*, London (1941).
Brown. *Proc. nat. Acad. Sci.*, **19**, 327 (1933).
Biol. Bull., **67**, 365 (1934) ; **70**, 8 (1936).
J. Morph., **57**, 317 (1935).
Physiol. Zool., **13**, 343 (1940).
Comparative Animal Physiology, London, 677 (1950).
The Action of Hormones in Plants and Invertebrates, N.Y., 171 (1952).
Brown, Ederstrom and Scudamore. *Anat. Rec.*, **75**, Suppl., 129 (1939).
Brown and Klotz. *Proc. Soc. exp. Biol. Med.*, **64**, 310 (1947).
Brown and Sandeen. *Physiol. Zool.*, **21**, 361 (1948).
Brown, Sandeen and Webb. *Anat. Rec.*, **111**, 569 (1951).
Brown and Scudamore. *J. cell. comp. Physiol.*, **15**, 103 (1940).
Brown and Wulff. *J. cell. comp. Physiol.*, **18**, 339 (1941).
Brown-Séquard. *C. R. Acad. Sci.* (Paris), **25**, 482, 508 (1847).
J. Physiol. (Paris), 2, 281, 451 (1859).
Budge. *Bewegungen d. Iris* (1855).
Butcher. *J. exp. Zool.*, 79, 275 (1938).
Cerletti and Berde. *Experientia*, **11**, 312 (1955).
Cott. *Adaptive Coloration in Animals*, London (1940).
Allæsthetic Selection and Evolutionary Aspects, in Huxley, Hardy and Ford's *Evolution as a Process*, London (1954).

Ergene. *Z. vergl. Physiol.*, **34**, 159 (1952).
Fabre and Lederer. *Bull. Soc. Chim. biol.* (Paris), **16**, 105 (1934).
Fox. *Ann. Rev. Biochem.*, **16**, 443 (1947).
Fröhlich. *Z. allg. Physiol.*, **11**, 269, 316, 351 (1910).
Fuchs. Winterstein's *Handb. vergl. Physiol.*, Jena, **3** (1). 1189 (1914).
Gabritschevsky. *J. exp. Zool.*, **47**, 251 (1927).
von Geldern. *Proc. Calif. Acad. Sci.*, **10**, 77 (1921).
Giersberg. *Z. vergl. Physiol.*, **7**, 657 (1928) ; **9**, 523 (1929) ; **13**, 258 (1930).
Gray. *Nature* (Lond.), **177**, 91 (1956).
Gross. *Pflügers Arch. ges. Physiol.*, **112**, 302 (1906).
Guth. *Pflügers Arch. ges. Physiol.*, **85**, 119 (1901).
Hadley. *Bull. Mus. comp. Zool. Harvard*, **69**, 108 (1929).
Hanstrom. *Zool. Jb., Abt. Anat.*, **56**, 387 (1933).
Proc. nat. Acad. Sci., **21**, 584 (1935).
Kungl. Svenska Vetensk. Akad. Handl., **16**, 1 (1937).
Kungl. Fysiogr. Sällsk. Handl., **49**, 3 (1938).
Healey. *J. exp. Biol.*, **28**, 298 (1951) ; **31**, 473 (1954).
Hempelmann. *Z. wiss. Zool.*, **152**, 353 (1939).
Héribaud. *C. R. Acad. Sci.* (Paris), **118**, 82 (1894).
Hertel. *v. Graefes Arch. Ophthal.*, **65**, 106 (1907).
Z. allg. Physiol., **6**, 44 (1907).
Hitchcock. *Biol. Bull.*, **80**, 26 (1941).
Hofmann. *Arch. mikr. Anat.*, **70**, 361 (1907). .
Pflügers Arch. ges. Physiol., **118**, 375 (1907) ; **132**, 43 (1910).
Hogben. *The Pigmentary Effector System*, Edin. (1924).
Proc. roy. Soc. B, **120**, 142 (1936).
Hogben and Landgrebe. *Proc. roy. Soc. B*, **128**, 317 (1940).
Hogben and Mirvish. *Brit. J. exp. Biol.*, **5**, 295 (1928).
Hogben and Slome. *Proc. roy. Soc. B*, **108**, 10 (1931) ; **120**, 158 (1936).

Hogben and Winton. *Proc. roy. Soc. B*, **93**, 318 ; **94**, 151 (1922) ; **95**, 15 (1923).

Huxley. *Proc. zool. Soc. Lond.*, **2**, 491 (1914).
J. Linn. Soc. (Zool.), **35**, 253 (1922).
Proc. VIII Int. Ornith. Cong., Oxon., 430–55, 1934 (1938).

Janda. *Zool. Anz.*, **115**, 177 (1936).

Janzen. *Z. Morph. Oekol. Tiere*, **24**, 327 (1932).
Zool. Anz., **101**, 35 (1932).

Johnson. *Trans. Amer. micr. Soc.*, **58**, 42 (1939).

Kammerer. *Naturwissenschaften*, **8**, 28 (1920).

Keeble and Gamble. *Proc. roy. Soc. B*, **65**, 461 (1899) ; **71**, 69 (1902).
Philos. Trans. B, **196**, 295 (1904); **198**, 1 (1905).

Kleinholz. *Biol. Bull.*, **69**, 379 (1935).
J. exp. Biol., **15**, 474, 492 (1938).
Pubbl. Staz. zool. Napoli, **17**, 53 (1938).

Koller. *Verh. dtsch. zool. Ges.*, **30**, 128 (1925).
Z. vergl. Physiol., **5**, 191 (1927) ; **8**, 601 (1928) ; **12**, 632 (1930).

Krüger and Kern. *Pflügers Arch. ges. Physiol.*, **202**, 119 (1924).

Kühn, A. *Z. vergl. Physiol.*, **32**, 573 (1950).

Kühn, A., and Heberdey. *Zool. Anz.*, Suppl. 4, 231 (1929).

Kühn, R., and Lederer. *Ber. dtsch. chem. Ges.*, **66**, 488 (1933).

Kuntz. *Bull. U.S. Bur. Fish.*, **35**, 1 (1916).

Lautz. *J. Genet.*, **51**, 502 (1953).

Lundstrom and Bard. *Biol. Bull.*, **62**, 1 (1932).

McCord and Allen. *J. exp. Zool.*, **23**, 207 (1917).

Magnus. *Z. Biol.*, **38**, 567 (1899).

Marenghi. *Arch. ital. Biol.*, **37**, 274 (1902).

Marshall. *Philos. Trans. B*, **226**, 423 (1936).

Mast. *Bull. U.S. Bur. Fish.*, **34**, 173 (1916).

Matthews. *J. exp. Zool.*, **58**, 471 (1931).
Biol. Bull., **64**, 315 (1933).

Meinertzhagen. *The Ibis*, **4**, 106, 187 (1940).

Millott. *Philos. Trans. B*, **238**, 187 (1954).
Endeavour, **16**, 19 (1957).

Mills. *J. exp. Zool.*, **64**, 231 (1932).

Mottram. *Proc. zool. Soc. London*, 663 (1915).

Müller. *Verh. phys.-med. Ges. Würzburg*, **10**, p. L (1860).

Neill. *J. exp. Biol.*, **17**, 74 (1940).

Odiorne. *Proc. nat. Acad. Sci.*, **19**, 329 (1933).

Osborn. *Proc. nat. Acad. Sci.*, **26**, 155 (1940).

Parker. *J. exp. Zool.*, **3**, 401 (1906) ; **89**, 451 (1942).
Biol. Rev., **5**, 59 (1930).

Proc. nat. Acad. Sci., **17**, 594 (1931), **20**, 306 (1934).
Biol. Bull., **68**, 1 (1935) ; **71**, 255 (1936).
Proc. Amer. philos. Soc., **77**, 223 (1937) ; **83**, 379 (1940) ; **85**, 18 (1941).
J. exp. Biol., **15**, 48 (1938).
Quart. Rev. Biol., **18**, 205 (1943) ; **30**, 105 (1955).
Animal Colour Changes and their Neurohumors, Cambridge (1948).

Parker and Brower. *Biol. Bull.*, **68**, 4 (1935).

Parker and Scatterty. *J. cell. comp. Physiol.*, **9**, 297 (1937).

Perkins. *J. exp. Zool.*, **50**, 71 (1928).

Perkins and Snook. *J. exp. Zool.*, **61**, 115 (1932).

Phisalix. *Arch. Physiol. norm. path.* (Paris), **4**, 209, 445 (1892) ; **6**, 92 (1894).

Priebatsch. *Z. vergl. Physiol.*, **19**, 453 (1933).

Prince. *Visual Development*, Edin., **1**, (1949).

Redfield. *J. exp. Zool.*, **26**, 275 (1918).

Rowlands. *J. exp. Biol.*, **29**, 127 (1952) ; **31**, 151 (1954).

van Rynberk. *Ergebn. Physiol.*, **2**, 347 (1906).

Sand. *Biol. Rev.*, **10**, 361 (1935).

Scharrer. *Z. vergl. Physiol.*, **7**, 1 (1928).

Schleip. *Zool. Jb., Abt. allg. Zool. Physiol.*, **30**, 45 (1910) ; **35**, 225 (1915).

Schmidt. *Arch. mikr. Anat.*, **93**, 414 (1920).

Schur. *Z. rat. Med.*, **31**, 373 (1868).

Sereni. *Boll. Soc. ital. Biol. sper.*, **2**, 377 (1927) ; **3**, 707 (1928) ; **4**, 749 (1929).
Z. vergl. Physiol., **8**, 488 (1928) ; **12**, 329 (1930).
Biol. Bull., **59**, 247 (1930).

Shelford. *Proc. zool. Soc. Lond.*, **2**, 230 (1902).

Smith, D. C. *J. exp. Zool.*, **58**, 423 (1931).

Smith, H. G. *Proc. roy. Soc. B*, **125**, 250 (1938).

Smith, P. E. *Anat. Rec.*, **11**, 57 (1916).

Smith, R. I. *Physiol. Zool.*, **15**, 410 (1942).

Spaeth. *Anat. Anz.*, **44**, 520 (1913).

Steggerda and Soderwall. *J. cell. comp. Physiol.*, **13**, 31 (1939).

Steinach. *Pflügers Arch. ges. Physiol.*, **47**, 289 (1890) ; **52**, 495 (1892).

Steven. *J. exp. Biol.*, **25**, 369 (1948).

Stoppani. *Endocrinology*, **30**, 782 (1942).

Sumner. *J. exp. Zool.*, **10**, 409 (1911).
Amer. Nat., **69**, 245 (1935) ; **73**, 219 (1936).
Biol. Rev., **15**, 351 (1940).

Sumner and Doudoroff. *Proc. nat. Acad. Sci.*, **23**, 211 (1937).

Sumner and Keys. *Physiol. Zool.*, **2**, 495 (1929).

Timbergen. *Wilson Bull.*, **60**, 6 (1948).
The Study of Instinct, Oxon. (1951).

Tschirkowski. *Neurol. Vestn.*, **11** (4) (1904). *Arch. Augenheilk.*, **55**, 119 (1906).

Waring. *Proc. roy. Soc. B*, **128**, 343 (1940).

Weale. *J. Physiol.*, **132**, 257 (1956).

Webb, Brown, Fingerman and Hines. *Anat. Rec.*, **111**, 569 (1951).

Webb, Brown and Graves. *Biol. Bull.*, **103**, 310 (1952).

Wells. *Nature* (Lond.), **129**, 686 (1932).

Young. *Proc. roy. Soc. B*, **112**, 228 (1933). *Quart. J. micr. Sci.*, **75**, 571 (1933). *J. exp. Biol.*, **12**, 254 (1935).

Zondek and Krohn. *Klin. Wschr.*, **11**, 405 (1932).

Zoond and Eyre. *Philos. Trans. B*, **223**, 27 (1934).