# CHAPTER II

THE EFFECT OF LIGHT ON METABOLISM

It is well known and universally recognized that the general behaviour of many organisms is regulated by light ; the contrast between the activities of nature by day and its stillness by night needs no stress. This is a widespread characteristic of vegetable life which exists so much more closely to the sun and the earth than do animals, but even among the latter dramatic changes are frequently evident, particularly in the lower forms. Thus among Protozoa, some Rhizopods change their form, contracting under the influence of light (Engelmann, 1882 ; Verworn, 1889) (Figs. 2 and 3), many species are activated by light (such as flat-worms, Loeb, 1893–94), while other creatures become inactive under its influence (maggots, Herms, 1911 ; and many insects, such as cockroaches, Gunn, 1940). Among the higher forms of life, in addition to a number of basic metabolic functions, the reproductive

Fig. 2.   Fig. 3.
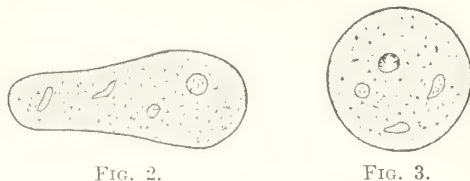
Figs. 2 and 3.—*Pelomyxa palustris* at rest (Fig. 2), and contracted under the influence of light (Fig. 3).

cycle and secondary features such as colour changes and behavioural habits are similarly regulated by light although in many cases other factors such as temperature, humidity and nutrition exert sometimes contributory, sometimes more potent effects. In this way the alternation of day and night has imposed a rhythmic diurnal cycle upon a number of the activities of living organisms (PHOTOPERIODISM) ; and it is to be remembered that in many of the phenomena thus involved darkness seems to be as important a stimulus as light. Indeed, in many cases the rhythm has become so fundamental that if the organism is placed in experimental circumstances wherein the natural alternation of light and darkness is changed to become out-of-phase, or if it is exposed to continuous light or darkness, many of these cyclic changes continue as if the normal 24-hour rhythm still persisted ; the rhythm originally imposed by external circumstances has eventually become autochthonous.
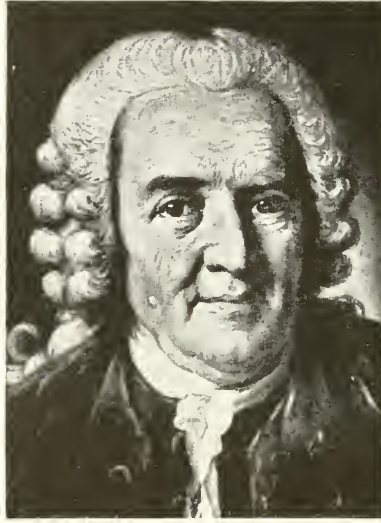
Fig. 4.—Carl Linnæus (1707–1778).

Carl Linnæus, son of a Lutheran Swedish pastor and Professor of Botany at Uppsala, is universally acknowledged as the Father of Scientific Botany. His main work was his *System of Nature* which passed through 12 editions in his lifetime following its initial publication in 1741. He had a passion for classification. Not only did he classify in a system based on their reproductive organs the 18,000 species of plants known to him, which he and his pupils travelled far and wide to collect (one of them, for example, accompanied Captain Cook on his first voyage, 1768–71) ; but he also classified animals, diseases and minerals—even past and present scientists in a system of military rank with himself as general. He introduced the now universally adopted nomenclature of plants and animals, first the *generic* name indicating the genus, and second the *specific* name indicating the species. His garden is still tended in Uppsala. The Linnean Society of London which possesses his library and collections was founded in 1788.

This portrait of " Carl v. Linné ætat. 67", lent me by the Linnean Society, is from the original by Krafft, the Swedish artist, who painted it in 1774 for the College of Physicians at Stockholm of which Linnæus was one of the founders.

The origin of such rhythms is speculative, but it is interesting to recall the environment of living creatures when first they experienced the drama of a day–night cycle on the earth. For millions of years living organisms never experienced conditions more varied than those of the warm but placid sea, but as the sea-weeds of the swamps spread onto the land, plants became exposed alternately to the stimulating conditions of a humid hot-house during the day and the depression of the comparative chill of night. Similarly, as Amphibians emerged to creep upon the land in the heat of the Palæozoic, and as they and the Reptiles matured in the torrid Jurassic and Cretaceous ages, it is difficult to realize the violence of the contrast between the extreme metabolic and nervous activity which must have occurred in the blaze of noon, and the sluggishness of sleep and the reduction of nervous energy which must have prevailed in the cold of night ; for chemical activity and the speed of nervous impulses are both dependent on temperature. It is probable, indeed, that the development of thermostasis and its ultimate evolution into homeostasis were the determining events which made possible the evolution and ultimate supremacy of Birds and Mammals on a cooling globe, and that the lack of the control of temperature was the main cause of the extinction of the Dinosaurs and the retreat of the Amphibians to a few degenerate types. But it is to be remembered that the period during which the primitive creatures which first inhabited the still-warm earth experienced this alternating climax of delirious activity each noon and fatigued torpidity each night, occupied some hundred million years ; and even although their descendants have long acquired the peace of thermostasis, it is not surprising that traces of the early turmoil still remain.

PHOTOPERIODISM IN PLANTS

Over 200 years ago, CARL LINNÆUS (1707–1778) (Fig. 4), who laid the groundwork of scientific botany at Uppsala, noted that many

FIGS. 5 AND 6.—SLEEP MOVEMENTS IN FLOWERS AND LEAVES.
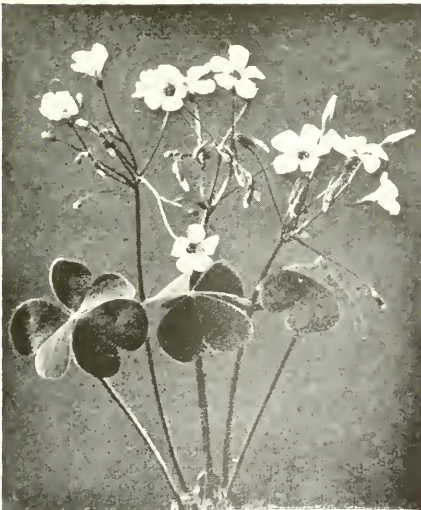

FIG. 5.—*Oxalis rosea* awake.   FIG. 6.—*Oxalis rosea* asleep.

flowers have a time of opening and closing so regular that he constructed
a flower-clock from which the time of day could be read—the poppy
opened at 6 a.m., the speedwell at mid-morning, the white campion in
the evening (to be pollinated by night moths), and so on (Figs. 5 and 6).
At a much later date, the " sleep movements " of leaves were similarly
studied by Darwin (1880) : those of the runner bean, for example, raise
themselves during the morning, become horizontal by noon, fall in the
afternoon and fold up at night.   The significance of these daily
rhythms, however, was largely neglected until they were intensively
investigated by the German botanist, E. Bünning (1931–56), who
showed that they were not simply an immediate response to the
passing stimuli of day and night, but were part of a rhythmic change
which has become characteristic and endogenous to the plant itself—a
24-hour rhythm in the intensity of endosmosis throughout its structure,
in the rate of growth, the rate of respiration, the activity of enzymes and
the entire metabolism, a rhythm to which the plant has become
habituated so that the periodicity persists for some time even if it is
placed in continuous darkness, and is only slowly readjusted if an
artificial rhythm is imposed upon it.[1]. Other factors may supervene,
the most important of which are temperature and nourishment, but
the most profound influence on basic activities is that of the sun, from
the energy of which all life is ultimately derived.

The pattern of the *flowering of many plants* is a good example of
this general tendency—and an important one, for floral initiation is a
fundamental factor marking the change from vegetative life to reproduc-
tive activity.   Although experimental work of considerable merit had
been done on the effects of artificially varying the periods of illumina-
tion on the growth and maturation of plants, particularly by Schübeler
(1880) in England, Tournois (1912) in France, and Klebs (1918) in
Germany,[2] it was left to two American botanists, Garner and Allard
(1920), to establish finally the important fact that in many species
flowering did not depend primarily on temperature or the intensity of
illumination but on *the daily lengths of the periods of light and darkness* ;
they therefore introduced the term PHOTOPERIODISM.   In many plants
the determining factor is the length of the day, and, as was first proved
by the Russian botanist, Cailahian (1936), the primary receptor organ
is the leaf ; even although the rest of the plant is covered, the exposure
of one leaf, or even part of a leaf, to the rhythm of light and darkness
determines the cycle, and if the leaves are removed and the plant
rendered naked to live on its stored food it immediately becomes

---

[1] See Grossenbacher (1939), Engel and Heimann (1949), Flügel (1949), Hagan
(1949), Heimann (1950–52), Enderle (1951), Vegis (1955), Bünning (1956), Wareing
(1956), and others.
[2] For review, see Smith, 1933.

indifferent to the alternating change between darkness and light. Moreover, if a plant of one type is denuded of leaves and the leaf of a plant with a different cyclic character is grafted onto it, the host-plant assumes the periodicity of the grafted leaf.[1]

Two different responses are well recognized. In summer-flowering plants (*long-day plants*) which bloom when the spring days lengthen, the formation of

FIG. 7.—THE EFFECT ON FLOWERING OF INTERMITTENT LIGHT DURING THE NIGHT.

On the *left* are two gladioli (long-day plants) grown in a control greenhouse with a normal solar day-and-night rhythm ; on the right, two similar plants grown with intermittent light during the night (Boyce Thompson Institute for Plant Research).

flowers is inhibited in darkness while during the periods of light some substance is presumably formed in the leaves which counteracts this inhibition ; in *short-day plants* which come to flower when the autumn days shorten, both dark and light periods are necessary for the development of the stimulus, each with opposite effects, one depending on light-energy and the other being inhibited by light. In summer-flowering plants artificial light during the night promotes flowering (Fig. 7) ; in autumn-flowering plants flowering in short days, light during the day promotes flowering but short periods of light during the night prevent it.

[1] Melchers (1936–37), Cailahian (1936–47), Loehwing (1938), Borthwick and Parker (1938–40), Hamner and Naylor (1939), Harder and v. Witsch (1940), Withrow *et al.* (1943), and others.

The mechanism of these photoperiodic responses is unknown but several facts are now established. It is significant that a brief exposure (1 sec. in some species) to light of a very low intensity (of the order of 1 ft. candle, that is, of the intensity of moonlight) is sufficient to determine the periodicity. The wave-length of the light is of importance, for the action-spectrum shows a specificity with maxima in the red and blue—a fact which suggests the presence of one or more absorbing pigments ; moreover, there are indications of an antagonism between the action of different spectral regions, while near infra-red radiation takes an active part in the effect (see Wassink and his co-workers, 1950–56). Such a pigment (or pigment-mixture) has not been isolated, but Borthwick and his colleagues (1948–54) speculated that it is an open-chain tetrapyrrol pigment, a distant relative of chlorophyll. With its aid a photosynthetic reaction takes place, the nature of which is unknown [1] with the probable result that one or more plant hormones,[2] perhaps both activating and inhibiting in their action, travel down the leaf-stalk and up the shoot to influence flowering ; the substance can travel through living cells and across grafts but not across an inanimate obstacle (Cailahian, 1940).

The fact that such a substance (or substances) has eluded chemical detection, has stimulated several alternative hypotheses.[3] However that may be, and whatever the intimate mechanism, the fact remains that the order of the procession of flowers through the seasons is largely determined by the diurnal periodicity of light and darkness.

Bonner. *Botan. Gaz.*, **110**, 625 (1949).
Bonner and Thurlow. *Botan. Gaz.*, **110**, 613 (1949).
Borthwick, Hendricks and Parker. *Botan. Gaz.*, **110**, 103 (1948).
Borthwick, Hendricks, Toole, E. H., and V. K. *Botan. Gaz.*, **115**, 205 (1954).
Borthwick and Parker. *Botan Gaz.*, **100**, 374 (1938) ; **101**, 806 (1940).
Borthwick, Parker and Hendricks. *Amer. Naturalist*, **84**, 117 (1950).
Bünning. *Jb. wiss Botan.*, **75**, 439 (1931). *Ber. dtsch. botan. Ges.*, **54**, 590 (1937). *Biol. Zbl.*, **64**, 161 (1944). *Flora*, **38**, 93 (1944). *Naturwissenschaften*, **33**, 271 (1946). *Naturforsch.*, **3b**, 457 (1948). *Planta* (Berl.), **38**, 521 (1950). *Ann. Rev. Plant Physiol.*, **7**, 71 (1956).
Cailahian. *C. R. Acad. Sci. U.R.S.S.*, **12**, 443 (1936) ; **27**, 160, 253, 370 (1940) ; **31**, 949 (1941) ; **47**, 220 (1945) ; **54**, 735, 837 (1946) ; **55**, 69 (1947).

Darwin. *The Power of Movement in Plants*, London (1880).
Enderle. *Planta* (Berl.), **39**, 570, (1951).
Engel and Heimann. *Planta* (Berl.), **37**, 437 (1949).
Engelmann. *Pflügers Arch. ges. Physiol.*, **29**, 387 (1882).
Flügel. *Planta* (Berl.), **37**, 337 (1949).
Garner and Allard. *J. agric. Res.*, **18**, 553 (1920).
Grossenbacher. *Amer. J. Botan.*, **26**, 107 (1939).
Gunn. *J. exp. Biol.*, **17**, 267 (1940).
Hagan. *Plant Physiol.*, **24**, 441 (1949).
Hamner and Naylor. *Botan. Gaz.*, **100**, 853 (1939).
Harder and van Senden. *Naturwissenschaften*, **36**, 348 (1949).
Harder and von Witsch. *Gartenbauwiss.*, **15**, 226 (1940).
Heimann. *Planta* (Berl.), **38**, 157 (1950) ; **40**, 377 (1952).
Herms. *J. exp. Zool.*, **10**, 167 (1911).

[1] Review, see Lang, 1952.   [2] p. 39.
[3] See Bünning (1937–50), Bonner and Thurlow (1949), Bonner (1949), Harder and van Senden (1949), van Senden (1951). Recent research indicates that the gibberillins are of fundamental importance in the photoperiodism of plants.

Klebs. *Flora*, **11–12**, 128 (1918).
Lang. *Ann. Rev. Plant Physiol.*, **3**, 265 (1952).
Loeb. *Pflügers Arch. ges. Physiol.*, **54**, 81 (1893) ; **56**, 247 (1894).
Loehwing. *Proc. Soc. exp. Biol. Med.*, **37**, 631 (1938).
Melchers. *Biol. Zbl.*, **56**, 567 (1936) ; **57**, 568 (1937).
Parker, Hendricks and Borthwick. *Botan. Gaz.*, **111**, 242 (1950).
Schübeler. *Nature* (Lond.), **21**, 311 (1880).
van Senden. *Biol. Zbl.*, **70**, 537 (1951).
Smith, F. *Meld. Norg. LandbrHöisk.*, **13**, 1 (1933).

Tournois. *C. R. Acad. Sci.* (Paris), **155**, 297 (1912).
Vegis. *Symbolae Botan., Upsalienses*, **14**, 1 (1955).
Verworn. *Psychophysiologische Protisten-studien*, Jena (1889).
Wareing. *Ann. Rev. Plant Physiol.*, **7**, 191 (1956).
Wassink, Sluysmans and Stolwijk. *Koninkl. ned. Akad. Wetens. Proc.*, **53**, 1466 (1950).
Wassink and Stolwijk. *Ann. Rev. Plant Physiol.*, **7**, 373 (1956).
Withrow, Withrow and Biebel. *Plant Physiol.*, **18**, 294 (1943).

PHOTOPERIODISM IN ANIMALS

DIURNAL METABOLIC RHYTHMS are equally remarkable among animals, for the cycle of day and night with its rhythm of changes in illumination, temperature and other environmental factors has so impressed itself upon living creatures in the course of their palæontological development that many of their metabolic processes vary with a corresponding periodicity, synchronized as it were by an internal physiological clock.

These physiological rhythms have received much study and have accumulated a considerable literature.[1] Among Mammals, including Man, the periodicity of *sleep and activity* is the most obvious,[2] possibly a survival of the nocturnal reduction of nervous activity in primæval Amphibians. Most animals are diurnally active ; but in nocturnal animals the cycle of activity is reversed.[3] A similar cyclic variation is seen in bodily *temperature*.[4] In Man the temperature through the day is higher than at night, but considerable variations occur in the characteristics of the curve ; in some individuals the peak is in the morning, in others in the afternoon and in others at an intermediate .time. The *blood constituents* show a variation affecting the hæmoglobin, hæmatocrit readings and plasma proteins,[5] while the variation in the eosinophil count is dramatic ; in Man, in the morning there is an eosinopenia[6] ; in nocturnal animals such as mice the count is high in the morning and low in the early hours of the night.[7] A similar rhythm acting independently of the intake of fluid affects the *urinary output*, involving not only the excretion of water but also that of electrolytes (Na, K and chlorides, etc.) and urea which persists even if the 24-hour day is disrupted for periods up to 6 weeks.[8] Even more fundamental cellular processes are involved such as *mitotic activity* which is maximal in the rest-period at

[1] See Kleitman (1949), Menzel (1952), Halberg (1953), Harker (1958).

[2] See Kleitman (1939).

[3] Rat—Richter (1922), Browman (1937) ; wood rat—Colton (1933) ; vole—Davis (1932) ; hedgehog—Herter (1934) ; mice—Achelis and Nothdurft (1939), Aschoff (1952), Kowalski (1955) ; wild mice—Johnson (1926).

[4] See Kleitman *et al.* (1937–38), Kleitman (1949), Halberg *et al.* (1953).

[5] Renbourn (1947).

[6] von Domarus (1931).

[7] Halberg and Visscher (1950–52).

[8] Gerritzen (1936–40), Mills (1951), Mills and Stanbury (1952), Mills *et al.* (1954), Lewis *et al.* (1956), Lewis and Lobban (1956).

midnight and minimal at noon, a rhythmic variation first noted in plants [1] and discovered in mammalian tissues (including the corneal epithelium) by van Leijden (1917), confirmed in the human epidermis by Cooper (1939) and noted in the cornea of tadpoles by Meyer (1954).[2] It is interesting that it is a physiological process not seen in cancer cells. As will be fully discussed in a subsequent volume, a diurnal variation of some 3–5 mm. Hg occurs in the *ocular tension*.[3]

Established by constant repetition, these rhythms persist for some time in the absence of environmental reinforcement when the external rhythm has been artificially altered or has ceased. The mechanism of these changes is unknown ; most of them are probably maintained by rhythmic changes of activity in the neuro-vegetative centres of the diencephalon, while the endocrine system, particularly the pituitary
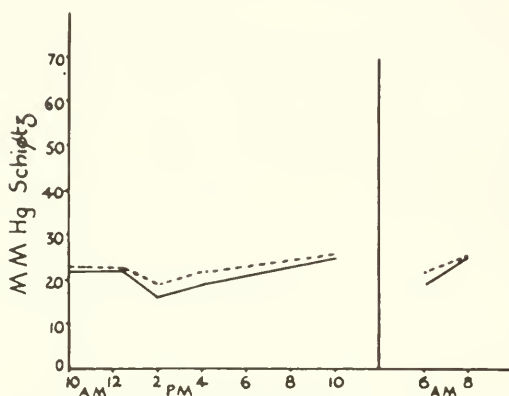

Fig. 8.—The Normal Diurnal Variation in the Intra-ocular
Pressure.

The abscissæ are times of the day ; the vertical line denotes when the patient was asleep.

complex, probably has some effect. Apart from the long-known centres controlling thermo-regulation and urinary output, functions such as the variation in circulating eosinophils are governed by the diencephalo-hypophyseal system through the secretion of cortico-steroids by the adrenal cortex (Hume, 1949 ; Porter, 1953), and the evidence is rapidly accumulating that a region in the same neighbourhood exerts control over the intra-ocular pressure (v. Sallman and Lowenstein, 1955 ; Gloster and Greaves, 1957). However they are controlled, these rhythms are real and autochthonous. Thus in man the normal variation in temperature persists for a considerable period after the commencement of habitual night work, and the diurnal rhythm of urinary flow survives a uniform intake of fluid throughout

[1] Kellicott (1904).
[2] See Blumenfeld (1939), Halberg (1953).
[3] Maslenikow (1904) ; see Duke-Elder (1952).   See also p. 560.

the 24 hours and the reversal of the sleep habit. Similarly, the normal phasic swing of the ocular tension is independent of the blood pressure, osmotic changes in the blood, illumination, the time of meals, feasting or fasting, or bodily activity ; the rhythm can only be altered by a complete reversal of the sleep habit established over some time (Raeder, 1925) (Fig. 8). The fact that such rhythms as the diurnal variation in temperature in the new-born infant, or the 24-hour periodicity of activity of the newly hatched chick kept under constant laboratory conditions (Aschoff and Meyer-Lohmann, 1954), are apparent from birth indicates that at any rate some of these fluctuations are fundamental and innate—an environmental influence of biological value which has with time so impressed itself upon organisms that it has become hereditarily transmitted.

Some of these diurnal variations, however, seem to depend on environmental stimulation. Thus the cyclic variation in the eosinophil count of mice was found by Halberg and his associates (1954) to be abolished by the enucleation of both eyes, although it partially returned some 5 months after blinding. The rhythm of diurnal activity of the minnow, *Phoxinus*, is said to be reversed on blinding (Jones, 1956). In man the variation in eosinophilia depends to some extent on activity (Halberg *et al.*, 1953), and illumination has a subsidiary influence (Appel and Hansen, 1952 ; Landau and Feldman, 1954).

The same *rhythms in general activity* are seen in Invertebrates, among which Insects provide some of the most dramatic examples (see Welsh, 1938 ; Wigglesworth, 1953). The habit of nocturnal activity and diurnal catalepsy shown by the stick-insect, *Dixippus*, for example, persists unchanged for some days in permanent darkness or in reversed illumination (Steiniger, 1933), a daily rhythm which applies to such activities as defæcation and oviposition (Kalmus, 1938). The same general tendency is seen in many other species.[1] The rhythm may, indeed, be acquired in the larval stage in response to diurnal changes of light, persist through the pupal stage and determine the activity in the adult.[2] A metabolic rhythm in which the CO_2 is higher (sometimes by 30%) during the night even although the animal is kept in constant darkness is seen in Crustaceans.[3] A similar diurnal rhythm of the opening and closing of the valves of the clam, *Venus mercenaria*, persists under laboratory conditions of constant illumination ; it is interesting that in this case there is also a persistent tidal rhythm and the interaction of the two produces a lunar cycle (Bennett, 1954). A similar phenomenon whereby an endogenous tidal rhythm displaces

[1] It is seen in some forest insects (Lutz, 1932 ; Park and Keller, 1932), mayflies (Harker, 1953), cockroaches (Gunn, 1940 ; Mellanby, 1940 ; Harker, 1954), millipedes (Park, 1935), and other species.
[2] In *Leptinotarsa*—Grison (1943).
[3] The crab, *Carcinus*—Henkes (1952) ; the woodlouse, *Oniscus*—Cloudesley-Thompson (1952).

the endogenous diurnal rhythm, is seen in the fiddler-crab, *Uca* (Brown *et al.*, 1952–54) and also in marine forms of the protozoon, *Euglena* (Pohl, 1948). A lunar as well as a diurnal rhythm of activity and oxygen consumption is seen in the earthworm, *Lumbricus* (Ralph, 1957), and in crayfish such as *Cambarus virilis* (Guyselman, 1957). The timing of these rhythms with respect to the solar day when the animals are kept in darkness has been altered by lowering the temperature (the fiddler-crab, *Uca*, Stephens, 1957).[1]

THE SEXUAL CYCLE OF ANIMALS, as with flowering in plants, is also frequently determined by the influence of light as expressed by the gradual change in the length of day in the annual solar cycle ; in this way the onset of the breeding season becomes rhythmic as though there has been implanted on the central nervous and hormonal systems a pattern of behaviour automatic and innate so that it can only be altered experimentally by a prolonged disturbance of the natural phases. In some species, it is true, particularly in Invertebrates and the lower Vertebrates, other factors such as temperature and humidity also enter into the question, but controlled experiments have shown that these and other extraneous circumstances, such as physical activity and feeding, are often secondary and in many cases can be excluded and that the most important factor is the *duration* of the period of light—not its intensity or wave-length. These phenomena have been particularly studied in animals inhabiting the northern hemisphere. Spring in these regions with its increasing days is the appropriate season for reproduction if survival is to be maintained, and in those species with a long gestation period, the shortening days of autumn are most suitable for mating. In general, when species with a breeding periodicity of this type are experimentally subjected to artificially lengthening days in late autumn or winter, they can be brought from their sexually quiescent condition into the ripeness typical of spring, while conversely, if the lengthening days of spring are artificially curtailed, sexual regression occurs ; indeed, it is possible by these means to bring some types (birds, for example) into breeding condition several times in the year—a change which applies not only to anatomical considerations such as the development of the gonads, but also to those habits and modes of conduct which are essentially sexual in origin such as (in birds) singing and migration.

Such phenomena have been investigated in many species of Invertebrates, Fishes, Amphibians, Reptiles, Birds and Mammals.

In the INVERTEBRATES, even among Protozoa, Ehret (1951) found that the diurnal rhythm of the mating reaction of *Paramœcium bursaris* persists for several days in complete darkness and can be altered by varying the illumination

[1] Compare p. 22.

at different periods of the daily cycle. In snails, a prolongation of the diurnal period of light beyond 13 hours stimulates egg-laying, while periods of 11 hours or less inhibit it (Jenner, 1951) ; it is interesting that short intervals of illumination during the dark periods of a short-day cycle stimulate egg-laying, showing that, as with short-day plants, the length of the dark period is an essential feature in the stimulus. Similarly the strawberry-root louse, *Aphis forbesi*, can be made to breed in midsummer instead of February by artificially curtailing the summer days (Marcovitch, 1923). A more dramatic influence is seen in the plant-louse, *Psylla* : individuals hatched in autumn differ from those hatched in spring but the winter-type can be produced in spring by subjecting the larvæ to an artificial diurnal rhythm in which the period of light is shortened (Bonne-maison and Missonnier, 1955).

Among FISHES, temperature has been shown to be a potent factor, but it has been demonstrated that the reproductive cycle of the trout can be photoperiodically determined (Hoover and Hubbard, 1937) ; similarly the activity of the gonads of certain AMPHIBIANS such as the clawed toad, *Xenopus lœvis*, (Shapiro and Shapiro, 1934) and REPTILES such as the lizard, *Anolis carolinensis* (Clausen and Poris, 1937), has been altered by means of artificial illumination.

BIRDS show more dramatic changes than most species, and these have received much attention probably because of their obvious habits of migration and singing, the sexual connection of which has been recognized since the time of Aristotle. For long the annual rhythm of the avian gonad was held to be determined by temperature. It is true that in the old custom of " muit " long prevalent in Holland, birds were brought into song in autumn by confining them in the dark in the middle of June and exposing them to light in September, and that by the similar ancient practice of "yogai", Japanese pet birds were brought into singing condition in January by providing them with extra hours of illumination in the autumn (Miyazaki, 1934). In this respect, however, zoologists waited on botanists ; for although Schafer (1907) had suggested that migration, because of its accurate periodicity, must depend on the mathematically regular changes in length of day rather than on the notoriously irregular variations in climate, it was not until the work of Garner and Allard on the influence of photoperiodism on the flowering of plants had been published in 1920 [1] that Eifrig (1924) propounded a similar hypothesis to explain the habits of birds, a conception eventually proved by the experimental work of Rowan (1925–38).

Rowan's classical work was on the junco finch, which migrates from wintering grounds in the middle United States to Alberta ; he found that even if the birds were retained in an aviary in Alberta, provided they were subjected to the artificial increase of daily illumination (2-3 mins.) that they would have experienced in the early spring in the States, their gonads matured and they burst into song in December despite the temperature of the Canadian winter (minimum, −50° F). These results were confirmed by Bissonnette (1930–32) in Connecticut experimenting on starlings ; and it is now amply established that among many birds of the temperate zones of the northern hemisphere, the testes of which normally reach a peak of activity as the days lengthen in late spring, an artificial increase of the period of illumination over some time brings on a precocious activity, while a curtailment or denial of light brings on the reverse changes.[2] On the other hand, confinement of male parrots in continuous

---

[1] p. 10.
[2] See among others : junco, *Junco hyemalis*—Rowan (1929), Jenner and Engels (1952) ; starling, *Sturnus vulgaris*—Bissonnette (1930–32) ; pheasant—Martin (1935), B. C. Clark *et al.* (1936–37) ; house sparrow, *Passer domesticus*—Riley (1936), Kirschbaum and Ringoen (1936) ; white-throated sparrow—Jenner and Engels (1952) ;

darkness for a month results in testicular activity, while continuous illumination produces a resting state (Vaugien, 1952). The same result follows a " natural " change in the day–night cycle, for if the birds in the northern hemisphere are transported to the southern, their breeding season is reversed (Rowan, 1926) ; while in regular migrants across the equator the stimulus for the recrudescence of sexual activity and enlargement of the gonads is the shortening of the days in March in southern lands (Rowan, 1938), an inherent habit which can only be broken if such species are retained for several years in the southern hemisphere and prevented from migrating (Marshall, 1937 ; Baker and Ranson, 1938). It would therefore seem established that the sexual cycle and the migration of birds, rhythms which have become innate, are determined essentially by photo-period, although it is to be remembered that periods of darkness may have an influence equal to or even more potent than light (Hammond, 1953 ; Kirk-patrick and Leopold, 1953), while temperature also has an adjuvant effect (Bissonnette, 1937 ; Farner and Mewaldt, 1952–53 ; Wilson et al., 1956).

Similarly among MAMMALS, male ferrets,[1] mice [2] and ewes [3] can be brought into œstrus in winter when normally they are in anœstrus by subjecting them to rhythmic periods of increased illumination for 2 months or more, while the gonads of the field-mouse have been shown to diminish by exposing the animals to increased periods of darkness (Baker and Ranson, 1932).[4] As would be expected, these changes do not apply to non-seasonable animals [5] or those that reach sexual maturity during hibernation [6] or æstivation.[7] Among those animals in which it is operative, however, and particularly among those with migratory habits, the periodic behaviour thus induced sometimes assumes legendary exactitude, a fact commented on since the days of Pliny ; the cuckoo arrives in England on " Cuckoo Day ", the early stream of swifts is expected to arrive on the last three days of April and the big arrival on May 24th, while in the late autumn each year the male markhor is said to descend from the high Hindu Kush into the valleys to meet the females on December 14th precisely, and the rut begins (Burton, 1951).[8]

The mechanism of the action of light in these photoperiodic activities varies, but in general is mediated through hormones the activity of which is largely determined by stimulation through the eyes. This complex matter will be discussed subsequently,[9] but at this stage it is convenient to note that in Crustaceans, several hormones are

white-crowned sparrow—Farner et al. (1953) ; dove, Zenaidura macroura—Cole (1933) ; Japanese white-eye, Zosterops—Miyazaki (1934) ; duck—Benoit (1934–35), Radnót (1953–55) ; quail—B. C. Clark et al. (1936–37), Hammond (1953) ; fowl—Radnót (1955), Radnót and Orbán (1956).

[1] Bissonnette (1932), Marshall and Bowden (1934–36), Hart (1951), Thomson (1954).

[2] Whitaker (1936).

[3] Hafez (1951).

[4] For further details of the mechanism involved, see p. 559.

[5] Guinea-pigs—Dempsey et al. (1933–34) ; rabbit—Smelser et al. (1934).

[6] Squirrel—Wells (1934–35), Johnson and Gann (1933).

[7] Alexander and Bellerby (1935–38), Bellerby (1938).

[8] In a similar manner the palolo (Polychæte) worms of the South Pacific shed their eggs or sperms in countless millions, sufficient to give the sea the appearance of vermicelli soup, at a specific time. These are eminently edible, and the natives of Samoa have learned to expect a great feast precisely at dawn one week after the November full moon.

[9] p. 547.

secreted in the eye-stalks and central nervous system and stored in the sinus glands and these regulate ovarian maturation and testicular development. In Vertebrates the pituitary gland exerts an analogous gonadotropic influence under the control of its associated centres in the diencephalon which in turn receive their stimulation from the retinæ.[1]

PHOTOPERIODISM IN PIGMENT MIGRATION. Pigment, the function of which is so closely related to light, would be expected to be peculiarly susceptible to its influence ; in its migration to cause colour changes,[2] rhythmic diurnal variations of a primitive type frequently survive. That a persistent rhythm of this kind occurs in the *migration of the retinal pigment* [3] in the eyes of a noctuid moth, *Plusia gamma*, was first reported by Kiesel (1894), an observation which has been repeated in several Arthropods with compound eyes and shown to persist even although the animals are kept for a considerable time in conditions of constant illumination and temperature or are reared from the larval stage in the laboratory in constant darkness.[4] The effect is well seen in the crayfish in the eye of which there is a tapetal reflecting pigment [5] obscured during the day but unprotected at night so that the eye then assumes an orange glow ; even if the animal is kept in conditions of constant darkness and temperature, the diurnal rhythm of orange " eye-shine " at night will continue automatically for months (Welsh, 1941). Similar rhythms affecting the retinal and tapetal pigments are seen in many species of Crustaceans (Henkes, 1952), and it would appear that these pigmentary movements are under hormonal control, a subject which will be discussed in a later chapter.[6]

Closely associated with the movements of the retinal pigment are the corresponding *movements of the rods and cones* of some of the lower Vertebrates. As with the retinal pigment, these movements are usually a direct response to light, but evidence was produced by Welsh and Osborn (1937) that these elements in the eye of the catfish underwent a diurnal rhythmic change of position even although the fish were kept in constant darkness ; the mechanism of this rhythmic activity is unknown.

The *integumentary chromatophore system* frequently shows similar cyclic activities. The responses of this pigmentary system to light are complex and will be studied in a later section [7] ; it is sufficient to note here that many animals show a rhythmic day–night change of colour wherein they pale by night and darken by day, a rhythm which may persist for a considerable time if they are kept in conditions of constant

---

[1] p. 556. [2] p. 82. [3] p. 170.
[4] In the beetle, *Bolitotherus cornutus*—Park and Keller (1932) ; and a number of Crustaceans such as fresh-water shrimps, *Macrobrachium* and others—Welsh (1930) ; crayfish, *Cambarus*—Bennitt (1932), Welsh (1939–41) ; crab, *Uca*—Smith (1948); Brown *et al.* (1951–54), Kleinholz (1937) ; and so on.
[5] p. 165. [6] p. 547. [7] p. 82.

illumination or darkness.[1]   Gamble and Keeble (1900) first reported
such a cyclic diurnal colour change which persisted under constant
illumination in the prawn, *Hippolyte varians*, but although subsequent
work has not confirmed this particular observation (Kleinholz and
Welsh, 1937), the phenomenon has been demonstrated in a number of
species of both Invertebrates and the lower Vertebrates.[2]   In some
cases these diurnal changes are largely masked by other factors such
as pigmentary changes adopted to mimic the background,[3] but the

FIGS. 9 AND 10.—DIURNAL RHYTHMS IN THE PIGMENT OF THE CRAB, *UCA*.

The black and white segments at the top of the graphs and in the corre-
sponding position immediately below the graphs represent the normal rhythm
of daylight and darkness.   The second tier of markings below indicate the
experimental variations introduced.   Ordinates : the degree of pigmentation
expressed in Hogben and Slome's scale, 1 representing complete concentration
of pigment, *i.e.*, the light phase, and 5 its complete dispersal, *i.e.*, the dark
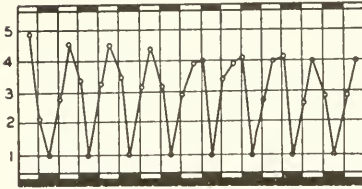phase (Brown and Webb, 1949).

FIG. 9.—The normal diurnal rhythm of
pigmentation (dark through the day
and light at night) is seen to continue
uninterruptedly after the animal has
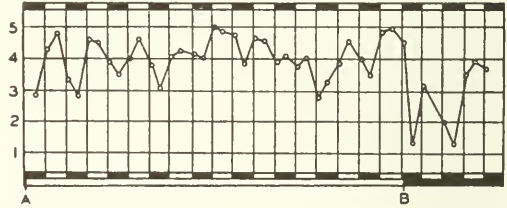been 9 days in darkness.

FIG. 10.—At the beginning of the experiment *Uca*
was exposed to continuous illumination (80 foot
candles) from A to B.   There is a decrease in
amplitude and then a gradual inhibition of the
rhythm until eventually the chromatophores
change irregularly.   At B the animals were trans-
ferred to continuous darkness, whereupon the
chromatophores became almost completely con-
centrated and thereafter a normal 24-hour rhythm
in phase with solar day–night was observed.

effect of the underlying rhythm is seen in the increased rapidity of
these secondary responses when they are in phase with the primary
diurnal cycle and their sluggishness when they antagonize it.   In other
animals the fundamental rhythm is preponderant so that secondary

[1] 8 to 9 weeks in the beach-louse, *Idotea*—Menke, (1911) ; 18 days in the lizard,
Anolis—Rahn and Rosendale (1941) ; and so on.
[2] Several Invertebrates such as the black sea-urchin, *Diadema antillarum*—Millott
(1950) ; many Crustaceans in addition to *Idotea* : the prawn, *Palæmon*—Keeble
and Gamble (1904), the fiddler crab, *Uca*—Abramowitz (1937), the Isopod, *Ligia*—
H. Smith (1938) ; a few Insects such as the stick-insect, *Dixippus*—Schleip (1910).
Compare, for example, Figs. 64–68.
A number of Vertebrates, particularly in their youth (Cf. Figs. 70 and 73) ; Cyclo-
stomes such as the lampern, *Lampetra*—Young (1935), Jones (1955) ; Amphibians
such as salamander larvæ and frogs—Hooker (1914), Welsh (1938) ; and Reptiles such
as the American horned " toad", *Phrynosoma*—Redfield (1918), the lizard, *Anolis*—
Rahn and Rosendale (1941), and the chameleon—Zoond and Eyre (1934).
[3] p. 82.

environmental factors have but a slightly modifying effect upon it. A good example of this is the crab, *Uca*, the responses of which have been extensively studied [1]; the diurnal rhythm of its colour change is remarkably constant, and within wide limits is independent of influences such as humidity and temperature, but the influence of metabolism on the phenomenon is exemplified in its retardation with a lengthening of the cycle on exposure to cold below $6°$ C (Figs. 9 and 10).

This rhythmic mechanism operating to disperse pigment in the day phase and concentrate it in the night phase of the cycle would seem to be adaptive in function, partly protective against deleteriously bright illumination, partly thermo-regulatory. In all species in which these colour changes occur the controlling factors are hormones differing in nature from the retinal pigment hormones but, like them, elaborated in Invertebrates by the neuro-secretory system and in Vertebrates by the neurohypophysis both of which show an endogenous rhythm. This question will be discussed in a subsequent chapter.[2]

The seasonal changes in colour of the coats of many Birds and Mammals are analogous phenomena which are also to some extent determined by photoperiod. It is well known that the majority of common birds undergo a post-nuptial moult immediately after the breeding season and a second pre-nuptial moult in spring when they assume their wedding robes. The times at which birds assume their nuptial and winter plumages are governed by a number of factors, the most potent of which is a pituitary hormone with an inherent cyclic activity depending in part on the length of the daily light periods (Witschi, 1935 ; Brown and Rollo, 1940 ; Lesher and Kendeigh, 1941 ; Kobayashi and Okubo, 1955). A similar control operates the seasonal moulting of many northern Birds and Mammals the colours of which change from a summer brown to a winter white.

Among Birds, the ptarmigan of the northern tundra or the high mountains (Höst, 1942), and among Mammals the varying hare (Lyman, 1943) and the ermine (Bissonnette and Bailey, 1944) are good examples of this ; these phenomena of moulting and change of colour can be induced out of season by artificially varying the diurnal periods of illumination. It is interesting that in the hare the eyes seem to be the normal receptors of this stimulus since if these are masked the changes do not occur. The pituitary seems to be the only endocrine gland involved since castration and thyroidectomy in the hare are without effect (Lyman, 1943), while hypophysectomy abolishes the cyclic moulting of ferrets (Bissonnette, 1935–38).

PHOTOPERIODICITY IN BIOLUMINESCENCE. The ability to produce light occurs widely but sporadically among bacteria, fungi, and most types of animals

---

[1] Abramowitz (1937–38), Brown and Webb (1947–49), Brown and Sandeen (1948), Webb (1950).

[2] p. 547.

from the Protozoa to the chordate Fishes ; it is a phenomenon which will be discussed in greater detail later.[1] It is well known that in most animal species the reaction appears intermittently in response to various stimuli, light having a general inhibitory effect, sometimes directly by destruction of the photogenic material in the light-producing cells, sometimes indirectly, acting through a central regulatory mechanism, hormonal or nervous (Harvey, 1925 ; Heymans and Moore, 1925 ; Moore, 1926). In the present connection it is interesting to remark that in a number of species there is a daily rhythm in the capacity to luminesce, a phenomenon seen even in unicellular Dinoflagellates (Harvey, 1952); and in some types of Insects [2] and perhaps in some jellyfish [3] and a balanoglossid [4] the rhythm may persist for several days so that the animal will light up at the normal time of the day even if kept in constant darkness.

A final expression of DIURNAL RHYTHMICITY is seen IN THE TIME-MEMORY OF SOME ARTHROPODS AND BIRDS. This curious and interesting phenomenon was first demonstrated in bees by von Stein-Beling (1929-35) who showed that within a cycle of 24 hours bees could be trained to visit an artificial feeding station at regular occasions throughout the day, a habit which could not be maintained if an attempt were made to operate within a cycle greater or less (e.g., 19 hours) than the normal solar diurnal rhythm. This ability has since been verified by a number of observers [5] and it has been confirmed in wasps [6] and ants [7] as well as in the Amphipod *Talitrus*.[8] So far as honey-gathering insects are concerned it is probably connected with the hours at which flowers periodically offer their nectar, but other activities are also involved. Thus Kalmus (1935) found that if larvæ and pupæ of *Drospohila*—an insect which normally emerges from its pupa before dawn—were kept in darkness during the daytime and artificially illuminated for 3 consecutive nights, the flies emerged in the evenings, remembering the time of the artificial dawn even although kept in perpetual darkness. Such time-keeping mechanisms or " internal clocks " are of wide occurrence, keeping time automatically with considerable precision, but regularly set and kept in pace by light stimuli. It would seem that the rhythm is influenced metabolically since it can be retarded by low temperatures (under 5° C, Kalmus, 1934) or by drugs ; thus Grabensberger (1934) found that by feeding quinine to trained bees, arrival at the sources of food was retarded, while it was accelerated by iodothyroglobin.

A similar apparently innate time-sense can be demonstrated in some Birds, which we will see [9] assumes considerable importance in their extraordinary ability to navigate over long distances. Thus Stein (1951) found that passerine birds could be trained to come to feed at a particular hour each day provided only that a 24-hour cycle were maintained, an acquirement retained for some considerable time although the birds were kept in constant illumination or had irregular feeding times ; experimental exposure to irregular periods of light and darkness, however, tends to disorientate this sense when it is used as an aid to navigation (Matthews, 1953-55).

[1] p. 736.
[2] Such as the firefly, *Photinus*—Buck (1937).
[3] *Pelagia*—Heymans and Moore (1924-25).
[4] *Ptychodera*—Crozier (1920).
[5] Wahl (1933), Kalmus (1934-54), Kleber (1935), v. Frisch (1937), and others.
[6] Verlaine (1929).
[7] Grabensberger (1934).
[8] Pardi and Papi (1952-53).
[9] p. 63.

Abramowitz. *Biol. Bull.*, **72**, 344 (1937). *J. exp. Zool.*, **76**, 407 (1938).
Abramowitz and Abramowitz. *Biol. Bull.*, **74**, 278 (1938).
Achelis and Nothdurft. *Pflügers Arch. ges. Physiol.*, **241**, 651 (1939).
Alexander and Bellerby. *J. exp. Biol.*, **12**, 306 (1935) ; **15**, 74 (1938).
Appel and Hansen. *Dtsch. Arch. klin. Med.*, **199**, 530 (1952).
Aschoff. *Pflügers Arch. ges. Physiol.*, **255**, 189, 197 (1952).
Aschoff and Meyer-Lohmann. *Pflügers Arch. ges. Physiol.*, **260**, 170 (1954).
Baker and Ranson. *Proc. roy. Soc. B*, **110**, 313 ; **112**, 39 (1932) ; **113**, 486 (1933).
Proc. zool. Soc. Lond., **108A**, 101 (1938).
Bellerby. *J. exp. Biol.*, **15**, 82 (1938).
Bennett. *Biol. Bull.*, **107**, 174 (1954).
Bennitt. *Physiol. Zool.*, **5**, 65 (1932).
Benoit. *C. R. Acad. Sci.* (Paris), **199**, 1671 (1934) ; **201**, 359 (1935).
C. R. Soc. Biol. (Paris), **118**, 664, 669, 672 ; **120**, 136, 905, 1326 (1935).
Bissonnette. *Amer. J. Anat.*, **45**, 289 ; **46**, 477 (1930).
J. exp. Zool., **58**, 281 (1931).
Physiol. Zool., **4**, 542 (1931) ; **5**, 92 (1932).
Proc. roy. Soc. B., **110**, 322 (1932).
Anat. Rec., **63**, 159 (1935).
Wilson Bull., **49**, 241 (1937).
Endocrinology, **22**, 92 (1938).
Bissonnette and Bailey. *Ann. N.Y. Acad. Sci.*, **45**, 221 (1944).
Blumenfeld. *Science*, **90**, 446 (1939).
Bonnemaison and Missonnier. *C. R. Acad. Sci.* (Paris), **240**, 1277 (1955).
Browman. *J. exp. Zool.*, **75**, 375 (1937).
Brown, Fingerman and Hines. *Biol. Bull.*, **106**, 308 (1954).
Brown, Fingerman, Sandeen and Webb. *J. exp. Zool.*, **123**, 29 (1952).
Brown and Rollo. *The Auk*, **57**, 485 (1940).
Brown and Sandeen. *Physiol. Zool.*, **21**, 361 (1948).
Brown, Sandeen and Webb. *Anat. Rec.*, **111**, 569 (1951).
Brown and Webb. *Anat. Rec.*, **99**, 674 (1947) ; **101**, 733 (1948).
Physiol. Zool., **21**, 371 (1948) ; **22**, 136 (1949).
Buck. *Physiol. Zool.*, **10**, 412 (1937).
Burton. *Illust. Lond. News*, **223**, 996 (1951).
Clark, B. C., Leonard and Bump. *Science*, **83**, 268 (1936) ; **85**, 339 (1937).
Clausen and Poris. *Anat. Rec.*, **69**, 39 (1937).
Cloudesley-Thompson. *J. exp. Biol.*, **29**, 295 (1952).
Cole. *The Auk*, **50**, 284 (1933).
Colton. *J. Mammol.*, **14**, 309 (1933).
Cooper. *J. invest. Derm.*, **2**, 289 (1939).
Crozier. *Anat. Rec.*, **20**, 186 (1920).

Davis. *J. anim. Ecol.*, **2**, 232 (1932).
Dempsey, Young, Myers and Jennison. *Anat. Rec.*, **57**, Suppl., 29 (1933) ; **58**, Suppl., 59 (1934).
Amer. J. Physiol., **109**, 307 (1934).
von Domarus. *Dtsch. Arch. klin. Med.*, **171**, 333 (1931).
Duke-Elder. *Amer. J. Ophthal.*, **35**, 1 (1952).
Ehret. *Anat. Rec.*, **111**, 528 (1951).
Eifrig. *The Auk*, **41**, 439 (1924).
Farner and Mewaldt. *Anat. Rec.*, **113**, 612, (1952).
Experientia, **9**, 219 (1953).
Farner, Mewaldt and Irving. *Science*, **118**, 351 (1953).
von Frisch. *Z. Tierpsychol.*, **1**, 9 (1937).
Gamble and Keeble. *Quart. J. micr. Sci.*, **43**, 589 (1900).
Gerritzen. *Acta med. scand.*, **89**, 101 (1936) ; Suppl., **108**, 121 (1940).
Gloster and Greaves. *Brit. J. Ophthal.*, **41**, 513 (1957).
Grabensberger. *Z. vergl. Physiol.*, **20**, 1, 338 (1934).
Grison. *C. R. Acad. Sci.* (Paris), **217**, 621 (1943).
Gunn. *J. exp. Biol.*, **17**, 267 (1940).
Guyselman. *Physiol. Zool.*, **30**, 70 (1957).
Hafez. *Experientia*, **6**, 423 (1951).
Halberg. *J. Lancet*, **73**, 20 (1953).
Halberg, Engel, Treloar and Gully. *Arch. Neurol. Psychiat.*, **69**, 462 (1953).
Halberg, Levy and Visscher. *Fed. Proc.*, **12**, 59 (1953).
Halberg and Visscher. *Proc. Soc. exp. Biol. Med.*, **75**, 846 (1950).
Amer. J. Physiol., **171**, 732 (1952).
Halberg, Visscher and Bittner. *Amer. J. Physiol.*, **179**, 229 (1954).
Hammond. *Science*, **117**, 389 (1953).
Harker. *J. exp. Biol.*, **30**, 525 (1953).
Nature (Lond.), **173**, 689 (1954).
Biol. Rev., **33**, 1 (1958).
Hart. *J. exp. Biol.*, **28**, 1 (1951).
Harvey. *J. gen. Physiol.*, **7**, 679 (1925).
Bioluminescence, N.Y. (1952).
Henkes. *J. exp. Biol.*, **29**, 178 (1952).
Herter. *Z. vergl. Physiol.*, **20**, 511 (1934).
Heymans and Moore. *J. gen. Physiol.*, **6**, 273 (1924) ; **7**, 345 (1925).
Hill and Parkes. *Proc. roy. Soc. B*, **115**, 14 (1934).
Hooker. *Amer. J. Anat.*, **16**, 237 (1914).
Hoover and Hubbard. *Copeia*, 206 (1937).
Höst. *The Auk*, **59**, 388 (1942).
Hume. *J. clin. Invest.*, **28**, 790 (1949).
Jenner. *Anat. Rec.*, **111**, 512 (1951).
Jenner and Engels. *Anat. Rec.*, **113**, 548 (1952).
Johnson. *J. Mammol.*, **7**, 245 (1926).
Johnson and Gann. *Anat. Rec.*, **57**, Suppl., 28 (1933).
Jones. *J. exp. Biol.*, **32**, 492 (1955) ; **33**, 271 (1956).

Kalmus. *Z. vergl. Physiol.*, **20**, 405 (1934); **25**, 494, 798 (1938).
Biol. generalis, **11**, 93 (1935).
Nature (Lond.), **173**, 657 (1954).
Keeble and Gamble. *Philos. Trans. B*, **196**, 295 (1904).
Kellicott. *Bull. Torrey Bot. Club*, **31**, 529 (1904).
Kiesel. *S. B. Akad. Wiss. Wien*, **103**, 97 (1894).
Kirkpatrick and Leopold. *Science*, **117**, 390 (1953).
Kirschbaum and Ringoen. *Anat. Rec.*, **64**, 453 (1936).
Kleber. *Z. vergl. Physiol.*, **22**, 221 (1935).
Kleinholz. *Biol. Bull.*, **72**, 24 (1937).
Kleinholz and Welsh. *Nature* (Lond), **140**, 851 (1937).
Kleitman. *Sleep and Wakefulness*, Chicago (1939).
Physiol. Rev., **29**, 1 (1949).
Kleitman, Titelbaum and Feiveson. *Amer. J. Physiol.*, **121**, 495 (1938).
Kleitman, Titelbaum and Hoffman. *Amer. J. Physiol.*, **119**, 48 (1937).
Kobayashi and Okubo. *Science*, **121**, 338 (1955).
Kowalski. *Folia biol.* (Warsaw), **3**, 55 (1955).
Landau and Feldman. *Acta endocr.* (Kbh.), **15**, 53 (1954).
van Leijden. *Proc. Sec. Sci. kon. ned. Akad. Wet.* (Amsterdam), **19**, 38 (1917).
Lesher and Kendeigh. *Wilson Bull.*, **53**, 169 (1941).
Lewis and Lobban. *J. Physiol.*, **133**, 670 (1956).
Lewis, Lobban and Shaw. *J. Physiol.*, **133**, 659 (1956).
Lutz. *Amer. Mus. Nov.*, **550**, 1 (1932).
Lyman. *Bull. Mus. comp. Zool. Harvard*, **93**, 391 (1943).
Marcovitch. *Science*, **58**, 537 (1923).
Marshall. *Nature* (Lond.), **129**, 344 (1932).
Philos. Trans. B, **226**, 423 (1936).
Proc. roy. Soc. B, **122**, 413 (1937).
Marshall and Bowden. *J. exp. Biol.*, **11**, 409 (1934) ; **13**, 383 (1936).
Martin. *Game Breeder and Sportsman*, **39**, 95 (1935).
Maslenikow. *Vestn. Oftal.*, **21**, 237 (1904).
Matthews. *J. exp. Biol.*, **30**, 243 (1953) ; **32**, 59 (1955).
Mellanby. *J. exp. Biol.*, **17**, 278 (1940).
Menke. *Pflügers Arch. ges. Physiol.*, **140**, 37 (1911).
Menzel. *Z. Altersforschung*, **6**, 26, 104 (1952).
Meyer. *Z. Zellforsch.*, **40**, 228 (1954).
Millott. *Biol. Bull.*, **99**, 329 (1950).
Mills. *J. Physiol.*, **113**, 528 (1951).
Mills and Stanbury. *J. Physiol.*, **117**, 22 (1952).
Mills, Thomas and Yates. *J. Physiol.*, **125**, 466 (1954).

Miyazaki. *Sci. Rep. Tohoku Univ., Biol. Ser.*, **9**, 183, 427 (1934).
Moore. *Amer. J. Physiol.*, **76**, 112 (1926).
Pardi and Papi. *Naturwissenschaften*, **39**, 262 (1952).
Z. vergl. Physiol., **35**, 459 (1953).
Park. *Ecology*, **16**, 152 (1935).
Park and Keller. *Ecology*, **13**, 335 (1932).
Pohl. *Naturforsch.*, **3b**, 367 (1948).
Porter. *Amer. J. Physiol.*, **172**, 515 (1953).
Radnót. *Orv. Hetil.*, **94**, 262 (1953).
Ophthalmologica, **127**, 422 (1954).
Acta morphol. hung., **5**, 369 (1955).
Radnót and Orbán. *Acta med. Budapest*, **8**, 369 (1956).
Raeder. *Klin. Mbl. Augenheilk.*, **74**, 424 (1925).
Rahn and Rosendale. *Proc. Soc. exp. Biol. Med.*, **48**, 100 (1941).
Ralph. *Physiol. Zool.*, **30**, 41 (1957).
Redfield. *J. exp. Zool.*, **26**, 275 (1918).
Renbourn. *J. Hyg.*, **45**, 455 (1947).
Richter. *Comp. Psychol. Monogr.*, **1**, 1 (1922).
Riley. *Proc. Soc. exp. Biol. Med.*, **34**, 331 (1936).
Anat. Rec., **67**, 327 (1937).
Rowan. *Nature* (Lond.), **115**, 494 (1925) ; **119**, 351 (1927) ; **122**, 11 (1928).
Proc. Boston Soc. nat. Hist., **38**, 147 (1926) ; **39**, 151 (1929).
Proc. nat. Acad. Sci. (Wash.), **16**, 520 (1930) ; **18**, 639 (1932).
Kongressbericht d. Weltgeflügelkongresses, **1**, vi, 142 (1936).
Biol. Rev., **13**, 374 (1938).
Proc. zool. Soc. Lond., **108A**, 51 (1938).
von Sallmann and Lowenstein. *Amer. J. Ophthal.*, **39** (2), 11 (1955).
Schäfer. *Nature* (Lond.), **77**, 159 (1907).
Schleip. *Zool. Jb., Abt. Zool. Physiol.*, **30**, 45 (1910).
Shapiro and Shapiro. *J. exp. Biol.*, **11**, 73 (1934).
Smelser, Walton and Whetham. *J. exp. Biol.;* **11**, 352 (1934).
Smith, H. *Proc. roy. Soc. B*, **125**, 250 (1938).
Smith, R. I. *Biol. Bull.*, **95**, 169 (1948).
Stein. *Z. vergl. Physiol.*, **33**, 387 (1951).
von Stein-Beling. *Z. vergl. Physiol.*, **9**, 259 (1929).
Biol. Rev., **10**, 18 (1935).
Steiniger. *Z. Morph. Oekol. Tiere*, **26**, 591 ; **28**, 1 (1933).
Stephens. *Physiol. Zool.*, **30**, 55 (1957).
Thomson. *Proc. roy. Soc. B*, **142**, 146 (1954).
Vaugien. *C. R. Acad. Sci.* (Paris), **234**, 1489 (1952).
Verlaine. *Bull. Ann. Soc. Ent. Belg.*, **69**, 115 (1929).
Wahl. *Z. vergl. Physiol.*, **18**, 709 (1933).
Webb. *Physiol. Zool.*, **23**, 316 (1950).
Wells. *Anat. Rec.*, **60**, Suppl., 53 (1934) ; **62**, 409 (1935).

Welsh. *Proc. nat. Acad. Sci.* (Wash.), **16,** 386 (1930).
Quart. Rev. Biol., **13,** 123 (1938).
Biol. Bull., **77,** 119 (1939).
J. exp. Zool., **86,** 35 (1941).
Welsh and Osborn. *J. comp. Neurol.,* **66,** 349 (1937).
Whitaker. *Proc. Soc. exp. Biol. Med.,* **34,** 329 (1936).

Wigglesworth. *Principles of Insect Physiology,* London, 5th Ed. (1953).
Wilson, Woodard and Abplanalp. *Biol. Bull.,* **111,** 415 (1956).
Witschi. *Wilson Bull.,* **47,** 177 (1935).
Young. *J. exp. Biol.,* **12,** 254 (1935).
Zoond and Eyre. *Philos. Trans. B,* **223,** 27 (1934).

Fig. 11.—Jacques Loeb (1859–1924).

It is good to have Jacques Loeb and Samuel Mast on the same page—the two great protagonists of the mechanistic and the vital interpretations of animal behaviour, both of whom propagated their views with unusual vigour—the first an intellectual descendant of Descartes, the second of Leibnitz and Goethe.

Jacques Loeb was assistant in physiology at the University of Würzburg where he was much influenced by his botanical colleague, Sachs ; he then went to Strasbourg, and thereafter, going to America, became professor of physiology at the Universities of Chicago and California, and finally head of the Division of General Physiology at the Rockefeller Institute for Medical Research in New York. I am indebted to that institution for his photograph. Samuel O. Mast, Professor of Zoology in Johns Hopkins University, was one of the band of men who have made Baltimore outstanding among the centres of learning in the world.

Fig. 12.—Samuel O. Mast (1871–1947).