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PHOTOTAXIS[1]

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Since this review was written, Vol. XVII, Part 1, of the Encyclopedia of Plant Physiology has been published. This volume contains three excellent reviews on phototaxis: "Chloroplastenbewegung", by W. Haupt (pp. 278-317), "Die Phototaxis der Algen", by W. Haupt (pp. 318-370), and "Phototaxis of purple bacteria", by R. K. Clayton (pp. 371-387).

INTRODUCTION

Light, through photosynthesis, is directly or indirectly the chief source of energy for living organisms. A number of light—controlled processes other than photosynthesis have been studied in plants: photoperiodic control of flowering, red and infrared light effects on germination, etc. We are beginning to realize the many-faceted importance of light in relating the response of an organism to its environment.

Phototaxis, the movement of an organism in response to a light stimulus, as opposed to phototropism, or light-oriented growth, has received little attention in recent years. Yet, phototactic responses supply many microorganisms (purple bacteria, at least 170 species of algae, fungi, etc.) with a mechanism for achieving optimum light conditions. Phototactic movements of chloroplasts in higher plants adapt the light-absorbing surface to existing light conditions. Phototaxis, though not confined to photautotrophs, may well prove to be ubiquitous among photosynthetic organisms.

Since existing reviews of the literature on phototaxis (Mainx, 1929; Mast, 1936, 1941; Manten, 1948; and a brief review by Stanier and Cohen-Bazire, 1957) are not comprehensive and, with the exception of that by Stanier and Cohen-Bazire are out of date, an extensive review of the literature in the field was deemed desirable. A number of researchers have recently become interested in phototaxis, and it is hoped that this review will be of use to them. Although it

may not be complete, this review, to the best knowledge of the author, contains a more extensive list of references on phototaxis than is elsewhere available. At the end of it is a list of 170 species of algae in which phototactic behavior has been observed.

This review covers phototaxis in bacteria, in algae, the phototactic movements of chloroplasts in algae and higher plants, and phototaxis in amebae.

EARLY OBSERVATIONS

The earliest speculations on light-induced orientation came from Ray in 1693. He formulated the theory that light orientation in plants is due to differential effects of intensity on the two sides of an organism until the organism is symmetrically placed with respect to the source of light. He believed that the light continues to act after the organism has oriented. This theory was accepted by DeCandolle (1832), and the idea that phototactic stimulation is due to differences in light intensity is sometimes referred to as the Ray-DeCandolle Theory.

The first scientific investigations of phototaxis were by Treviranus (1817) early in the nineteenth century. He suspended the green algae *Draparnaldia glomerata* and *Ulothrix subtilis* var. *compacta* (called *Conferva mutabilis* and *Conferva compacta* by Treviranus) in a vessel of water and found that on exposure to broad daylight the zoospores always moved to the shade thrown by the brim. He thought that this avoidance reaction was due to the high intensity of the light.

In the middle and latter parts of the nineteenth century, a considerable amount of work was done on the physiological effects of light on plants, including a surprising amount on desmids. This work on desmids was probably due to interest aroused earlier in the century by the controversy as to whether as green, locomoting organisms, they ought to be classed as animals or plants, as well as to curiosity about their mechanism of locomotion.

PHOTOTAXIS IN DESMIDS

Ralfs (1848), in his monograph on desmids, describes their movement to the surface of mud brought into the laboratory and presumes that this movement is due to the stimulus of light "rather than to any voluntary effort". *Tetmemorus granulatus* and *Penium brebissonni* were observed to show this effect particularly strongly. Apparently light-induced movements to the surface of mud were also observed

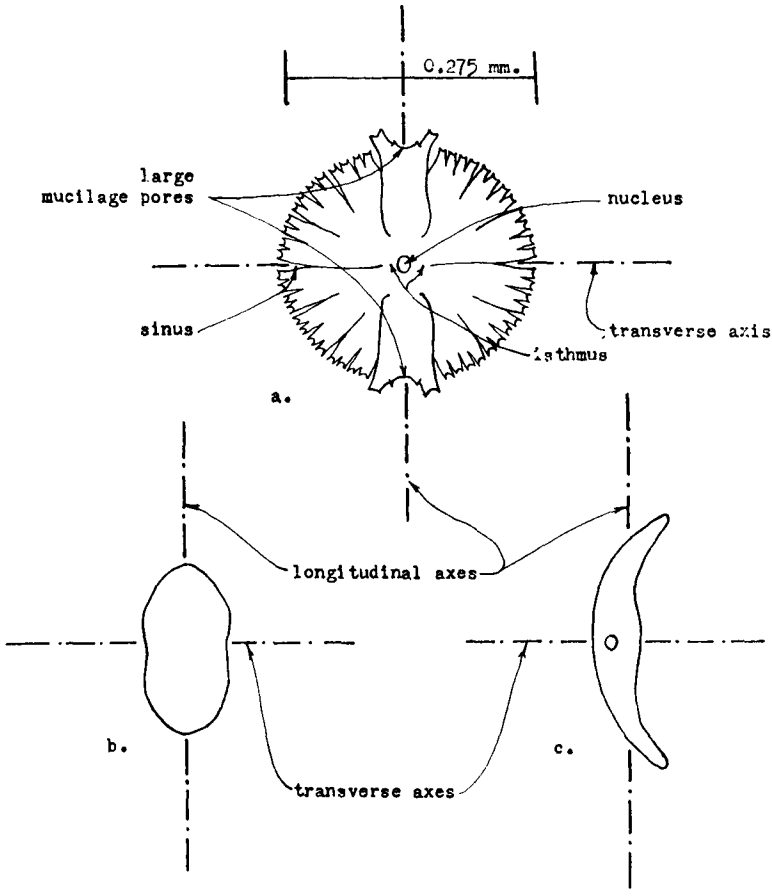

Fig. 1. Desmid cells. a. *Micrasterias rotata* var. *evoluta*. b. *Penium curtum*. c. *Closterium moneliferum*.

by him in filaments or cells of *Oscillatoria, Nostoc, Anabaena* and *Palmella.*

At the same time, Braun (1851) also noted light-induced movements in desmids. Among the species that he studied, *Penium curtum* moved most rapidly. The motion was described as very different from that of diatoms. He observed that the cells quickly turned to align the long axis (longitudinal, see Fig. 1) in the direction of the light source. The relative age of the semicells of *P. curtum* is readily determined, since the deposition of iron in the middle layer of the cell wall makes the older semicell appear darker. Braun noted that the younger semicell always oriented to the light source (p. 217). Pritchard (1861) stated

that desmids "...travel towards the light; appear on the side of the vessel on which the light falls . . .".

CONTROVERSY ON THE NATURE OF PHOTOTAXIS

Thuret (1850) accepted the Ray-DeCandolle Theory of phototaxis, but a controvery soon arose when Nägeli (1860) and Cohn (1865, 1866) proposed that phototaxis is a response to the direction of light, sun responses, for example, being due to the parallel nature of sunlight. Nägeli, like Treviranus, found that flagellates and swarm-spores collected at the side of a porcelain dish nearest the window, although the intensity of light there was frequently lower than elsewhere, due to the shadow of the side of the dish. Famintzin (1867a, 1867b) sided with Thuret.

It remained for Strasburger (1878) to settle temporarily the controversy by showing that the nature of the response appeared to depend upon the organism studied. In studying many kinds of swarm-spores, including fungal as well as algal representatives, he found two types of phototactic reactions: *a)* a response to gradation in white light intensity, e.g., swarm-spores of *Haematococcus; b)* a response to the direction of the light stimulus, e.g. swarm-spores of *Botrydium.*

Strasburger observed that organisms which showed positive phototaxis at moderate light intensities exhibited negative phototaxis when the intensity was very high (see also Stahl, 1880a; Berthold, 1882; Verworn, 1889; Oltmanns, 1892). He recorded phototactic irritability in several colorless forms, demonstrating that obvious pigmentation is not a requirement for phototactic organisms (see section titled "Phototaxis in achlorophyllous organisms", p. 169).

Cohn (1865) was the first to study the effects of different colors of light on phototaxis in microorganisms. Using colored glass filters to study the responses, he concluded that blue is phototactically most effective. Strasburger confirmed Cohn's work in experiments with a number of swarm-spores. At first, he used three colored solutions as filters and a yellow sodium light. Later, he dispersed sunlight into a five-cm. spectrum with a large prism and used a 0.4-mm. slit to isolate portions of this spectrum.

Strasburger studied the effect of temperature on phototaxis in *Haematoccocus* swarm-spores which he found at a given intensity to be negatively phototactic at 4°C., positively phototactic at 16 — 18°C., and very strongly positive at 35°C. Similar results were obtained with some other forms (e.g., swarm-spores of *Ulothrix* and *Ulva*), but

phototaxis could not be reversed in some other forms by manipulating the temperature (e.g., *Scytosiphon, Chilomonas*). Behavior similar to that of *Haematococcus* was found by Massart (1891) in *Chromulina,* where the phototactic response changes from positive to negative with a decrease in temperature.

THE WORK OF ENGELMANN

In 1876, the first of a remarkable series of papers by Engelmann appeared. Engelmann is most often remembered for his statement that photosynthesis is correlated with the absorption of light by chlorophyll and for his work in determining the first action spectrum of photosynthesis. It was probably his investigations on phototaxis which led him to perform these experiments. His investigations on phototaxis began (1879a) with observations of creeping motility in *Oscillatoria,* diatoms, *Beggiatoa* and *Thioploca.* He classified the latter two organisms as bacteria; they are now considered to be colorless blue-green algae.

Using a microspectrum projected on a slide, he studied phototaxis in purple bacteria, diatoms and blue-green algae (1881, 1882a, 1888a, 1888b). In *Bacterium photometricum* (modern name *Chromatium*) he could demonstrate no phototactic reaction in a beam of parallel light. Using sunlight, gas-light and incandescent light as sources in an attempt to compensate for inequality of energy across the spectrum, he found that *B. photometricum* collected in a band in the infra red between 800 and 900 mμ, in a less distinct band in the yellow at about 590 mμ, and in still less distinct bands in the green between 550 and 520 mμ. The absorption spectrum of a thin layer of bacteria was similar to the action spectrum he had obtained. Despite the displacement of the bacteriochlorophyll absorption curve from those of chlorophyll *a* and *b,* he recognized similarities to the curves that he had obtained with algae and concluded that *B. photometricum* is capable of photosynthesis. VanNiel has confirmed this in relatively recent years. Engelmann concluded that phototaxis in bacteria, because of its correlation with photosynthesis, is based on a chemotaxis for oxygen.

In further studies on phototactic phenomena, Engelmann elucidated the light-spot congregation phenomena first described by Cohn (1866). He found that sudden reduction in light intensity caused a "shock reaction", as a result of which the direction of movement was changed; however, the converse was not true, a sudden rise in intensity, if not great enough to cause shock stoppage of movement, had no effect.

Thus organisms were prevented from crossing a boundary between light and dark (or dim light) after having once entered the light zone, which therefore acted as a trap.

Engelmann studied phototaxis in *Paramecium bursaria* which contains *Chlorella,* which causes, under anaerobic conditions, aggregation of the paramecia in a spectrum at the spots of maximum absorption of chlorophyll. In trying to localize light sensitivity, Englemann found that it seemed to be located at or near the eye-spot in green flagellates, but that the sensitivity to light was spread over the entire cell in green ciliates (1882b).

PROGRESS DURING THE LATTER PART OF THE NINETEENTH CENTURY

In 1880 there appeared two papers on phototaxis in desmids. Göbel worked on *Micrasterias,* Stahl mainly on *Closterium moneliferum.* Göbel (1880, p. 318) reported that the plane of the disc of *Micrasterias* oriented at right angles to the direction of a light beam. Bendix (1957) found no light conditions which would consistently induce this position. With a stimulating light beam entering a dish of desmids at a grazing angle to the bottom, the cells generally remained flat on the bottom at a range of intensities from below the threshold of positive phototaxis to intensities inhibiting negative phototaxis.

Stahl (1880b) was led to investigate the phototactic behavior of *Closterium moneliferum* upon observation of apparently phototactic accumulations of this species in collected mud samples. Being familiar with the work of Braun, he expected the cells of *Closterium* to orient with the younger semicell toward the light source; however, he observed that, although the cells oriented with respect to the light source, either semicell could be toward the light. Using diffuse daylight, he noted that the longitudinal axis (see Fig. 1) of the cell lined up in the plane of the light. Stahl (1880b) found that, although *Closterium moneliferum* could glide along the bottom of a container in response to a phototactic stimulus, the dominant mode of locomotion was an end-for-end flipping. Bendix (1957) reported the same two types of motion in *Micrasterias rotata* var. *evoluta,* where, however, flipping was a less common occurrence (see Fig. 2).

Stahl made phototactic studies on other forms, similar to the work done by Strasburger and published the same year. He did not come to the same conclusions regarding the two types of phototaxis and, in particular, was unable to repeat Strasburger's work on *Bryopsis.*

Klebs (1885) and Aderhold (1888) thought that desmid movement is connected with localized secretion of gelatinous material through pores on one end of the cell; Kol (1927) has also emphasized this connection. Klebs (1885) observed that *Pleurotaenium* oriented in the direction of the light beam at low intensities and perpendicular to the beam at high intensities. He was not sure that light caused the movements he observed in *Micrasterias, Euastrum* and *Cosmarium.* Schenk (1894) stated in his textbook that many desmids

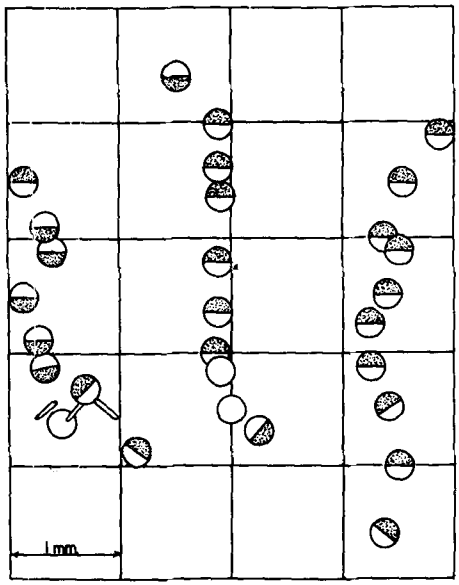

Fig. 2. Typical positive phototactic movement of *Micrasterias* cells showing gliding and flipping motions.

show heliotactic movements and that the orientation in light is correlated with the expulsion of slime through the cell membrane.

Klebs (1896) also studied phototaxis in the Chaetophoraceae (Ulotrichales), in which he found the microzoospores to be more light-sensitive than the macrozoospores. This was confirmed by Pascher (1907) and similar behavior was reported in *Ulothrix* by West and Fritsch (1927). Dodel-Port (1876) did a number of experiments on phototaxis in *Ulothrix zonata.* Verworn (1889) studied phototaxis in different colored lights, using sunlight as a source and the following filters: cobalt and ruby glasses, potassium bichromate and am-

moniacal copper oxide solutions. He concluded that short wave lengths were most effective in the phototaxis of *Navicula brevis* (diatom). Oltmanns (1892) observed negative phototaxis at high light intensities in *Volvox, Spirogyra* (filaments), *Mesocarpus* and *Funaria* (moss). Francé (1893) made an extensive study of eyespots in 31 species of algae, concluding that the eyespot functions as a light-receiving organ.

THE TWENTIETH CENTURY BEGINS

Although the beginning of the twentieth century saw more descriptive work extending the range of organisms in which phototaxis had been observed, it was marked by attempts to elucidate phototactic phenomena, a reflection of increasing knowledge of physics and concomitant instrumentation.

Pfeffer (1903) comprehensively reviewed the early literature on phototaxis. He stated that zoospores orient with the anterior end in the direction of phototactic movement and that many zoospores without eye-spots are phototactic. Francé (1909) believed the pigments in eye-spots to be light-sensitive and thought that the lenses in the eye-spots concentrate light. Richter (1903) observed phototaxis in diatoms. Holmes (1903) studied phototaxis in *Volvox.* Desroche (1912) found that phototaxis in *Chlamydomonas* approximately followed Weber's Law. Using *Rhodospirillum rubrum,* Molisch (1907) observed that purple bacteria respond more strongly to abrupt than to gradual changes in light intensity. Strzeszewski (1913) studied the effect of light intensity on phototactic accumulation of the purple bacterium *Chromatium.* Schiller (1907) observed that in the gametes of *Ulva* the eye-spot is nearly always directed toward the source of light. Rothert (quoted in Ewald, 1912) found some narcotics to inhibit phototaxis in *Gonium* and *Pandorina.*

Mast began his work on phototaxis with studies on *Volvox globator* (1907); his most detailed work, however, over a period of years, was done on *Euglena* and *Amoeba* (see pages 156, 170). He obtained an action spectrum for phototaxis in *Euglena* and found that *Gonium* gave essentially the same curve, with a maximum at 485 mμ, but that the related forms *Pandorina* and *Spondylomorum* showed a maximum at 535 mμ and a broader based curve (*Gonium, Pandorina* and *Spondylomorum* are in the same order of the green algae, whereas *Euglena* is in a separate phylum). These curves suggested participation of carotenoids in the response, and the differences between the genera were

assumed to be correlated with differences in the carotenoid pigments they contain.

Mast believed that the responses he observed in white light were due to the time-rate of change of light intensity. For example, in *Gonium* the rate of change in intensity, not the absolute magnitude of the change, influenced the response. A large but very gradual intensity change produced no effect, whereas a smaller but abrupt change produced a response analogous to shock reactions in *Euglena*. Mast was in strong disagreement with Loeb (Loeb and Maxwell, 1910) who held that the light-orienting stimulus in all animals is dependent upon the amount of stimulating energy, a given amount of stimulating energy (intensity $\times$ time) always producing the same effect, no matter how these two factors vary. According to this theory, a weak agent acting a long time would cause the same response as a strong one acting a short time. As Mast has pointed out, this theory does not account for the differences in behavior of many organisms when subjected to the same light intensity change abruptly or gradually.

MISCELLANEOUS OBSERVATIONS, 1915 TO 1945

Laurens and Hooker (1918) obtained a balanced energy action spectrum of phototaxis for *Volvox* which proved to be similar to that for *Euglena* as obtained by Mast. As late as 1928, experiments were still being performed in which action spectra were being obtained without regard to the differences in radiant energy in various parts of the spectrum obtained from a white light source. Dangeard (1928) used a spectrograph to determine the action spectrum of phototaxis for a number of organisms. He thought that the extreme variability of response which he obtained was due to differences in the balance between chlorophyll and xanthophyll in different samples of the organisms he worked with. Some of this, at least, may have been due to the differences in radiant energy distribution at different wave lengths between the various light sources he employed.

Durston (1925) found positive phototaxis in the brine flagellate *Dunaliella salina* to be brought about by blue or yellow, but not by red, light. This organism has been more intensively studied by Blum and Fox (1933). Phototactic action spectra were obtained by using an incandescent source and Corning glass filters to isolate wave-length bands. They determined the position of the light source at which response was barely detectable at 5 min. for each filter. The relative light intensity was calculated, using the inverse square law, the emis-

sion spectrum of the source (calculated, not experimentally determined) and spectrophotometrically determined transmission factors for the filters. Red and green forms of *D. salina* were found to have approximately the same responses (max. at about 500 mμ), from which it was assumed that the same substance is photoactive in both cases. The sensitivity of the red form is relatively less at shorter wave-lengths and greater at longer wave-lengths. The difference was thought to be due to differences in non-photoactive pigment screening of the photoactive substance. The phototactic response was retained in virtual absence of molecular oxygen.

Mainx and Wolf (1940) measured the swimming rate of *Pandorina morum* at various intensities in the positive and negative phototactic regions. They felt that the data indicated the presence of two independent antagonistic reactions involved in phototaxis.

Phototaxis in dinoflagellates has been reported by Kofoid and Swezy (1921), Entz (1930) and Metzner (1930). Metzner also (1919, 1921) studied the effects of photodynamic agents upon "non-phototactic" organisms. He was able to induce phototaxis with an action spectrum corresponding to that of the photodynamic agent. Unfortunately, he did not know that some of his organisms were normally phototactic under the proper conditions.

Pincussin (1930) reported that desmids oriented in a light beam make a 45° angle with the substratum. He does not state the angle of the incident beam with the substratum. Bendix (1957, p. 18), in observations of orientation in ten desmid species, found 45° orientation only when the light beam was at 45° with the substratum or transiently during the process of flipping end-for-end.

THE WORK OF LUNTZ

Luntz (1931a, 1931b, 1932) made a quantitative study of phototaxis in *Eudorina elegans, Volvox minor, Chilomonas* and *Chlamydomonas.* Absolute energy values were determined with a Moll thermopile standardized with a Hefner candle. For *E. elegans, V. minor* and *Chlamydomonas* he found a maximum at 492 mμ, no reaction in the red, and a weak reaction at 366 mμ. The thresholds for *Eudorina* and *Chlamydomonas* were the same, that for *Volvox* considerably higher. Colorless *Chilomonas* had a maximum at 366 mμ and was equally sensitive to all visible lines. The absolute threshold at 492 mμ was about 10^3 times as high as that for the other three organisms. The threshold at 366μ was the same for all four organisms. Threshold

values for *Eudorina, Volvox* and *Chilomonas* are given in Table I. The thresholds for movement in *Eudorina* and *Volvox* were lower than those for orientation. Bendix (1957) found this to hold true for *Micrasterias rotata* var. *evoluta* also.

TABLE I
PHOTATACTIC THRESHOLDS DETERMINED BY LUNTZ (1931a)

Organism	Orientation threshold erg/cm.²/sec.	Movement threshold erg/cm.²/sec.
Eudorina elegans	0.04	0.01
Volvox minor	0.06	0.04
Chilomonas	9.00	—

Luntz studied the high intensity inflection from positive to negative phototaxis in *Volvox, Chlorogonium* and *Eudorina.* He hypothesized that a light stimulus causes two opposite reactions whose strengths

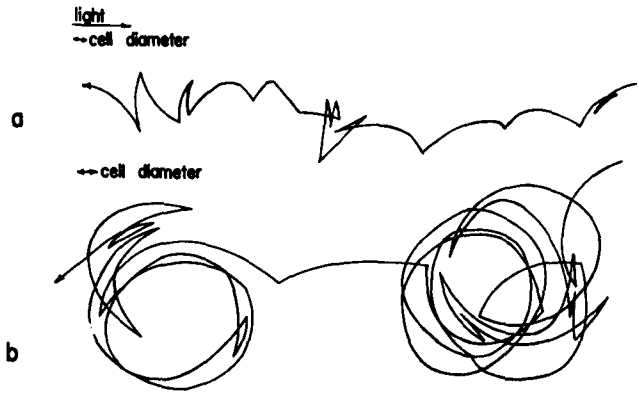

Fig. 3. Positive phototactic movement of diatoms
a. *Amphora montana;* b. *Nitzchia palea.* (Nultsch, 1956).

are differently influenced by light intensity. The observed behavior represents the difference between the two reactions.

PHOTOTAXIS IN EUGLENA

Euglena is an organism on which particularly many phototactic studies have been performed. Famintzin (1867a), Stahl (1880a) and Engelmann (1882b) observed *Euglena* to exhibit positive phototaxis in weak light and negative phototaxis in strong light. Wager (1900)

describes detailed observations on phototactic motion in *Euglena viridis* and gives diagrams of organelles associated with phototaxis similar to that of Gössel (see Fig. 4).

Engelmann (1882b) established that the response of *Euglena* to a decrease in intensity resulted in aggregation in brilliant spots in a field of light and that the response to an increase in light intensity resulted in aggregation in dark spots. Thus spots act like traps: organisms enter in the course of random movement through the field, but shock reactions prevent exit. Bünning and Tazawa (1957) found negative phototaxis in *E. gracilis* to be a clear shock effect.

Individual cells of *E. gracilis* were confined in quartz capillaries by Tchakhotine (1936). Micro-beam irradiation elicited a phototactic response only when directed on the eye-spot. Blue and blue-violet only were phototactically effective. Irradiation with 2800 Å blinded the organisms to visible phototactic stimuli. He concluded that the stigma was a primitive visual organ mediating the phototactic response.

Mast (1936) held that there are two types of light response in *Euglena*: one depends upon the rate of change in luminous intensity and results in orientation and aggregation; the other depends on changes in the energy levels received and involves the degree of activity.

The peaks in various determinations of action spectra are shown in Table II. Mast (1917) was the first investigator of *Euglena* to recognize the need to correct action spectra data for radiant intensity differences at different wave lengths. He obtained a peak at 485 mμ,

TABLE II

ACTION SPECTRUM MAXIMA FOR POSITIVE PHOTOTAXIS IN *Euglena*

Investigator	Date	Maximum — mμ
Strasburger	1878	c. 415 — 435
Engelmann	1882b	c. 470 — 490
Loeb and Maxwell	1910	460 — 510
Loeb and Wasteneys	1916	450 — 506
Mast	1917	485
Bracher	1937	420 — 460
Bünning and Schneiderhöhn	1956	490 — 500
Wolken and Shin	1958	465 and 630—"photokinesis"
		420, 440, 468, 508—"phototaxis" (see text)

with the limits of response at 410 and 540 mμ. The blue peak implicated carotenoids present in the eye-spot.

Bünning and Schneiderhöhn (1956) obtained action spectra for positive and negative phototaxis in *Euglena gracilis,* using interference filters. They found different action spectra for the two responses: the positive phototactic response had a major maximum at 490—500 mμ and a secondary maximum at 415—430 mμ; the negative phototactic response had a single major maximum at 415 mμ. They think that the two reactions are dependent on the same substance and that the differences in action spectra are due to a modifying influence exerted upon the responses by the absorption by stigma carotenoids.

Wolken and Shin (1958) distinguished between "photokinesis" = non-directed swimming rate affected by light and "phototaxis" = light-directed orientation. In *E. gracilis* photokinesis in white fluorescent light saturated at 40 fc (0.16 mm./sec.), then decreased with increasing light intensity. Plane polarized light obtained with a polarizer proved to be phototactically more effective than non-polarized light (saturation at 13 fc, 0.18 mm./sec.). An action spectrum with maxima at 465 and 630 mμ was obtained with Corning and Wratten filters to isolate narrow wavelength bands.

"Phototactic" action spectra resulted by comparing the relative numbers of organisms accumulating in areas of a cell illuminated through two filters. Light-grown, dark-grown and dark adapted cells showed maximum responses at 420 and 490 mμ. Additional peaks at 468 and 508 mμ were observed in polarized light, which these authors feel may indicate that more than one light-absorbing pigment is present within the eye-spot or that other pigments in the cell were involved in the response.

The enhanced "photokinetic" efficiency of plane polarized light suggests that the molecules of the absorbing pigment are similarly oriented in the eye-spot. Additional peaks in the "phototactic" action spectrum are more difficult to interpret. A satisfactory explanation has not yet been proposed.

THE NATURE OF PHOTIC ORIENTATION

Verworn (1894) postulated the following theory to explain orientation: when euglenae are not oriented, opposite sides are unequally illuminated, the flagella beat more effectively in one direction than in the other, and this results in turning the organisms until opposite sides are equally illuminated. The flagella then beat equally in both

directions and the organisms continue on a straight course. This is essentially the Ray-DeCandolle Theory applied to *Euglena.*

Jennings (1904) felt that if only the anterior end of *Euglena* is sensitive to changes in luminous intensity, then all turning from the light results in reduction in illumination, and all turning toward the light results in increase in illumination of the sensitive substance. Photopositive specimens turn until they face the light, photonegative specimens until they face the opposite direction. The stimulus which induces turning then ceases and the organisms continue directly toward or away from the light. Torrey (1907) disagreed with Jennings and felt that Jennings' own data indicated that orientation is due to the local effect of unequal stimulation on either side of the organism.

Engelmann (1882b) determined that if a shadow was passed from the posterior to the anterior end of *Euglena,* there was no response until the stigma was reached. This was confirmed by Mast (1911) who explained orientation this way: a transparent layer of plasma is present in front of the eye-spot of this flagellate, while the rest of the protoplast is fairly opaque; rotation on the longitudinal axis, which normally occurs during movement, illuminates the eye-spot for only part of each rotation, causing a shock reaction during each revolution; the shock reactions cause the direction of the axis to be changed until the direction of the axis and that of the light coincide.

Mast makes a strong point that the stimulus ceases after the organism has become oriented and that the organism then continues directly to or from the light because it tends to take a straight course and because, if for any reason it is turned from this course, the orienting stimulus immediately acts and induces shock reactions which bring it back on course. He does not accept the Ray-DeCandolle Theory, according to which the organism would be held on course by continuous action of the light. To the present author it seems that if light causes a course correction whenever the organism deviates from a straight line, then light is continuously acting to hold the organism on its course.

BEHAVIOR IN TWO BEAMS

Mast (1911) studied the behavior of several free-swimming species of *Euglena* and two in the crawling state (a number of other genera were also tested) subjected to two beams of light at 90°. He found that they moved approximately on the diagonal between the directions of the two beams.

In similar experiments, Buder (1917) found that *Euglena* moved at an angle related to the intensities of the two beams, which seemed to indicate quantitative proportionality between stimulus and response. Mast and Johnson (1932) felt that the behavior in two beams has no bearing on the quantitative relation between stimulus and response, but could be explained on the assumptions that the eye-spot is a photoreceptor and that the stimulating effect of light varies with the angle of incidence.

MOVEMENT IN DIATOMS

Diatoms are unique among non-flagellate phototactic microorganisms in that there is definite information about their means of locomotion, and one is not forced to rely on nebulous theories regarding the nature of "slime movement" to explain motion. Many diatoms have the ability to move. This ability is correlated with the presence of a raphe in each valve wall. The raphe is a sigmoid cleft running the length of the organism. According to current belief, based on the extensive work of Müller (1889, see Smith 1955, p. 671 for a list of references), movement is due to a flow of cytoplasm along the free face of the raphe. Propulsion of the frustule is in the opposite direction to that of the streaming at the area of contact with the substratum. Movement is due to currents in the medium set up by the protoplasmic streaming which can be demonstrated by observation in dilute india ink (Smith 1955).

Heidingsfeld (1943), on the basis of her observations of phototaxis in light isolated by two filters, concluded that *Navicula radiosa* is phototactically most sensitive to short wave lengths. Cells with their long axis parallel to the beam responded fastest, whereas cells perpendicular to the beam did not respond until random movement brought them parallel. There was no evidence that light caused orientation, however.

Nultsch (1956) obtained phototactic action spectra for several diatoms, using Schott filters and metal interference filters. He distinguished three classes of movement among the organisms he worked with: *Navicula* type = movement predominantly in a straight line; *Amphora* type = path randomly irregular; *Nitzschia* type = path devious but with two consistent radii of curvature (see Fig. 3). Average speeds were 3 to 10μ/sec., while maximum speeds ranged from 4 to 14 μ/sec. There was a noticeable effect of temperature only above 30°C. Four species were positively phototactic at 3 to 10,000

lux (meter-candles). *Nitzschia stagnorum* was indifferent above 2500 lux. Short wave lengths, around 550 mμ, were most effective in phototaxis.

PHOTOTAXIS IN PHAEOPHYCOPHYTA AND RHODOPHYCOPHYTA

Phototaxis in the Phaeophycophyta (brown algae) and Rhodophycophyta (red algae) has not been studied so extensively as in other algae and in bacteria. Phototactic behavior has been observed in the spores of brown algae by Thuret (1850) and Cohn (1866). Kylin (1918) stated that everyone who has studied brown algae has observed phototaxis in swarmers, and he refers to phototaxis in his later work on brown algae (1933). Fritsch (1935) considered it common in the Ectocarpales.

Papenfuss (1935) reported that conjugation was not observed in *Ectocarpus siliculosis* while the female gametes were motile, but always after the female gamete attached to the side of the hanging drops toward the light. He also found the great majority of zooids to be positively phototactic, but a certain unexplained proportion was negative or neutral in phototactic response. He found that disturbance due to handling tended to produce a negative response. In other work on the brown algae, Kotte (1923) noted that the spermatozoids of *Fucus serratus* were negatively phototactic, and Abe (1935) has observed phototaxis in swarmers of *Heterochordaria, Scytosiphon* and *Sorocarpus.*

Phototaxis in *Porphyridium cruentum* (a primitive member of the Rhodophycophyta) was first reported by Dangeard (1930) and was confirmed by Vischer (1935), Geitler (1944), Pringsheim and Pringsheim (1949) and others. Geitler reports the maximum rate of phototactic movement as 60 μ/hr. Creeping motility is known in some other members of the red algae which may well prove to be phototactic on further investigation.

MOVEMENT IN BLUE-GREEN ALGAE

Cyanophyceae exhibit three types of movement: linear translation[2], axial rotation, and oscillation. These movements, in so far as present evidence indicates, are not due solely to phototactic stimuli. Since all studies of the mechanism of cyanophycean locomotion have a bear-

[2] Translation of a body is such motion that all plane sections of the body remain parallel to their respective first positions.

ing on the mechanism of response to light stimuli, this discussion will include some reference to experiments in which phototaxis was not a factor.

Apparently the first paper on autonomic movements of filamentous Cyanophyceae was published in the middle of the eighteenth century by Adamson (1767). Famintzin (1867a) found *Oscillatoria insignis* to be negatively phototactic in direct sunlight and positive in diffuse daylight. He felt that light was the main stimulus for motion, since comparatively slight motion was observed in the dark. Movements may long continue in the dark, however (Borzi, 1879; Pieper, 1915; Harder, 1917; Schmid, 1921). Hansgirg (1882), who worked with four species of *Oscillatoria,* Phillips (1904), Pieper (1913) and Harder (1920) agreed with Famintzin that movement was more rapid in light than in dark. Hansgirg thought the movement to be due to "diosmotic processes" resulting from a turgor gradient along the entire filament, and the reversal in direction to be due to reversal of the pressure gradient caused by an external stimulus (1883). Plasmolytic experiments do indicate a difference in osmotic properties in different parts of the filament, but no gradient, has been demonstrated (Burkholder, 1934).

In contrast to Famintzin and Hansgirg, Verworn (1889) found filamentous blue-green algae to be positively phototactic in direct sunlight. Schmid (1923) thought that brown species, such as *Oscillatoria jenensis,* with a high proportion of phycoerythrin, were negatively phototactic, and that green species, such as *O. cortiana,* were positively phototactic; but this generalization has proved to be invalid. In experiments with nine species of *Oscillatoria,* Burkholder (1934) reported the phototactic sign to vary within the genus: one species, *O. splendida,* being negatively phototactic, whereas the other eight were positive.

Correns (1897) thought that velocity was proportional to the diameter of the filament. Harder (1918) observed that the velocity of filaments varied with the light intensity after 24 hours of dark adaptation. The speed of primary hormogonia of *Nostoc* increases with light intensity between 5 and 900 mc., with a strong increase up to 100 mc. Older hormogonia are indifferent to intensity changes over a range of 5 to 2222 mc. Burkholder (1934) observed no variation in velocity between 0.01 to 2613 mc. in *Oscillatoria formosa* after 20 hours of dark adaptation. These experiments were done under

conditions in which orientation of the filaments was excluded by illuminating in a direction perpendicular to the plane in which the organisms were allowed to glide, which may well account for the observed lack of response.

Harder (1917) made use of the phototactic response of young hormogonia of *Nostoc punctiforme* and *Anabaena variabilis* to obtain pure cultures. This technique was used on a number of other blue-green algae by Allen (1952).

EFFECTS OF LIGHT OF DIFFERENT WAVE LENGTHS

Verworn (1889) observed a phototactic reaction in all regions of the visible spectrum with *Glaucothrix gracillima.* Pieper (1913) established that diaphototaxis, or orientation in such a manner that optimum light absorption may be permitted, occurs in *Oscillatoria* filaments under moderate light intensities, the filaments orienting perpendicular to the direction of the incident light. He studied the behavior of *O. formosa* with several light sources and filters, obtaining the results shown in Table III. The light for these experiments was obtained by use of solutions of various colored substances. The transmission band widths are given as 25—80 mμ on the basis of work of others but were not actually measured by Pieper; he does not indicate whether these widths are half-widths or 'total' band widths. At the optimal intensities of red and yellow he obtained diaphototaxis. Dark-adapted cultures gave optimal positive phototaxis in white light at lower intensities than light-grown cultures, indicating an adaptive factor in the phototactic reaction.

Dangeard (1928) exposed various species of *Oscillatoria* to the spectrum from a spectrograph and found that they collected in the orange,

TABLE III

DIRECTION AND STRENGTH OF PHOTOTAXIS IN *Oscillatoria formosa* UNDER VARIOUS LIGHT CONDITIONS (AFTER PIEPER, 1915)

	Low intensity	High intensity
white light	+	—
red light	++	++
yellow light	++	++
green light	+	—
blue light	—	—

red and infra red. The response was constant for a given species but varied slightly from species to species, probably correlating with interspecific pigment differences.

ROLE OF THE MUCILAGE

Engelmann (1879a) thought that motion was due to rhythmic longitudinal waves traversing the filaments, coupled with the secretory mechanism. Many investigators since Engelmann, including Lauterborn (1896), Verworn (1889), Schröder (1902) and Harder (1918), have also thought that the secretion of mucilage is the cause of movement. Theories of propulsion by mucilaginous secretion are difficult to apply, however, to movements of filaments not in direct contact with the substratum.

Fechner (1915) reported that the mucilage of Cyanophyeae was anisotropic, but Krenner (1925) and Nikilitschek (1934) contested this. The envelope of mucilage forms a complete cylinder only in the rare instances in which the threads are moving freely. Usually the envelope is U-shaped in cross section with the opening on the underside, where the gliding thread is in direct contact with the substratum. The envelope itself is fixed to the substratum only at the starting point (Nikilitschek, 1934). Frey-Wyssling and Stecher (1954) have shown that *Nostoc* slime contains submicroscopic cellulose fibrils which are responsible for many of its physical properties.

Hansgirg (1883) and Zuelzer (1911) have observed mucilage spirals left by filaments as they moved. In careful observations of the movements of filaments of *Oscillatoria jenensis* over soil surfaces, Schmid (1921) saw fine mucilage strands which remained stretched from particle to particle and which were twisted as a result of the rotation of the filaments[3]. The mucilage tracks were made up of two threads. This was confirmed by Nikilitschek (1934). Schmid held that the right or left rotation of filaments was constant for a given species of *Oscillatoria.* He thought that the mucilage was secreted through pores, but others feel it is probably a modification of the outer part of the cell wall.

Hosoi (1951) placed filaments of *Oscillatoria princeps* on a thin agar film on a cover slip used as the roof of a moist chamber and then observed them with dark-field and phase microscopy. In dark-

[3] *Nostoc* does not rotate as it moves (Ulrich, 1926).

field illumination, the slime is brightly illuminated and can be seen to move spirally about the filaments, even when movement of the filament is stopped with micromanipulator needles. When the filament voluntarily comes to rest, the mucilage ceases to move.

Ulrich (1929) thought that movement was due to contractile waves traversing the filament. Schulz (1955), using Ulrich's method, could not confirm Ulrich's observations that active contractions were the likely origin of the gliding motions. He made an electron microscopic study of the structure of the cell walls of 11 species, using supersonic distintegration to obtain wall fragments, and found what he interpreted as many mucilage pores. Such pores had been reported by Phillips (1904) and Schmid (1921), but Mühldorf (1935, 1938) and Ulrich (1926) were unable to find them.

Fechner (1915) thought that both forward progression and the typical accompanying rotation were accounted for by the radial swelling of the mucilage, on an axis inclined to the axis of the filament, squeezing the filament forward and away from the smaller end of the sheath. This is not applicable to some forms with interrupted sheaths. Prell (1921) proposed the hypothesis that movement was caused by the flowing pressure of gelatinous strands extruded through numerous spirally arranged pores along the entire length of the filament. When secretion resumed, the jelly strands had a different purchase with respect to the substratum, and the filaments moved in the opposite direction. It is difficult to see how such a mechanism accounts for movement restricted to a single plane.

REVERSAL OF DIRECTION OF MOVEMENT

Nienburg (1916) used a very small beam of light controlled by different sizes and shapes of apertures manipulated so as to illuminate one or both ends or only the middle of a single filament creeping on a microscope slide. He found that a change from dark to light had no influence on the direction of movement. Speed was apparently accelerated by increased light intensity, but the temperature may not have been adequately controlled. All parts of a filament were equally sensitive to light. Nikilitschek (1934) found that *Oscillatoria* threads illuminated by a circular area of light exhibit reversal of movement as soon as one third to one half of the filament has passed into the dark. Darkening is effective in causing reversal only if the end that is momentarily directed forward comes under its influence. Burkholder

(1934) found a greater frequency of reversal at higher light intensities.

The hormogonia of *Nostoc* reverse direction when the light intensity is suddenly lowered. A sudden increase in intensity from 0 to 12,000 mc. gave no reversal. Only when the previous period of illumination had lasted a definite minimum time did a lowering of intensity result in reversal. The factors concerned in reversal are: *a*) period of illumination, *b*) period of shading, *c*) drop in intensity between the two periods. Filaments were exposed to white light at 200 mc. for two minutes, then darkened, then illuminated again. When the shade period lasted more than a minimum of 15 seconds, reversal always occurred, and the length of the rest-period in the succeeding light period varied inversely with the duration of the shade-period. When the shade period was greater than 80 sec., movement was resumed upon subsequent illumination without any rest period in the light (Harder, 1920).

PHOTOTAXIS IN PURPLE BACTERIA

Buder (1919) worked on phototaxis in purple bacteria where he succeeded in resolving the single aggregation Engelmann observed in the blue-green region of the spectrum into three weak but distinct regions at approximately 530, 490 and 470 mμ. Comparison of the absorption spectra of suspensions of living bacteria with the action spectrum for phototaxis led him to believe that the entire pigment complex was active in the perception of light. Van Niel (1944) concurred in this opinion. Carotenoids would be responsible for the aggregation at 530, 490 and 470 mμ; whereas bacteriochlorophyll would be responsible for observed aggregations at 900, 850, 800, 590 mμ and in the far violet.

Schrammeck (1934) made further studies on purple bacteria. He determined the smallest decrease in intensity which would suffice to evoke a phototactic response and found the liminally effective decrease to be 5% of the initial intensity. This has served as a key case in support of the Weber Law which requires that the least perceptable change in an environmental factor be a constant fraction of the original intensity of the factor. Clayton (1953a) found Weber Law adherence over a much narrower range when he repeated this work.

French (1938) studied the rate of photosynthesis in *Rhodospirillum rubrum* at different wave lengths. He explained the accumulation of

bacteria in a spectrum in regions of maximum absorption of bacteriochlorophyll by chemotaxis brought about by a carbon dioxide gradient due to unequal consumption of carbon dioxide in parts of the spectrum of different efficiency for photosynthesis. Aggregation would then be due to avoidance of high carbon dioxide concentrations. Fischer (1939) studied the effect of rate of change in light intensity on phototaxis in *Chromatium.*

Schlegel (1956) has demonstrated negative phototaxis at high light intensities in four species of purple bacteria: *Chromatium vinosum, Chr. Okeni, Thiospirillum jenense, Rhodospirillum rubrum.*

THE WORK OF MANTEN

Manten has obtained an action spectrum of phototaxis in *Rhodospirillum rubrum* (1948), taking advantage of the fact that this organism exhibits a bright light spot trap phenomenon of the type first described by Cohn. The spirilla will cross a boundary from a less phototactically stimulating area into one that is more so, but will not do the reverse. Manten constructed an optical apparatus which enabled him to have two adjacent areas in a microscope field that could be controlled with respect to wave length and intensity. The two areas were illuminated by beams from two prisms cemented together with a thin layer of Canada balsam in such a fashion that no evidence of a double boundary could be established. One area was set as a standard at a given wave length region, and at each wave length the intensity of the second area required to give uniform distribution of the bacteria across the two areas was determined, that is, it was determined which intensity of the second area was phototactically equivalent to the first one.

Manten concluded that bacteriochlorophyll was responsible for most of the response, with a secondary contribution by carotenoids. Manten's results also give an action spectrum for photosynthesis in this organism. Manten thinks that the phototactic response in *Rhodospirillum rubrum* is correlated with the photosynthetic rate. Would his method have distinguished between responses dependent or independent of photosynthetic rate?

THE WORK OF CLAYTON

Since Manten's action spectrum did not indicate participation of the predominant carotenoid, spirilloxanthin, Clayton (1935a) de-

cided to repeat this work with light of greater spectral purity. He also repeated the work of Schrammeck. He constructed a monochromator yielding a half-width of 5 to 7.5 mμ and used a phototube with AC amplification to measure intensity. Above 570 mμ this action spectrum agreed with Manten, showing characteristic bacteriochlorophyll maxima at 590 and 870 mμ. Below 570 mμ there were some differences, making it more likely that spirilloxanthin participates as well as carotenoids present in small quantities. The scarcer carotenoids were still more active in proportion to their concentration in *Rhodospirillum*, however. Manten used a different strain of *R. rubrum* from Clayton. At 15 fc., Wolken and Shin (1958) have obtained an action spectrum for *R. rubrum* with maxima at 420, 465, 490 and 530 mμ.

Differences in action spectra for phototaxis in *Rhodospirillum rubrum* obtained by different investigators prove to be due to a difference in the behavior of young and old cultures which is correlated with changes in the pigments present (Goodwin and Sissins, 1955). When mature, *R. rubrum* cultures synthesize almost exclusively spirilloxanthin.

Thomas and Nijenhuis (1950) noted that the saturating light intensities for photosynthesis and phototaxis in *R. rubrum* were equal and varied in the same manner under the influence of cyanide and urethane. This study was not carried to fully saturating light intensities. Clayton (1953b) made simultaneous determinations of the saturating light intensities for phototaxis and photosynthesis in *R. rubrum* which he observed to be generally unequal. The ratio varied widely under different environmental conditions. Clayton established that the saturating intensity for phototaxis is markedly influenced by the nature of the photosynthetic substrate. This finding is in accord with Manten's hypothesis that phototaxis and photosynthesis are closely related in this organism but suggests that the phototactic response does not depend on a change in the photosynthetic steady-state. Clayton felt that the data could be accounted for by a transient disturbance or fluctuation in the photosynthetic process which must reach a threshold value to evoke a response. Such a transient effect could occur at higher intensities than that which corresponds to saturation for photosynthesis, as based on measurements of the steady state.

In a study of the effect of drugs, Clayton (1955) found that methylene blue inhibited phototaxis at 0.2×10^{-3} M., tetrazolium had no ef-

fect at 0.2×10^{-3} M. but inhibited at 1×10^{-3} M., and dinitrophenol had no effect at 0.5×10^{-3} M. but a slight effect at 1.0×10^{-3} M.

It is assumed that, through the pigment system, a decrease in light intensity leads to a suitable (perhaps electric) stimulus for an irritable system, the excitation of which leads to a phototactic response (Clayton, 1953c). Separation of photoreceptive system and primary irritable mechanism is indicated by the existence of a chemotactic response elicited by oxygen in particular. Clayton suggested that there was an apparent duality of mechanism between phototaxis of purple bacteria and algae, arising from a difference in the mechanism of photosynthesis, with algal phototaxis bearing a closer similarity to the visual process of vertebrates. This generalization would seem to be partly based upon the incorrect assumption that the algal response is always carotenoid dependent.

PHOTOTAXIS IN ACHLOROPHYLLOUS ORGANISMS

ALGAE

Rothert (1901, p. 372) observed phototaxis in colorless *Chlamydomonas multifilis*. Buder (1917), in studies on *Polytoma* and *Polytomella*, found that only forms with eye-spots were light-sensitive. Shettles (1937) studied phototaxis in the colorless, eyespotless, nonorienting flagellate, *Peranema* (Euglenales). *Peranema* responds only to rapid increases in light intensity. The entire organism is sensitive to light, but the flagellum is most sensitive, the posterior end least sensitive.

Pringsheim (1937) cites as reasons for thinking that the stigma is the light-perceiving organ in phototaxis: *a*) action spectra maxima agree with the absorption of stigma pigments, *b*) forms lacking a stigma are not phototactic. Neither of these statements holds true for all phototactic organisms. He cites as one example of *b*), colorless unicellular members of the Volvocales, in which species lacking a stigma do not respond phototactically, while those with a stigma do. As an exception to *b*), he mentions *Chilomonas* which is phototactic without a stigma.

Gössel (1957) used 15 interference filters with maxima from 389 to 533 mμ to obtain action spectra for phototaxis in achlorophyllous strains of *Euglena gracilis*. In *E. gracilis* var. *bacillaris* with both photoreceptor and stigma (see Fig. 4), negative phototaxis only was ob-

served, with a maximum at 410 mμ. In *E. gracilis* var. *bacillaris* PBZ-G4, which has a photoreceptor but no stigma, both positive and negative phototaxis were observed. The action spectra for both positive and negative phototaxis in this strain had maxima at 410 mμ, but

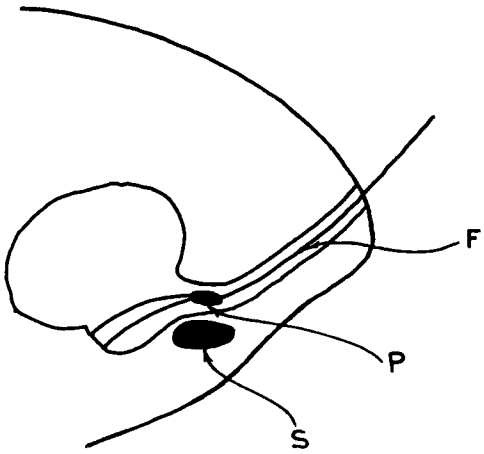

Fig. 4. Front end of *Euglena gracilis* cell showing stigma (S), photoreceptor (P) and flagellum (F.). (After Gössel, 1957).

the secondary maxima did not coincide. *Astasia longa*, lacking both photoreceptor and stigma, was not phototactic under any conditions tested. Gössel concluded that the stigma is not involved in negative phototaxis and that positive phototaxis is due to a periodic darkening of the stigma by the eye-spot. Bünning and Tazawa (1957) agree with these conclusions.

Phototactic behavior has been observed in the swarmers of the following fungi: *Synchytrium taraxaci* (Fischer, 1882), chytrids (Rothert 1901, p. 371), *Chytridium vorax* and *Polyphagus Euglenae* (Strasburger, 1878), *Phizophidium pollinis* (Müller, 1911). Other than these few examples, no attempt will be made to cover phototaxis in fungi in this review.

AMOEBAE

The first observations of the shock reaction of movement cessation due to a large, sudden increase in light intensity were made by Engelmann (1879b) on *Amoeba.* He noted that if the intensity was increased gradually, movement would continue. Mast (1910) held that

the movement-stopping response was due to the rate of change in light intensity. The shock reaction varies from a momentary retardation in streaming in a localized region in a pseudopod to total cessation of movement with reversal in direction of streaming on recovery (Mast, 1941).

Harrington and Leaming (1900) established that shorter wavelengths of light were most effective in producing negative phototaxis. Most of the work on amoebae is concerned with negative phototaxis; however, Schaeffer (1917) had some evidence for positive phototaxis in very weak light. Feeding amoebae are not phototactic (Folger, 1925).

Davenport (1897) observed that *Amoeba proteus* orients in a light beam. In unilaterally illuminated amoebae the pseudopods develop more freely on the shaded side, which results in gradual turning from the light. Localized illumination causes, by its gelating effect, an increase in thickness and in the elastic strength of the plasmagel in the region illuminated. This effect is not transmitted to other regions, and there are no impulses produced, but the effect of localized gelation and the consequent contraction are transmitted, resulting in coordinated action, according to Mast (1932b).

SHOCK RESPONSE AND RECOVERY IN AMOEBAE

Folger (1925) designated the period from the beginning of illumination to response as "reaction time," the time that illumination must continue as "stimulation period", the time stimulation need not continue as "latent period". As intensity increases, the latent period increases rapidly from 1 second at 500 mc. to a maximum of 6 seconds at 1000 mc., then decreases gradually to 0.75 second at 11,000 mc. He concluded that two processes are involved, the first occurring only in light, the second in light or in dark; and that the action of light probably results in the formation of a substance which induces the response. Folger (1927) thought that cessation of movement in amoebae resulting from mechanical stimulation involves the same processes as cessation produced by an increase in illumination. Therefore, the latter could not be due to photochemical changes, since the former could not cause photochemical changes.

After an amoeba responds to a rapid increase in illumination, some time must elapse before it will respond again to the same increase. This is the "refractory period." Recovery consists of two phases: the

first (1-2 min.) takes place regardless of a change in light intensity, the second (10-20 sec.) proceeds only if the intensity is decreased (Folger, 1925). Mast (1941) felt that recovery from high intensity shock indicates that an increase in light intensity induces changes which internal factors in the organism continuously tend to oppose and eliminate. If this is true, the more rapidly a given amount of energy is received, the less time there is for recovery and consequently the greater will be the effect of a given quantity of light. This might account for the increase in the amount of energy required for a shock response with a decrease in intensity in weak light but does not account for the increase in the amount of energy required with an increase in intensity in strong light.

EFFECTS OF ENVIRONMENT AND ADAPTATION IN AMOEBAE

The quantity of light energy required to induce cessation of movement was found to depend on the chemical composition of the surrounding medium (Mast and Hulpieu, 1930). In general, the quantity of energy required varied directly with the viscosity of the cytoplasm.

There is no fixed threshold of response. Mast (1941) felt that variation in the amount of energy required to induce cessation of movement is due, at least in part, to adaptation. Mast and Stahler (1937) observed that dark-adapted amoebae, when exposed to light, gradually increase their rate of locomotion to a maximum and then remain at this level. The time required to reach this maximum level decreases from 15 minutes at 225 mc. to a minimum of 7 minutes at 15,000 mc., then increases to 30 minutes at 40,000 mc. The maximum rate of locomotion increases from 130 μ/min. at 50 mc. to 220 μ/min. at 15,000 mc., then decreases 150 μ/min. at 40,000 mc. The increase in rate of locomotion with increase in light intensity is due to the action of longer wave lengths. Mast and Stahler felt that the effects were probably caused by changes in the rate of sol-gel and gel-sol transformations, in which case, both of these transformations would have to be augmented by longer wave lengths and retarded by shorter wave lengths.

EFFECTS OF REPRODUCTIVE PROCESSES ON PHOTOTAXIS

Borzi (1883, quoted in Pfeffer 1903, p. 324) already observed that the gametes of *Enteromorpha compressa* lost their phototactic irritability on copulation. Carter (1926), in her studies on the Ulvaceae,

found that the positive phototaxis of gametes changes to negative phototaxis on fusion. This has been further studied by Miyake and Kuneida (1931) and by Kylin (1930). Föyn (1929) obtained similar results with *Cladophora* and *Ulva.* In *Enteromorpha intentinalis,* Kylin found (1930, p. 460) that freshly discharged zoospores were usually positively phototactic, but occasionally negatively phototactic. Commonly, the positively phototactic zoospores become negatively phototactic after 30-40 minutes. The negatively phototactic spores are the first to attach. Smith (1946) reported that reversal of phototaxis on initiation of gametic fusion makes it easy to locate fusing paris of *Chlamydomonas* gametes when gametes of opposite sex are mixed. Fritsch (1935) stated that isogametes commonly change from positive to negative phototaxis on fusion.

Mainx (1931) assembled several reports on the phototactic behavior of isogametes, showing that they may change from positive to negative phototaxis before or after copulation. He showed that sexual colonies of *Volvox aureus* change from strong positive to strong negative phototaxis during oögenesis and that the sign of phototaxis changes on copulation of the gametes of *Hydrodictyon utriculatum.* As soon as eggs become visible in *V. aureus* colonies, the inflection intensity (transition from positive to negative phototaxis) moves rapidly to lower light intensities. If sexual reproduction does not occur, phototactic sensitivity is lost as the culture degenerates. Colonies with ripening "parthenospores" are always strongly negatively phototactic, the threshold and point of inflection coinciding!

Bendix (1957) reported that the cells of *Micrasterias rotata* var. *evoluta* lose most of their phototactic response shortly before division and do not regain it until reorganization of the daughter cells is complete (see Fig. 5). Normal phototactic sensitivity is not regained until some hours after cellular reorganization can be visually judged to be complete. This suggested that in this organism either both phototaxis and division are dependent upon a limited common energy source which is sufficient for only one of these processes at a time or that phototaxis and division use a common precursor which preferentially goes to the division mechanism during division.

EFFECTS OF ENVIRONMENTAL FACTORS ON PHOTOTAXIS

Strasburger (1878) observed that environmental factors influenced phototactic response: any increase in temperature, without a change

in intensity of illumination, tended to produce a positive phototactic response; a decrease in temperature tended to produce a negative response (work on *Euglena*). Mast (1911) noted that strongly positive *Euglena* specimens, in a beam of constant light intensity, become less active as the temperature decreases, come to rest at 10° C., become more active under further decrease, with a maximum at 5° C., at which temperature they are as strongly negatively phototactic as they were previously positive.

Mast (1918) studied the effects of chemicals on phototaxis in the colonial form *Spondylomorum quaternarium*. Negative specimens be-

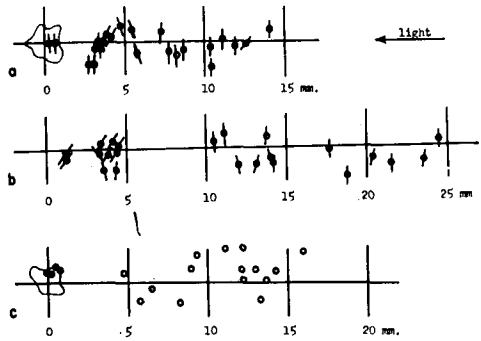

Fig. 5. Loss of phototactic sensitivity by dividing *Micrasterias* cells.

a. Position of a group of cells containing five cells undergoing nuclear division after six hours photic stimulation. Attached pairs of daughter cells have not moved as far as non-dividing cells. 440 mμ.

b. Cells from 'a' after 11 hours. Separated daughter cells still show very little response and are more poorly oriented than non-recently divided cells.

c. Position of a group of cells containing two pairs of cells which have undergone caryokinesis and cytokinesis and have formed about ¼ of their new semicells. After 9 hours the recently divided cells still have not moved. 690 mμ.

Open circles = undivided cells, solid circles = daughter cells of recent divisions, lines through circles = orientation of transverse axes of cells, wavy outlines = starting position of group of cells.

came strongly positive on addition of chloroform, ether, chloral hydrate or acids. All inorganic and organic acids tested were found to have no effect on positive phototaxis. Formalin, sugar, oxygen, hydrogen peroxide, $MgSO_4$, $CaCl_2$, KNO_3 had no influence. Burkholder (1933) found normal phototactic movement in *Oscillatoria* in the pH range 6.4 — 9.5. Movement was hindered outside this range.

Mainx (1929) conducted an extensive study of phototaxis in a number of algae. He studied the effects of the following agents on phototaxis: pH, oxygen tension, temperature, anaesthetics, alcohols, osmotic pressure, previous light exposure, etc. He found that conditions which lower the threshold of positive phototaxis raise the energy level at which the transition from positive to negative phototaxis takes place. The full effect of changes in external factors lasted more than two hours after removal from the stimulus, and the cells adapted back to their original values in one or two days. Light pretreatments had to be longer than others for effect, and the return to equilibrium sensitivity was also slower. Mainx felt that this indicated a qualitative difference in the action of light as compared to the other stimuli. He also found that addition of ferrous sulfate produced strong positive phototaxis in non-reactive old cultures of *Eudorina elegans* and *Volvox aureus.* This may have been due to the low iron content of culture media at that time compared to modern media with chelating agents holding optimal amounts of iron in solution. Unfortunately, he did not have equipment for determining light intensities and reported only distances from light sources. We can judge, however, that the threshold values he obtained were quite low, since he reports thresholds as far as six meters from a 0.5 watt source behind a frosted diffusing glass!

Halldal (1956, 1957) studied phototaxis in *Platymonas subcordiformis* and other motile green algae and dinoflagellates in which irregular positive and negative phototactic behavior at a given light intensity proved to be partially correlated with the concentration of calcium and magnesium ions in the medium. Movement was relatively independent of oxygen and carbon dioxide tension. In experiments with different ratios of calcium chloride to magnesium chloride in the medium, he found positive phototaxis when Ca/Mg was less than 1:6; random motion at 1:6; and negative phototaxis at Ca/Mg ratios greater than 1:6. It is possible that Kleb's (1896) observations that phototaxis in the microspores of *Ulothrix zonata* was strongly influenced by the composition of the medium were related to a similar phenomenon.

DIURNAL PHOTOTACTIC VARIATION

Diurnal variations in the phototactic behavior of *Euglena* were reported by Bracher (1919, 1937), Pohl (1948) and Bruce and Pitten-

drigh (1956). Bracher (1919) observed that the shore form *Euglena deses* moves most rapidly at 15° C. and becomes sluggish at temperatures below 5° C. or above 25° C. *Euglena deses* burrows below the surface of the mud when the light intensity falls below a critical value. Under ordinary daylight, it lives on the mud surface, but at the approach of high tide it burrows. The tidal rhythm of emergence and burrowing persists three days in the laboratory (1937). In daylight, a minimum of 33 to 40 fc. is required to maintain the organisms on the mud surface. Under artificial light, higher intensities are required to bring them to the surface, due to deficiency in the blue end of the spectrum. Using Wratten filters, the region 420 to 460 mμ was determined to be most effective, and no response was observed in the red. A Weston photo-electric cell was used for the energy measurements. Bracher concluded that the phototactic response in *Euglena deses* was influenced by the number of organisms per unit area, temperature, water content of the mud, time of day and by tide.

Pohl (1948) observed an endogenous diurnal variation in the phototactic behavior of *Euglena gracilis*. Bruce and Pittendrigh (1956) have recently extended this work. They measured phototaxis by sending a light beam through an algal suspension in a carrell flask, so that the beam intercepted about 22% of the culture volume. The entire culture was illuminated with a 4-watt fluorescent tube. The beam of light served as a "light-trap" for phototactic cells. The beam fell upon a photocell connected to an automatic recording system which registered the decrease in light transmitted by the culture as organisms accumulated in the beam. The beam was on one-half hour in two hours.

Their results showed that *Euglena* cells became phototactically inactive when exposed to continuous dark; that the phototactic rhythm persisted for a while in the dark but did not persist in continuous light; that persistence of the phototactic rhythm in the dark was dependent upon the cells receiving sufficient photosynthetic energy from the test light; that from 17 — 33° C. rhythm persistence in the dark is temperature-independent; and that the diurnal rhythm persists even when cells are growing so rapidly that they divide more frequently than once every 24 hours.

An arhythmic population can be made rhythmic by a single light stimulus. They are not certain that this stimulus initiates rhythms in cells or establishes synchrony in a population of rhythms with random-

ly distributed phrases. This problem illustrates the difficulty in dealing with cell populations rather than individual cells.

Bruce and Pittendrigh suggested that the *Euglena* rhythm possesses certain features characteristic of a class of periodic phenomena known in physics as self-sustained relaxation oscillations. (Pittendrigh and Bruce, 1957).

Fauré-Fremiet studied the natural tidal rhythms of several sand-dwelling microorganisms. In *Chromulina psammobia* he found positive phototaxis and a tendency to disperse during low tide; negative phototaxis and positive thigmotaxis at high tide, producing a tendency to go into the sand (1950). The phototactic rhythm was maintained in the laboratory for eight days. The period was a little over 24 hours. He felt that the difficulty of experimental modification of the responses indicated the presence of an endogenous physiological rhythm. The response was not affected by LiCl, KCl, NaCl, $MgCl_2$, nitrates, acetates, duponol, increase in CO_2, etc. A similar tidal-phototactic rhythm was observed in the diatom *Hantzschia amphioxys* (1951). Fauré-Fremiet (1948) also observed positive phototaxis in *Strombidium oculatum* due to a symbiotic green alga (not *Chlorella*). Phototactic control of diurnal vertical migration in marine dinoflagellates is discussed in Hasle (1950).

OTHER RECENT WORK ON ALGAE

Brucker (1954) studied phototactic behavior in *Lepocinclis texta* which he found to be positively phototactic, even at high light intensities. Organisms dark-adapted through 40 hours darkness had a threshold at 0.4 — 1.3 mc, while organisms light-adapted from daylight or artificial light over 50 lux, had a threshold at 20 — 21 mc, i.e., decreased sensitivity. This difference was shown not to be a true phototactic light adaptation but a difference due to the difference in the carbonic acid concentration in the medium with cells in different light-dependent physiological states. "Dark-adapted" cells thresholded at 20 mc. when the carbonic acid concentration of the medium was artificially increased.

Mayer and Poljakoff-Mayber (1957) reported that *Chlamydomonas moewussii* is not phototactic (five other species of *Chlamydomonas* are), but CO_2-tactic. The chemotactic response was influenced by light intensity.

Millot (1957, p. 19) has recently stated that " . . . there is still

some doubt as to whether the light absorbed by the eye-spot pigment is directly concerned in excitation, or whether the pigment acts as a light filter for the real receptive area, which is ill defined". Hartshorne (1953) thought that there is good reason to believe that the eye-spots of Euglenophycophyta and Chlorophycophyta are structurally and functionally different. In the Euglenophycophyta the eye-spot consists of an irregular mass of pigment granules. In the Chlorophycophyta the eye-spot has a definite outline and appears to be more homogeneous. In *Euglena* the eye-spot is adjacent to the base of the flagellum. This is generally not so in the Chlorophycophyta where position is variable, even within a single genus.

Hartshorne studied phototaxis in an eye-spotless mutant of *Chlamydomonas reinhardi* produced by ultra-violet irradiation. He found that lack of the eye-spot was not associated with complete insensitivity to light, although the eye-spotless mutant reacted with much less uniformity and precision than the wild type. Perception of light is therefore not restricted to the eye-spot. It seems that the relative light sensitivity of eye-spot and cytoplasm varies from organism to organism.

Bendix (1957) studied phototaxis in the unicellular desmid *Micrasterias rotata* var. *evoluta* which is particularly favorable experimental material, since it is highly pigmented (100 cells suffice for spectrophotometric determination of pigments) and easy to observe because of large size (275 μ in diameter) and low velocity (3 mm./hr. maximum). Cells placed in the beam dispersed by a large prism clearly showed two separate phototactic responses, one in the plane of the beam (PN response) and one perpendicular to the beam (L response). The L response is uni-directional, causing cells to move out of the long wave length end of the visible spectrum but no farther than 570 mμ. It was observed in a range of intensities from an irradiance too low to support division to an irradiance high enough to irreversibly inhibit division. This response was independent of the direction of the energy gradient across the region in which it was observed and was not correlated with the red chlorophyll absorption peak.

As intensity increases, the PN response goes to a positive maximum and back to zero to a null response region, goes to a negative maximum and again returns to zero. The threshold of the positive PN response in white light is a little below 2 fc., in monochromatic light goes as low as 5×10^{-4} μw/cm^2 at 690 mμ (approximately 1.5×10^5 quanta/sec./cell). The positive PN response saturates in white light between

2 and 6 fc., in monochromatic light at as low an irradiance as 5×10^{-3} $\mu w/cm^2$ (690 mμ). The action spectrum for this response obtained with a monochromator indicated that chlorophyll *a* and probably another, as yet unidentified, chlorophyll act as the photoreceptors. The positive PN response is lost at 100-5000 $\mu w/cm.^2$.

Micrasterias cells orient during both positive and negative phototactic movements so that the longitudinal axis (see Figs. 1, 6) is parallel to the stimulating light beam. The orientation mechanism can be selectively destroyed without affecting movement.

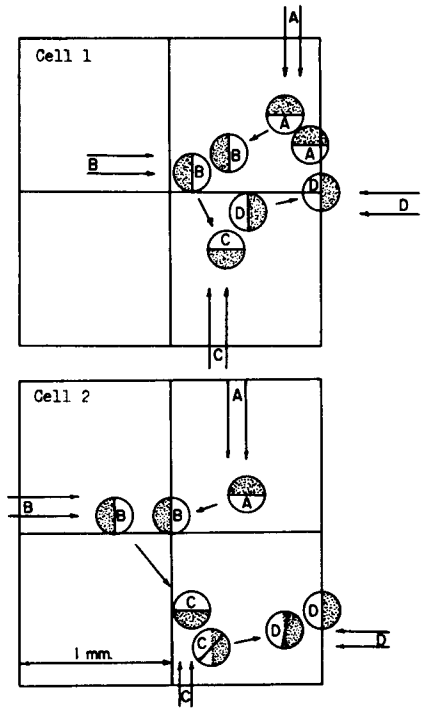

Fig. 6. Change in orientation of *Micrasterias* cells with change in direction of incident light from monochromator. Cells rotated 90° in beam three times. 690 mμ, 16 $\mu w./cm.^2$.

THE WORK OF HALLDAL

Halldal (1958) distinguishes between "phobo-phototaxis" = shock reaction causing accumulation in a light spot, and "topo-phototaxis"

= active orientation in relation to light source as well as movement toward or away from it. He determined topo-phototactic action spectra for five species of Volvocales, gametes of two *Ulva* species, and three members of the Dinophyceae.

Two methods were employed in determination of these action spectra. A modification of Manten's method (Manten, 1948), in which algae were placed between two opposed beams: a reference beam of constant intensity and wave-length, and a variable wave length exciting beam (in the range 10-800 ergs/cm^2 sec.), which could be adjusted in intensity until the cells swam toward neither light source. In the second method, a spectrum with an intensity gradient perpendicular to the wave-length scale was projected on one side of an algae-containing vessel, the other side of which was illuminated with light uniform in wave length and intensity. Algae then collected on the side of the vessel where the projected spectrum was more effective than the reference beam. The action spectrum was obtained by measuring energy and wave length along the boundary of the collection area. The projected spectrum with an intensity gradient was obtained with a V-shaped slit and a photographic wedge.

A number of check experiments were run in which both intensity and wave length of the reference beam were varied in order to test the representative nature of a curve based on any given reference beam value. The action spectra values proved to be independent of the wave length and intensity of the reference beam. This was taken to indicate that determinations were being made below the saturating intensity for phototaxis in these organisms.

Halldal concluded that two, possibly three, pigments were involved in phototaxis in the organisms which he studied. The members of the Volvocales and the *Ulva*-gametes had the same action spectra (maximum at 493 mμ, small shoulder at 435 mμ); *Goniolax catenella* and *Peridinium trochoideum* had curves similar but not identical to this group (maximum at 475 mμ, small shoulder at 435 mμ). *Prorocentrum micans* gave a maximum at 570 mμ. Action spectra for positive and negative phototaxis were the same in the Volvocales. Absorption spectra of living suspensions of the Volvocales and Dinophyceae did not indicate the presence of any pigment corresponding to the phototactic action spectra. The same major fat-soluble pigments were present in both *Peridineum* and *Prorocentrum*. None of the active pigments has been successfully isolated.

Halldal concluded that the photosensitive spot for topo-phototaxis was at or near the flagellar base, but that it was not the stigma nor any organ connected to it. The stigma, when present, is assumed to act only as an auxiliary body, which on some occasions will improve the precision of the movement.

PHOTOTACTIC MOVEMENTS OF CHLOROPLASTS

Phototaxis has been observed in higher plants as a movement of chloroplasts or effects on cyclosis. The chloroplasts of certain algae also exhibit phototactic movements. Until recently, this phenomenon has mainly been studied in mosses and waterplants, among higher plants, since this material is particularly favorable for the necessary observations.

Böhm (1856) was the first to notice that the position of chloroplasts in the cell is light-dependent. He studied chloroplast movements in over 100 species of Crassulaceae and later in some members of the Saxifragaceae. Famintzin (1867b) observed the movements of chloroplasts in the leaves of the moss, *Mnium,* and found that yellow light gives the same effect as darkness and that blue gives the 'daylight' arrangement of chloroplasts. Frank (1872) studied the effect of light on chloroplasts and concluded that red light had the same effect as darkness. Stahl (1880a), using *Lemna trisulca,* came to the same conclusion. DeBary and Strasburger (1877) found that light caused movements of the chloroplasts in *Acetabularia.* The early work on phototaxis in chloroplasts is summarized in Pringsheim (1912).

CHLOROPLAST MOVEMENTS IN *Mougeotia*[4]

In the saccoderm desmid, *Mougeotia,* Stahl (1880a, 1880b) found that the cell as a whole oriented in the light, but that the nucleus, which is centrally imbedded in the chloroplast, did not show preferential orientation in the light beam. Observing the movements of the plate-shaped chloroplast of *M. scalaris* he concluded: *a*) that in diffuse light the plane of the chloroplast was at right angles to the incident beam; *b*) that in sunlight the edge of the chloroplast was towards the source. Moore, who reviewed the early work on phototactic chloroplast movements and performed extensive experiments himself (1888a),

[4] Known as *Mesocarpus* in the nineteenth century.

also worked on *Mougeotia* (1888b). He found that if a chloroplast was placed so as to receive diffuse light from two sources at 90°, then:

a) if the chloroplast was originally perpendicular to the stronger beam, it remained in this position;

b) if the chloroplast was originally parallel to the stronger beam, it rotated so as to become perpendicular to it.

c) if the relative intensities of the two beams were interchanged, the chloroplast rotated 90°.

The chloroplast changed shape and became at least partially peripheral in full sun. Moore concluded that the position of the chloroplast depended on light intensity in the following manner:

a) diffuse light = perpendicular to beam,
b) weak sun = parallel to beam,
c) full sun = parastrophe.

Lewis (1898) made a series of observations to determine the effect of duration of the light stimulus on chloroplast movements in *Mougeotia.* He studied the effect of diffuse light on turning the chloroplasts from vertical to horizontal and the effect of strong sunlight on turning the chloroplast from horizontal to vertical. In the latter case he found 90 sec. illumination necessary for full 90° rotation in the subsequent dark period. Diffuse light reactions were normal in hydrogen, but carbon dioxide stopped all movement.

EXPERIMENTS WITH FILTERED LIGHT

Senn (1908) studied chloroplast movements in *Phaseolus* and other plants, concluding that only blue causes parastrophe (see Table IV for definitions of terms relating to chloroplast placement) and that red slowly induces apostrophe. *Mougeotia* was an exception, parastrophe being brought about by blue and epistrophe by red.

Linsbauer and Abramowicz (1909), using light filtered through $K_2Cr_2O_7$ and $(Cu(NH_3)_4)(OH)_2$, came to the conclusion that the apostrophe-epistrophe reaction was phototactic, but that the epistrophe-apostrophe reaction was associated with the assimilation of carbon dioxide. Nothmann-Zuckerkandle (1915), investigating the effects of colored light on protoplasmic movements in *Elodea canadensis,* found streaming most pronounced under the influence of red light and slowest in violet.

Voerkel (1934) obtained quantitative data on the influence of color and intensity of light on the transposition of chloroplasts in cells

of *Funaria hygrometrica.* He found that the apostrophe-epistrophe reaction at constant intensity was elicited most efficiently by blue light. The effects of various colors of light were in the following ratio: blue 270 : yellow-blue 52 : yellow-green 1. Very intense red did not induce epistrophe. He could not induce parastrophe with even very high intensity visible light and thought that only long ultraviolet could do it. The influence of blue on apostrophe-epistrophe was connected with carotenes.

THE WORK OF ZURZYCKA AND ZURZYCKI

Zurzycka and Zurzycki have in recent years carefully investigated phototaxis of chloroplasts in higher plants. They (1953, p. 675) state

TABLE IV
TERMS RELATING TO CHLOROPLAST POSITION IN THE CELL

Chloroplast condition	Position in the cell	Orientation of chloroplasts with respect to incident beam	Corresponding light condition
apostrophe	against internal cell walls	parallel	darkness
epistrophe	against walls perpendicular to incident light beam	perpendicular	dispersed light
parastrophe	against walls perpendicular to leaf surface or parallel to incident light beam	parallel	direct sun or very strong artificial light

that "It appears that light is the main and in normal conditions almost the only factor causing tactic chloroplast movements. Other stimuli cause these movements only exceptionally." They (1950) studied the influence of temperature on the phototactic movements of chloroplasts. The rapidity of the epistrophe-parastrophe movement depends on temperature in accord with the Van't Hoff Law, with a coefficient of 1.26. The Van't Hoff coefficient for the epistrophe-apostrophe reaction is 1.47. The apostrophe-epistrophe and parastrophe-epistrophe reactions show no marked dependence on temperature.

Protoplasmic viscosity has a marked influence on the velocity of chloroplasts in epistrophe, but in apostrophe the movement is independent of viscosity (Zurzycka and Zursycki, 1951).

ACTION SPECTRA FOR CHLOROPLAST PHOTOTAXIS

Zurzycka (1951) investigated the reactions of chloroplasts in *Lemna trisulca* to color and intensity of light. She found epistrophe in high intensity and apostrophe in the dark. As sources she used an Osram 35 w. 12 v. lamp and a 250 w. 125 v. Ostram projection lamp. In the absence of a monochromator, six narrow transmission band Fuess gelatin filters were used. Copper sulfate solutions served as infrared filters. Light intensity was determined with a thermopile and galvanometer.

The results obtained by Zurzycka agree with those of Voerkel on the relative effects of blue and red on the epistrophe-apostrophe reaction, but the epistrophe-parastrophe reaction in *Lemna trisulca* seemed to be different from that in *Funaria*. She found two maxima for this effect, at 600+ mμ and 500— mμ, and thought that Voerkel's results may have been due to the nature of his experimental setup. Her general conclusions were that the apostrophe-epistrophe reaction is due to carotenes or xanthophylls and that the epistrophe-parastrophe reaction is a negative phototaxis correlated with chlorophyll absorption. She went even further and suggested that these data are evidence that "The direction of the maximal absorption by chlorophyll must therefore be perpendicular to the direction of maximum absorption by carotenoids". This conclusion seems unwarranted.

Discrepancies in the results obtained with red light by various experimenters have been resolved by Babushkin (1955b) who showed that the effect is produced not by red but by infrared which was not adequately filtered out in some experiments. Zurzycka obtained a "red" effect, using a 3% $CuSO_4$ solution as an infrared filter. Babushkin found that 6% $CuSO_4$ transmitted sufficient infrared to produce the effect but that 6% $CuSO_4$ + infrared opaque glass eliminated all chloroplast movement in red light. This was confirmed by production of chloroplast movements with an incandescent source and an RG-8 filter which transmits only infrared (not "phototaxis", since this term refers to movements produced by visible light). Phototaxis in chloroplasts is therefore caused only by blue light.

Babushkin (1955b) obtained action spectra for chloroplast phototaxis, using a prism-produced spectrum and a microspectrograph with

500-750 watt projection lamps as sources. The wave-length scale was checked with the mercury lines 404-7 and 436 mμ. Thin, fluorescent light-grown leaves were used. Before an experiment plants were kept in the dark two days.

Where chloroplasts move to front cell walls, a leaf looks less transparent. This permitted the development of a contact print method in which a 20 x 40 mm. leaf piece, upon which a spectrum had been projected, was placed on photographic paper and illuminated. The paper was developed so as to accentuate the contrast. Light intensity was regulated so that where chloroplasts were in epistrophe, no light was transmitted and the paper was white; where the chloroplasts remained in apostrophe, the paper was dark.

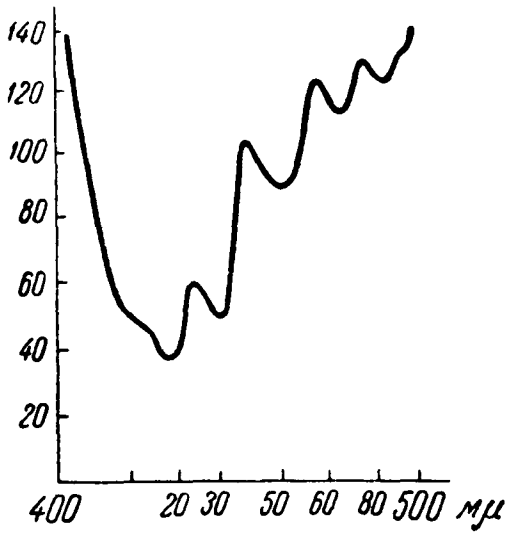

Fig. 7. Action spectrum for chloroplast phototaxis in tobacco. Vertical units = ergs/cm.²sec. (Babushkin, 1955a).

The action spectrum he obtained (Figure 7) had five maxima: 420, 430, 450, 462 and 477 mμ (all ± 2-5 mμ). The broadest maximum was at 450 mμ (440-455 mμ). Some maxima were believed probably to be compound. The action spectrum is corrected for energy differences across the spectrum. The action spectrum indicated participation of chlorophylls and several carotenoids. The main maxima

are due to violaxanthin (420 mμ) and chlorophyll *a* (430 mμ). The entire chloroplast pigment complex seems to participate in the response.

ADAPTATION TO LIGHT INTENSITY

Zurzycka and Zurzycki (1954) examined the effects of a gradual change in light intensity to determine whether phototactic effects were due to shock reactions from sudden intensity changes. They found that the final positions (epistrophe, parastrophe) were the same, whether the change in intensity was sudden or gradual, and that the course of the phototactic reaction did not depend on the time the previous intensity lasted.

Since 1952 Babushkin (1955a, 1955b, 1955c) has engaged in an intensive study of the effect of light intensity on phototaxis in chloroplasts, primarily working with tobacco. Observations were made with a microscope mounted over a thermostatically controlled chamber with a window equipped to take filters. The source was a mercury vapor lamp (EGAR-2) from which the 436 mμ line was isolated with a filter and passed through a collimator. Light intensity in the chamber was controlled by either or both, varying the source-chamber distance and neutral filters. In some experiments "light wedges" were used which produced a continuous gradient in light intensity.

Two wedges were employed, one transmitting 16-68%, the other 68-83% of the incident light. In each experiment intensity measurements were made on the beam falling on the wedge, then the location of the desired chloroplast condition with respect to the wedge produced gradient was determined.

Phototactic behavior of chloroplasts was characterized by determining the light intensity at which full epistrophe was attained (I_1) and the intensity at which the epistrophe-parastrophe transition began to take place (I_2). The method was sensitive to $\pm$ 5 ergs/cm^2 sec. for I_1 and $\pm$ 20 ergs/cm^2 sec. for I_2. Tobacco was used because the top row of palisade cells is easily visible without injury to the leaf.

TABLE V

THE EFFECT OF TEMPERATURE ON CHARACTERISTICS OF CHLOROPLAST PHOTOTAXIS IN TOBACCO. LIGHT INTENSITIES IN ergs/cm^2 sec. (Babushkin 1955a).

	10°C		15°C		20°C		25°C	
Exp. No.	I_1	I_2	I_1	I_2	I_1	I_2	I_1	I_2
1	10	1600	12	1520	20	1460	22	1400
2	14	1600	18	1560	20	1470	26	1380

Temperature increase in the 10-25°C range causes an increase in I_1 and a decrease in I_2 (Table V). A comparison was made between plants grown in sunlight and under artificial illumination, in which several cell layers were observed. I_1 and I_2 were lowest for surface cells in fluorescent light grown plants, but lowest for the deepest observed layer in sunlight-grown plants. The direction of change for I_1 and I_2 with depth of cell layer was opposite for low (artificial illumination) and high (sunlight) intensity light grown plants.

Under conditions of artificial illumination, leaves at different levels in a plant are at different distances from the source, and receive different light intensities; whereas isolated sunlight-grown plants receive essentially the same intensity on all leaves, and differences in phototactic behavior are determined mainly by the age of the leaf. The younger the leaf the lower I_1 and I_2 under comparable light conditions. Under fluorescent light, light intensity is relatively a more important factor in determining phototactic behavior than leaf age.

A study of phototactic behavior of wild plants of the shade-loving species *Impatiens parviflora* and *Asarum europaeum* indicated that the higher the light intensity under which an individual plant grew, the greater the interval between I_1 and I_2. The more light-loving a species was, the greater the interval between I_1 and I_2 (Table VI).

TABLE VI

VALUES OF I_2-I_1 FOR VARIOUS PLANTS IN ergs/cm² sec. (Babushkin, 1955a)

Species	$I_2 - I_1$
Asarum europaeum	20 — 176
Impatiens parviflora	138 — 550
Majanthemum difolium	$\geqslant$ 110
Convallaria majalis	$\geqslant$ 274
Carex caespitosa	$\geqslant$ 317
Aspidistra plectogyne	920
Nicotiana tabacum	945 — 3344*
Zea mays	1740 — 2160
Helianthus annuus	2200 — 3410
Phaseolus vulgaris	$\leqslant$ 2600

*extremes of range for different strains

CHLOROPLAST PHOTOTAXIS AND METABOLISM

The effect of phototactic chloroplast movements on photosynthesis has been investigated by Zurzycki (1955) and Babushkin (1955c). Zurzycki used a micro-technique based on a capillary tube respirometer which could be used for measurements of gaseous metabolism in leaves several millimeters square or algal filaments several millimeters long, with an accuracy of 10^{-3} µl. Chloroplast movements were studied in *Funaria, Lemna, Mougeotia* and *Spirogyra,* the last as control material in which the chloroplasts could not move. Changes in chloroplast arrangement and photosynthesis were correlated at low intensities only. At low intensities increase of assimilation area (apostrophe-epistrophe and parastrophe-epistrophe reactions) is related to change in photosynthetic rate. As long as the photosynthetic rate increases proportionally to the light intensity, the chloroplasts are in epistrophe. Full parastrophe is reached at the point of photosynthetic light saturation (Zurzycki, 1955).

A strong reduction or complete blocking of photosynthesis by hydroxylamine hydrochloride or sodium azide in *Lemna trisulca* inhibited or stopped entirely those phototactic movements which started with the profile chloroplast arrangement (paratrophe-epistrophe, parastrophe-apostrophe, apostrophe-epistrophe) and had no effect on phototactic movements beginning from the horizontal chloroplast position (epistrophe-parastrophe, epistrophe-apostrophe). Seventy per cent reduction in the respiratory rate by berberine sulphate brought no change in the phototactic movements (Zurzycki and Zurzycka, 1955).

Babushkin (1955c) studied photosynthetic behavior manometrically and with $C^{14}O_2$. He used tobacco leaves grown under 2000 lux of fluorescent light so that the compensation point would be as low as possible. He found that the lower the I_1, the higher the photosynthetic rate. When photosynthetic rate was plotted against light intensity, marked dips occurred which coincided with the apostrophe-epistrophe and epistrophe-parastrophe transitions. $C^{14}O_2$ studies indicated that the photosynthetic rate decrease actually takes place first, since it shows up on three-minute exposures which are insufficient to cause chloroplast movement. Phenylurethane decreases phototaxis as well as photosynthesis.

On the basis of his work, Babushkin makes the following statements regarding phototaxis. Photosynthesis and phototaxis cease in chloroplasts with the destruction of chlorophyll. The action-spectrum of

phototaxis at short wave lengths indicates participation of both chlorophyll and carotenoids. The magnitude of I_1 correlates with the shape of the photosynthetic efficiency curve. Transition periods in chloroplast position in the cell correlate with minima in photosynthetic rate curves. He concludes that chloroplasts have a single pigment system operating in phototaxis and the light phase of photosynthesis. The action-spectrum of phototaxis can be explained only by the assumption that the products of photoreaction are different for red and blue light. Bendix (1957) has also suggested that light absorbed at the two peaks of chlorophyll absorption is not equally effective in phototaxis *(Micrasterias)*.

CLASSIFICATION OF PHOTOTACTIC ORGANISMS

Engelmann (1882b) classified phototactic organisms into three groups (Table VII). In modern terms we would say that phototaxis is dependent upon photosynthesis in organisms belonging to Group I but independent of it in those belonging to Group III. *Paramecium bursaria* is a special case, since phototaxis in it is presumably induced by endozoic *Chlorella*.

TABLE VII

ENGELMANN'S CLASSIFICATION OF PHOTOTACTIC ORGANISMS

Group	Examples	Dependence upon oxygen
I	*Navicula, Pinnularia* and most other diatoms; most filamentous blue-green algae; cells of higher plants with moveable chloroplasts.	Light influences gas exchange only; movement stops in dark or under artificially produced decrease in oxygen tension, due to oxygen lack; no shock reaction.
II	*Paramecium bursaria*	Change in respiration results from change in gas exchange; when oxygen adequate, no phototaxis; when oxygen insufficient, strong phototactic sensitivity to oxygen concentration differences.
III	*Euglena viridis*	Uninfluenced by oxygen; shock reaction present.

Luntz (1931a) classified phototactic reactions into "kinetic reactions" dependent only on the quantity of radiant energy absorbed and "orientation reactions" dependent on a change in lateral light intensity. Since there is some evidence for photic orientation in all phototactic groups of microorganisms other than the purple bacteria and Rhodophycophyta, and since no organism is yet known which possesses a phototactic reaction that bears a quantitative relation with the amount of light energy absorbed over a wide range of energy levels, this classification seems rather artificial.

Manten (1948) divided phototactic organisms into two groups:

GROUP I	GROUP II
Purple bacteria, some blue-green algae *(Oscillatoria), Paramecium bursaria.* Except for *P.* bursaria, systematically rather primitive organisms.	Swarmspores, unicellular flagellates, some colonial green algae.
1) Lack eye-spots.	1) Possess eye-spots
2) Do not orient in light beam.	2) Orient in light beam.
3) Phototaxis correlated with photosynthesis (i.e., chlorophyll(s) characteristic of organism). Move laterally in a spectrum.	3) Phototaxis correlated with carotenoids in eye-spot. Differences in action spectra for various organisms suggest that the carotenoid involved is species-dependent.
4) Relatively high intensity threshold of response.	4) Respond to very small amounts of light.
5) No negative phototaxis at high intensities.	5) Negative phototaxis at high intensities.

The following exceptions to this classification can be cited:
(1) Desmids, which orient in a beam despite absence of eye spots (e.g., *Micrasterias, Penium, Closterium*).
(2) *Micrasterias rotata* var. *evoluta:* eye-spotless, responds to very small amounts of radiant energy; negative phototaxis at high light intensities.
(3) Diatoms: eye-spotless, most sensitive to short wave lengths (carotenoids). *Navicula brevis* (Verworn, 1889), *Nav. radiosa* (Heidingsfeld, 1943), *Nav. buderi, Amphora montana, Nitzchia palea, N. stagnorum* (Nultsch, 1956).

(4) Oscillatoriae, which exhibit negative phototaxis at high light intensities: *Oscillatoria insignis* (Famintzin, 1867a), *O. formosa* (Pieper, 1915), *O. jenensis* (Schmid, 1923), *O. splendida* (Burkholder, 1934).

(5) *Prorocentrum micans:* dependent upon neither a chlorophyll not a carotenoid for phototactic movement (Halldal, 1956).

(6) Purple bacteria: exhibit negative phototaxis at high light intensities (Schlegel, 1956).

(7) Phototactic movements of chloroplasts of cells without eyespots, some of which are definitely correlated with carotenoids.

(8) *Amoeba proteus*: eye-spotless; most strongly influenced by short wave lengths (carotenoids) (Harrington and Leaming, 1900).

In view of the apparent existence of a considerable number of exceptions to Manten's classification, a more general classification of phototactic responses seems to be indicated. Stanier and Cohen-Bazire (1957) made a classification of phototactic organisms similar to Manten's, except that they include diatoms in Group II and therefore do not limit Group II to organisms with eye-spots. This removes the exceptions to Manten's classification listed above, except for (4) (5), (6), (8) and *Micrasterias,* in which phototaxis does not correlate with carotenoids but otherwise fits into Group II by one phototactic response and into neither group by the other response.

It seems that existing classifications of phototactic organisms are not based on sufficiently fundamental characteristics of response to hold up as more facts are added to the picture. Perhaps, when more action spectra are available, it will be possible to classify phototactic response on the basis of the pigment(s) involved, rather than by groups or organisms. Present evidence suggests three types of phototaxis on this basis:

I. Reactions in which chlorophyll(s) participate but are not necessarily the sole photochemical agents.

II. Reactions photochemically independent of photosynthesis and/or chlorophyll.

A. Dependent primarily on carotenoids.

B. Dependent on pigments other than carotenoids.

A given organism could have different forms of phototaxis serving different physiological purposes and interacting to produce the final observed behavior.

ALGAE IN WHICH PHOTOTAXIS HAS BEEN OBSERVED

In order to determine how widespread the phototactic response is, it seemed desirable to compile a list of organisms in which phototaxis has been observed. Since the most comprehensive available data relate to algae, the tabulation has been confined to them. The list has been arranged in the framework of the most modern system of classification of the algae (Papenfuss, 1955) and shows that there is no major group of algae in which phototaxis has not been found. Twenty one families of the Chlorophycophyta are represented on the list, as well as the Charophycophyta, Euglenophycophyta, Chrysophycophyta (six families), Pyrrophycophyta, Cryptophyceae, six families of the Phaeophycophyta, the Cyanophyceae, and the Rhodophycophyta. Such widespread occurrence suggests that the response may be ubiquitous when studied in more forms, and that absence of phototactic responses in an alga may be an exception. This is the opinion of Stanier (1957, p. 57) who has stated "Probably all motile phototrophic microorganisms are capable of directed movement with respect to light".

Although this is the most comprehensive list of organisms that exhibit phototaxis that has been compiled to the best of the author's knowledge, comprising some 170 species, it is by no means complete, and any additions by readers will be welcomed.

TABLE VIII
ORGANISMS EXHIBITING PHOTOTAXIS

PHYLUM CHLOROPHYCOPHYTA	
Class Chlorophyceae	
Order Volvocales	
Suborder Volvocineae	
Family Chlamydomonadaceae	*Carteria ovata* (Buder, 1917)[5]
	Chlamydomonas alboviridis
	C. multifilis (Rothert, 1901)
	C. pisiformis (Loeb and Wasteneys, 1916)
	C. pulvisculus (Elfving, 1886; Aderhold, 1888)
	C. reinhardi (Hartshorne, 1953)
	C. variabilis (Buder, 1917)
	Chlorogonium euchlorum (Schulze, 1927;) Mainx, 1929)
	Platymonas subcordiformis (Halldal, 1957)
	Polytoma (Buder, 1917)

[5] References are given wherever possible; the author's records do not include sources of information for all species listed.

TABLE VIII. (Cont.)

	Dunaliella ct. *euchlora* (Halldal, 1958; Durston, 1925; Blum and Fox, 1933)
	D. salina (Halldal, 1956)
	D. viridis (Halldal, 1956)
Family Polyblepharidaceae	*Polytomella agilis* (Pringsheim, 1937)
	P. uvella
	Stephanoptera gracilis (Halldal, 1956)
Family Haematococcaceae	*Haematococcus lacustris* (Strasburger, 1878; Aderhold, 1888)
	H. pluvialis (Mainx, 1929)
Family Spondylomoraceae	*Chlamydobotrys gracilis* (Schulze, 1927)
	Spondylomorum quaternarium (Buder, 1917; Mast, 1918)
Family Volvocaceae	*Eudorina elegans* (Buder, 1917; Mainx, 1929; Luntz, 1931a)
	Gonium pectorale (Mast, 1916; Mainx, 1929)
	Pandorina morum (Rothert, 1901; Mast, 1919; Mainx, 1940)
	Volvox aureus (Buder, 1917; Mainx, 1929)
	V. globator (Mast, 1907, 1932a)
	V. minor (Luntz, 1931a)
Suborder Tetrasporineae	
Family Palmellaceae	*Palmella* (Ralfs, 1848)
	Tachygonium[6]
Order Zygnematales	
Suborder Zygnematineae	
Family Zygnemataceae	*Spirogyra* (Oltmanns, 1892; Lepeshkin, 1909)
	Mesocarpus (*Mougeotia*) *scalaris** (Stahl, 1880a)
Suborder Desmidineae	
Family Desmidiaceae	*Closterium archerianum*
	Cl. dianae
	Cl. didymotocum
	Cl. lineatum (Aderhold, 1888)
	Cl. moneliferum (Stahl, 1880b)
	Cl. striatolum (Aderhold, 1888)
	Cosmarium botrytis (Aderhold, 1888)
	Cos. meneghinii (Aderhold, 1888)
	Desmidium cylindricum (Aderhold, 1888)
	D. swartzii (Aderhold, 1888)
	Euastrum ansatum (Aderhold, 1888)
	E. insignis (Aderhold, 1888)
	Micrasterias rotata (Gőbel, 1880; Stahl, 1880b)
	M. rotata var. *evoluta* (Bendix, 1957)
	Penium brebissonii (Ralfs, 1848)
	P. curtum (Braun, 1851)
	P. digitus (Aderhold, 1888)

[6] Taxonomic status of this species uncertain.

TABLE VIII. (Cont.)

	Pleurotaenium coronatum (Aderhold, 1888)
	Pl. nodulosum (Aderhold, 1888)
	Tetmemorus brebissonnii (Ralfs, 1848)
Order Ulotrichales	
Family Ulotrichaceae	*Ulothrix subtilis* var. *compacta* (Treviranus, 1817)
	U. subtilissima (Bolte, 1920)
	U. tenuis
	U. zonata (Dodel-Port, 1876; Strasburger, 1878; Klebs, 1896)
Family Chaetophoraceae	*Chaetophora** (Moore, 1888)
	*Draparnaldia glomerata*** (Treviranus, 1817; Moore, 1888)
Family Pleurococcaceae	*Protococcus* (= *Pleurococcus*)
Family Monostromaceae	*Monostroma latissimum* (Carter, 1926)
Family Ulvaceae	*Enteromorpha compressa* gametes (Borzi, 1883)
	E. intestinalis (Kylin, 1930)
	Ulva lactuca gametes and zoospores
	U. rigida gametes (Halldal, 1958)
	U. taeniata gametes (Halldal, 1958)
Order Sphaeropleales	
Family Sphaeropleaceae	*Sphaeroplea* antherozoids
Order Oedogoniales	
Family Oedogoniaceae	*Oedogonium* swarm-spores (Mast, 1911)
Order Schizogoniales	
Order Chlorococcales	
Family Chlorellaceae	*Chlorella*
Family Hydrodictyaceae	*Hydrodictyon reticulatum*[7] (Mainx, 1929)
Order Cladophorales	
Family Cladophoraceae	*Chaetomorpha aerea* (Strasburger, 1878)
	Cladophora laetevirens gametes and zoospores
Order Siphonocladales	
Order Siphonales	
Family Bryopsidaceae	*Bryopsis plumosa* gametes
Order Dasycladales	
Family Dasycladaceae	*Acetabularia** (DeBary and Strasburger, 1877)
PHYLUM CHAROPHYCOPHYTA	
Class Charophyceae	
Order Charales	
Family Characeae	*Chara vulgaris** (Moore, 1888)
PHYLUM EUGLENOPHYCOPHYTA	
Class Euglenophyceae	
Order Euglenales	

[7] In older literature also as *H. utriculatum.*

TABLE VIII. (Cont.)

Family Euglenaceae	*Euglena acus*
	E. deses (Bracher, 1919, 1937; Mast, 1927)
	E. gracilis (Mast & Gover, 1922; Pohl, 1948; Bünning & Schneiderhöhn, 1956)
	E. gracilis var. *bacillaris* (Gőssel, 1957)
	E. lacustris[8]
	E. limosa
	E. spirogyra (Mast, 1911)
	E. oxyuris
	E. stagnalis[8]
	E. viridis (Aderhold, 1888; Wager, 1900; Loeb & Wasteneys, 1916; Buder 1917)
	Lepocinclis texta (Bolte, 1920; Mast, 1927a; Brucker, 1954)
	Phacus acuminatus (Gőssel, 1957)
	P. longicaudus (Mast, 1911)
	P. pleuronectes (Mast & Gover, 1922)
	P. triquiter (Mast, 1911)
	Trachelomonas hispida
	T. intermedia (Buder, 1917)
	T. volvocina (Buder, 1917)
Family Peranemaceae	*Peranema trichophorum* (Mast & Hawk, 1936; Shettles, 1937)

PHYLUM CHRYSOPHYCOPHYTA

Class Xanthophydeae	
Order Heterochloridales	
Order Rhizochloridales	
Order Heterocapsales	
Order Heterococcales	
Order Heterotrichales	
Order Heterocloniales	
Order Vaucheriales	
Family Botrydiaceae	*Botrydium granulatum* swarm-spores (Strasburger, 1887)
Family Vaucheriaceae	*Vaucheria** (Stahl, 1880a; Moore, 1888)
Class Chrysophyceae	
Subclass Chrysophycidae	
Order Chrysomonadales	
Family Chrysomonadaceae	*Chromophyton* (= *Chromulina* ?)
	Chromulina psammobia (Fauré-Fremiet, 1950)
	C. rosanofii (Dangeard, 1928)
	C. woroniana
Order Isochrysidales	
Family Synuraceae	*Synura uvella* (Mainx, 1929)
Family Coccolithophoraceae	*Coccolithus huxleyi* (Mjaaland, 1956)

[8] Taxonomic status of these species uncertain.

TABLE VIII. (Cont.)

Order Ochromonadales	
Order Prymnesiales	
Order Rhizochrysidales	
Order Chrysocapsales	
Order Chrysotricales	
Subclass Silicoflagellatophycideae	
Order Siphonotestales	
Order Steriotestales	
Class Bacillariophyceae	
Order Centrales	
Order Pennales	
Family Naviculaceae	*Amphora montana* (Nultsch, 1956)
	Navicula brevis (Verworn, 1889)
	N. buderi (Nultsch, 1956)
	N. minuscula (Meinholds, 1911)
	N. radiosa (Heidingsfeld, 1943)
	Pinnularia
	Hantzchia amphioxus (Fauré-Fremiet 1951)
Family Nitzschiaceae	*Nitzschia communis* (Nultsch, 1956)
	Ni. dissipata (Meinhold, 1911)
	Ni. palea (Meinhold, 1911; Nultsch, 1956)
	Ni. stagnorum (Nultsch, 1956)
PHYLUM PYRROPHYCOPHYTA	
Class Dinophyceae	
Subclass Desmophycidae (Desmokontae)	
Order Desmomonadales	
Order Thecatales	
Family Prorocentraceae	*Prorocentrum micans* (Hasle, 1950; Halldal, 1956, 1958)
Subclass Dinophycidae (Dinokontae)	
Order Gymnodiniales	
Order Blastodiniales	
Order Peridiniales	
Family Glenodiniaceae	*Hemidinium nasutum* (Metzner, 1930)
Family Peridiniaceae	*Peridinium cinctum* (Metzner, 1930)
	P. trochoideum (Halldal, 1956, 1958)
	P. umbonatum (Metzner, 1930)
Family Goniaulaceae	*Goniaulax catenella* (Halldal, 1956, 1958)
	G. polyedra (Hasle, 1950)
Family Ceratiaceae	*Ceratium cornutum* (Metzner, 1930)
	C. furca (Nordli, 1957)
	C. fusus (Hasle, 1950; Nordli, 1957)
	C. lineatum (Nordli, 1957)
	C. tripos (Hasle, 1950; Nordli, 1957)
Order Rhizodiniales	
Order Dinocapsales	
Order Dinoccocales	
Order Dinotrichales	

TABLE VIII. (Cont.)

CLASSES OF UNCERTAIN SYSTEMATIC POSITION	
Class Cryptophyceae	
Order Cryptomonadales	
Family Cryptomonadaceae	*Chilomonas curvata* (Strasburger, 1878)
	C. parametium
	Cryptomonas ovata (Pringsheim, 1937)
Class Chloromonadophyceae	
PHYLUM PHAEOPHYCOPHYTA	
Class Phaeophyceae	
Order Ectocarpales	
Family Ectocarpaceae	*Ectocarpus siliculosus* (Fritsch, 1935; Papenfuss, 1935)
	E. tomentosus (Kylin, 1918)
	Sorocarpus uvaeformis (Abe, 1935)
Order Sphacelariales	
Order Cutleriales	
Order Tilopteridales	
Order Dictyotales	
Order Chordariales	
Family Chordariaceae	*Chorda filum* (Kylin, 1918)
	Heterochordaria abietina (Abe, 1935)
Family Spermatochnaceae	*Stilophora rhizodes* (Kylin, 1918)
Order Sporochnales	
Order Dictyosiphonales	
Family Punctariaceae	*Asperococcus bulbosus* (Kylin, 1918)
	Scytosiphon lomentarium (Abe, 1935)
Order Laminariales	
Family Laminariaceae	*Laminaria digitata*
	L. saccharina
Order Fucales	
Family Fucaceae	*Fucus serratus* (Kotte, 1923)
PHYLUM SCHIZOPHYTA	
Class Cyanophyceae	
Order Chroococcaceae	
Family Chroococcaceae	*Holopedia*
	Merismopedia revoluta (Carter, 1933)
Order Chamaesiphonales	
Order Hormogoniales	
Family Oscillatoriaceae	*Beggiatoa* (Engelmann, 1879a; Winogradsky, 1887)
	Glaucothrix gracillima (Verworn, 1889)
	Microcoleus vaginatus (Allen, 1957)
	Oscillatoria acroginea-coerulea (Hansgirg, 1882)
	O. agardhii (Troizkaja, 1921)
	O. amphibia (Funk, 1923)

TABLE VIII. (Cont.)

	O. cortiana
	O. frölichii (Hansgirg, 1882)
	O. formosa (Pieper, 1913; Burkholder, 1934)
	O. insignis (Famintzin, 1867; Hansgirg, 1882)
	O. jenensis (Schmid, 1921, 1923)
	O. nigra (Hansgirg, 1882)
	O. princeps (Hosoi, 1951)
	O. sancta (Burkholder, 1934)
	O. splendida (Burkholder, 1934)
	Lyngbya aestuarii (Allen, 1958)
	Phormidium autumnale (Allen, 1958)
	P. foveolarum
	Symploca (Schmid, 1918)
	Thioploca (Engelmann, 1879a)
Family Nostocaceae	*Anabaena cylindrica* (Allen, 1958)
	A. variabilis (Harder, 1917)
	Nostoc muscorum (Allen, 1958)
	N. punctiforme (Harder, 1917)
	N. sphaerocarpa (Allen, 1958)
	Pseudanabaena brevis (Carter 1933)
Family Rivulariaceae	*Calothrix parientina* (Allen, 1958)
Family Scytonemataceae	*Fremyella diplosiphon* (Allen, 1958)
	Plectonema boryanum (Allen, 1958)
	Pl. calothricoides (Allen, 1958)
	Pl. gracillimum
	Scytonema julianum (Geitler, 1922)
	Tolypothrix tenuis (Allen, 1958)
PHYLUM RHODOPHYCOPHYTA	
Class Rhodophyceae	
Subclass Bangiophycidae	
Order Porphyridiales	
Family Porphyridiaceae	*Porphyridium cruentum* (Dangeard, 1930; Vischer, 1935; Geitler, 1944)
Order Goniotrichales	
Order Bangiales	
Order Rhodochaetales	
Order Compsopogonales	
Subclass Florideophycidae	
Order Nemalionales	
Order Gelidales	
Order Gigartinales	

* = organisms in which phototactic movements of chloroplasts have been observed.

** = organisms in which chloroplasts as well as the organism as a whole move phototactically.

BIBLIOGRAPHY

ABE, K. 1935. Zur Kenntnis der Entwicklungsgeschichte von *Heterochordaria*, *Scytosiphon*, und *Sorocarpus*. Sci. Rep. Tohoku Imp. Univ. Ser. iv-Biol. **9**: 329-337. [p. 329]

ADAMSON, M. 1767. Un mouvement particulier découvert dans une plante appellée *Tremella*. Mem. Acad. Sci. Paris: 415-431.

ADERHOLD, R. 1888. Beiträge zur Kenntnis richtender Kräfte bei der Bewegung niederer Organismen. Jena Zeits. Naturwiss. **22**: 310-342.

ALLEN, MARY BELLE. 1952. The cultivation of Myxophyceae. Arch. Microbiol. **17**: 34-53.

———. 1958. [Personal communication]

BABUSHKIN, L. N. 1955a. [Adaptation of the chloroplast phototactic apparatus to light intensity]. Doklady Akad. Nauk S.S.S.R. **102**: 1215-1218. Referat. Zhur. Biol. 1956. No. 62609. [In Russian]

———. 1955b. [The phototactic action spectrum of chloroplasts]. *Ibid.* **103**: 333-335. Referat. Zhur. Biol. 1956. No. 48639. [In Russian]

———. 1955c. [On the relationship between chloroplast phototaxis and phytosynthesis]. *Ibid.* **103**: 507-510. Referat. Zhur. Biol. 1956. No. 76249. [In Russian]

BANCROFT, F. W. 1913. Heliotropism, differential sensibility, and galvanotropism in *Euglena*. Jour. Exp. Zool. **15**: 383-428.

BARANETZSKI, J. 1876. Influence de la lumière sur les plasmodia des Myxomycètes. Mem. Soc. Sc. Nat. Cherbourg **19**: 321-360.

DE BARY, A., and STRASBURGER, E. 1877. *Acetabularia mediterranea*. Bot. Zeit. **35**: 745-758. [p. 747]

BENDIX, S. W. 1957. Phototaxis in the desmid *Micrasterias rotata* var. *evoluta*. Thesis, Univ. Calif.

BERTHOLD, D. 1882. Beiträge zur Morphologie und Physiologie der Meeresalgen. Jahrb. Wiss. Bot. **13**: 569-717.

BLUM, H. F., and FOX, D. L. 1933. Univ. Calif. Pub. Physiol. **8**: 21-30.

BÖHM, J. A. 1856. Beiträge zur näheren Kenntnis des Chlorophylls. Sitz. Kais. Akad. Wiss. Wien. Math.-Nat. Kl. **22**: 479-512.

BOLTE, ELIZABETH. 1920. Über die Wirkung von Licht und Kohlensäure auf die Beweglichkeit grüner und farbloser Schwärmzellen. Jahrb. Wiss. Bot. **59**: 287-324.

BORZI, A. 1879. Note alla morfologia e biologia delle alghe Ficromacee. Nuov. Giorn. Bot. Ital. **11**: 347-388. [p. 385]

———. 1883. [Quoted in Pfeffer 1903, p. 324]

BRACHER, ROSE. 1919. Observations on *Euglena deses*. Ann. Bot. **33**: 93-102.

———. 1937. The light relation of *Euglena limosa* Gard. Part I. The influence of intensity and quality of light on phototaxy. Jour. Linn. Soc. Bot. **51**: 23-42.

BRAUN, A. 1851. Betrachtungen über die Erscheinung der Verjügung in der Natur, insbesondere in der Lebens- und Bildungsgeschichte der Pflanze. 363 pp.

BRUCE, V. G., and PITTENDRIGH, C. S. 1956. Temperature independence in a unicellular "clock." Proc. Nat. Acad. Sci. **42**: 676-682.

BRUCKER, W. 1954. Beiträge zur Kenntnis der Phototaxis grüner Schwärmzellen. I. Die Lichtempfindlichkeit von *Lepocinclis texta* und ihre Abhängigkeit von der Vorbelichtung und vom Kohlensäregehalt des Mediums. Arch. Protist. **99**: 294-327.

BUDER, J. 1917. Zur Kenntnis der phototaktischen Richtungsbewegungen. Jahrb. Wiss. Bot. **58**: 105-220.

————. 1919. Zur Biologie des Bacteriopurpurins und der Purpurbakterien. Jahrb. Wiss. Bot. **58**: 525-628.

BÜNNING, E., and SCHNEIDERHÖHN, GISELA. 1956. Über das Aktionspectrum der phototaktischen Reaktionen von *Euglena*. Arch. Mikrobiol. **24**: 80-90.

————, and TAZAWA, M. 1957. Über die negative-phototaktische Reaktion von *Euglena*. Arch. Mikrobiol. **27**: 306-310.

BURKHOLDER, P. R. 1933. Movement in the Cyanophyceae. The effect of pH upon movement in *Oscillatoria*. Jour. Gen. Physiol. **16**: 875-81.

————. 1934. Movement in the Cyanophyceae. Quart. Rev. Biol. **9**: 458-459.

DECANDOLLE, A. P. 1832. Physiologie végétale.

CARTER, NELLIE. 1926. An investigation into the cytology and biology of the Ulvaceae. Ann. Bot. **40**: 665-689.

————. 1933. A comparative study of the algal flora of two salt marshes. II. Jour Ecol. **21**: 128-208. [pp. 153, 158]

CLAYTON, R. K. 1953a. Studies in the phototaxis of *Rhodospirillum rubrum*. I. Action spectrum, growth in green light and Weber Law adherence. Arch. Microbiol. **19**: 107-124.

————. 1953b. II. The relation between phototaxis and photosynthesis. *Ibid.* 125-140.

————. 1953c. III. Quantitative relations between stimulus and response. *Ibid.* 140-165.

————. 1955. Tactic responses and metabolic activities in *Rhodospirillum rubrum*. *Ibid.* **22**: 204-213.

COHN, F. 1865. Über die Gesetze der Bewegung mikroscopischen Thiere und Pflanzen unter Einfluss des Lichtes. Jahrb. Schless. Ges. Vaterl. Cult. **42**: 35-36.

————. 1866. Ueber die Gesetze der Bewegung der mikroskopischen Pflanzen und Thiere unter Einfluss des Lichtes. Hedwigia **5**: 161-168.

CORRENS, G. 1897. Über die Membran und die Bewegung der Oscillarien. Ber. Deut. Bot. Ges. **15**: 139-148.

DANGEARD, P. A. 1928. Le déterminisme des mouvements chez les organismes inférieurs. Ann. Protist. **1**: 3-10.

————. 1930. Sur la mobilité de certaines cellules de *Porphyridium cruentum* Naegeli. Comp. Rend. Acad. Sci. [Paris] **190**: 819-821.

DAVENPORT, C. B. 1897. Experimental Morphology. 280 pp.

DESROCHE, P. 1912. Reaction des *Chlamydomonas* aux agens physiques. [Quoted in Halldal, 1958]

DODEL-PORT, A. 1876. Beiträge zur Kenntnis der Schwärmsporen von *Ulothrix zonata*. Bot. Zeit. **34**: 177-185.

DURSTON, A. D. 1925. The light reactions of *Dunaliella salina*. Thesis, Stanford Univ. [Quoted in Blum and Fox, 1933]

ELFVING, E. 1886. Über die Einwirkung von Äther und Chloroform auf die Pflanzen. Oefversigt Finska Vet. Soc. Förh. **28**.

ENGELMANN, TH. W. 1879a. Ueber die Bewegungen der Oscillarien und Diatomeen. Bot. Zeit. **37**: 49-56.

————. 1879b. Über Reizung contraktilen Protoplasmus durch plötzliche Beleuchtung. Pflüger's Arch. Ges. Physiol. **19**: 1-7.

————. 1881. Zur Biologie der Schizomyceten. *Ibid.* **26**: 537-545.

———. 1882a. Ueber Sauerstoffausscheidung von Pflanzenzellen im Mikrospectrum. Bot. Zeit. **40**: 419-426.
———. 1882b. Über Licht- und Farbenperception niederster Organismen. Pfluger's Arch. Ges. Physiol. **29**: 387-400.
———. 1883. *Bacterium photometricum.* Ein Beitrag zur vergleichenden Physiologie des Licht- und Farbensinnes. *Ibid.* **30**: 95-124.
———. 1888a. Ueber Bacteriopurpurin und seine physiologische Bedeutung. *Ibid.* **42**: 183-188.
———. 1888b. Die Purpurbacterien und ihre Beziehungen zum Lichte. Bot. Zeit. **46**: 661-669, 677-689, 693-701, 709-720.
ENTZ, G. 1930. Über gehemmte Lebens- und Absterbe-Erscheinungen einiger Dinoflagellaten. Arb. Ungar. Biol. Forschungsinst. **3**: 206-243. [p. 227]
EWALD, W. F. 1912. On artificial modification of light reactions and the influence of electrolytes on phototaxis. Jour. Exp. Zool. **13**: 591-612.
FAMINTZIN, A. 1867a. Die Wirkung des Lichtes auf Algen und einige andere ihnen verwandte Organismen. Jahrb. Wiss. Bot. **6**: 1-44.
———. 1867b. Die Wirkung des Lichtes und der Dunkelheit auf die Verteilung der Chlorophyll-körner in den Blättern von *Mnium* sp. *Ibid.* 45-49.
FAURÉ-FREMIET, E. 1948. Le rythme de marée du *Strombidium oculatum.* Bull. Biol. France-Belgique. **82**: 3-23.
———. 1950. Rhythme de marée d'une *Chromulina* psammophile. *Ibid.* **84**: 207-214.
———. 1951. The tidal rhythm of the diatom *Hantzschia amphioxys.* Bio. Bull. **100**: 173-177.
FECHNER, R. 1915. Die Chemotaxis der Oscillarien und ihre Bewegungserscheinungen überhaupt. Zeit. Bot. **7**: 289-364.
FISCHER, A. 1882. Untersuchungen über die Parasiten der Saprolegnieen. Jahrb. Wiss. Bot. **13**: 298.
FISCHER, W. 1939. Die phototaktische Reaction von *Chromatium* bei plötzlichen und allmählichem Lichtabfall. Doct. Diss. Breslau.
FOLGER, H. T. 1925. A quantitative study of reactions to light in *Amoeba.* Jour. Exp. Zool. **41**: 261-291.
———. 1926. The effects of mechanical shock on locomotion in *A. proteus.* Jour. Morph. & Physiol. **42**: 359-370.
———. 1927. The relation between the responses by *Amoeba* to mechanical shock and to sudden illumination. Bio. Bull. **53**: 405-412.
FÖYN, B. 1929. Vorlaufige Mitteilung über die Sexualität und den Generationswechsel von *Cladophora* und *Ulva.* Ber. Deut. Bot. Ges. **47**: 495-506.
FRANCÉ, R. H. 1893. Zur Morphologie und Physiologie der Stigmata der Mastigophoren. Zeit. Wiss. Zool. **56**: 138-164.
———. 1908. Experimentelle Untersuchungen über Reizbewegungen und die Lichtsinnesorgane der Algen. Zeit. Ausb. Entwlehre. **2**: 29-43.
———. 1909. Untersuchungen über die Sinnesfunktion der Augenflecke bei Algen. Arch. Hydrobiol. **4**: 37-48.
FRANK, G. 1872. Über die Veränderung der Lage der Chlorophyll-Körner und der Protoplasma in der Zelle, und deren innere und äussere Ursachen. Jahrb. Wiss. Bot. **8**: 216-303.
FRENCH, C. S. 1938. The rate of CO_2 assimilation by purple bacteria at various wave lengths of light. Jour. Gen. Physiol. **21**: 71-87.
FREY-WYSSLING, A., and STECHER, H. 1954. Über den Feinbau des *Nostoc*-Schleimes. Zeits. Zellf. **39**: 515-519.

FRISCH, K. v., and KUPELWEISER, H. 1913. Über den Einfluss der Lichtfarbe auf die phototaktischen Reaktionen neiderer Krebse. Biol. Cent. **33**: 517-552.

FRITSCH, F. E. 1935. Structure and reproduction of the algae.

FUNK, G. 1923. Über Bewegungen der Kolonien von *Oscillatoria amphibia* Ag. Beih. Bot. Cent. I. **39**: 257-320.

GEITLER, L. 1922. Neue und wenig bekannte Blaualgen. Ber. Deut. Bot. Ges. **40**: 283-287.

————. 1944. Furchungsteilung, simultane Mehrfachteilung, Lokomotion, Plasmoptyse und Ökologie der Bangiaceae *Porphyridium cruentum*. Flora **137**: 300-333.

GÖBEL. 1880. Jour. Roy. Micros. Soc. **3**: 318.

GOODWIN, T. W., and SISSINS, M. E. 1955. Changes in carotenoid synthesis in *Rhodospirillum rubrum* during growth. Bioch. Jour. **61**: xiii-xiv.

GÖSSEL, I. 1957. Über das Aktionsspektrum der Phototaxis chlorophyllfreier Euglenen und über die Absorption des Augenflecks. Arch. Mickrobiol. **27**: 288-305.

HALLDAL, P. 1956. Phototaxis in flagellates. Carnegie Inst. Wash., Yearbook **1955–1956**: 259-261.

————. 1957. Importance of Ca and Mg ions in phototaxis of motile green algae. Nature **179**: 215-216.

————. 1958. Action spectra of phototaxis and related problems in Volvocales, *Ulva*-gametes, and Dinophyceae. Physiol. Plant. **11**: 118-153.

HANSGIRG, A. 1882. Nova pozorovani o pohybech drkalek. Neue Beobachtungen über die Bewegungen der Oscillarien. [Abstract]. Bot. Cent. **12**: 361-364.

————. 1883. Bemerkungen über die Bewegungen der Oscillarien. Bot. Zeit. **41**: 831-843.

HARDER, R. 1917. Ernährungsphysiologische Untersuchungen an Cyanophyceen, hauptsächlich dem endophytischen *Nostoc punctiformis*. Zeit. Bot. **9**: 143-242. [p. 161]

————. 1918. Über die Bewegung der Nostocaceen. *Ibid.* **10**: 177-244.

————. 1920. Über die Reaktionen freibeweglicher pflanzlicher Organismen auf plötzliche Aenderungen der Lichtintensität. *Ibid.* **12**: 353-462.

HARRINGTON, N. R., and LEAMING, E. 1900. The reactions of *Amoeba* to light of different colors. Amer. Jour. Physiol. **3**: 9-18.

HARTSHORNE, J. N. 1953. The function of the eyespot in *Chlamydomonas*. New Phytol. **52**: 292-297.

HASLE, G. R. 1950. Phototactic vertical migration in Marine Dinoflagellates. Oikos **2**: 162-175.

HEIDINGSFELD, I. 1943. Phototaktische Untersuchungen an *Navicula radiosa*. Doct. Diss. Breslau.

HÖFLER, K. 1926. Über Eisengehalt und lokale Eisenspeicherung in der Zellwand der Desmidiaceen. Sitz. Akad. Wiss. Wien. Math-Nat. **135**: 103-166.

HOLMES, S. J. 1903. Phototaxis in *Volvox*. Biol. Bull. **4**: 319-326.

HOSOI, A. 1951. Secretion of the slime substance in *Oscillatoria* in relation to its movement. Bot. Mag. Tokyo **64**: 14-17.

JENNINGS, H. S. 1904. Contributions to the study of the behavior of lower organisms. Carnegie Inst. Wash. Pub. #16. 256 pp.

KLEBS, G. 1885. Über Bewegung und Schleimbildung der Desmidiaceen. Biol. Cent. **5**: 353-367.

———. 1896. Die Bedingungen der Fortpflanzung bei einigen Algen und Pilzen. 543 pp.

KOFOID, C. A., and SWEZY, OLIVE. 1921. The free-living unarmored Dinoflagellata. Mem. Univ. Calif. **5**: 1-534.

KOL, E. 1927. Über die Bewegung mit Schleimbildung einiger Desmidiaceen aus der Hohen Tatra. Folia Cryptogamica Szeged **1**: 435-442.

KOTTE, W. 1923. Zür Reizphysiologie der *Fucus*—Spermatozoiden. Ber. Deut. Bot. Ges. **41**: 24-32.

KRENNER, J. A. 1925. Ueber die Bewegung der Oscillarien. Arch. Protist. **51**: 530-541. [p. 532]

KRIEGER, W. 1939. Die Desmidiaceen Europas mit Berücksichtigung der ausserauropäischen Arten. *In:* Rabenhorst, L. Kryptogamen-Flora von Deutschland, Osterreich und der Schweiz. 2nd Ed. Bd. 13, Abt. 1, Teil 2. 117 pp.

KYLIN, H. 1918. Studien über die Entwicklungsgeschichte der Phaeophyceen. Svensk. Bot. Tidsskr. **12**: 1-64. [p. 3]

———. 1930. Über Heterogamie bei *Enteromorpha intestinalis*. Ber. Deut. Bot. Ges. **48**: 458-464.

———. 1933. Über die Entwicklungsgeschichte der Phaeophyceen. Lunds. Univ. Årsskr. N.F. 2, **29**: 1-102.

LAURENS, H., and HOOKER, H. D., JR. 1918. The relative sensitivity of *Volvox* to spectral lights of equal radiant energy content. Anat. Rec. **14**: 97-98.

———. 1920. Studies on the relative physiological value of spectral lights. II. The sensibility of *Volvox* to wave-lengths of equal energy content. Jour. Exp. Zool. **30**: 345-368.

LAUTERBORN, R. 1896. Untersuchungen über Bau, Kernteilung, und Bewegung der Diatomeen. 165 pp. [p. 130]

LEPESCHKIN, W. W. 1909. Zur Kenntnis der photonastischen Variationsbewegung und der Einwirkung des Beleuchtungswechsels auf die Plasmamembran. Beih. Bot. Zent. **24**: 308-356.

LEWIS, F. J. 1898. The action of light on *Mesocarpus*. Ann. Bot. **12**: 418-421.

LINSBAUER, K., and ABRAMOWICZ, E. 1909. Untersuchungen über die Chloroplastenbewegungen. Sitz. Kais. Akad. Wiss. Wien. Math.-Nat. I, **118**: 418-241.

LOEB, J., and MAXWELL, S. S. 1910. Further proof of the identity of heliotropism in animals and plants. Univ. Cal., Pub. Physiol. **3**: 195-197.

LOEB, J., and WASTENEYS, H. 1916. The relative efficiency of various parts of the spectrum for the heliotropic reactions of animals and plants. Jour. Exp. Zool. **20**: 217-236.

LUNTZ, A. 1931a. Untersuchungen über die Phototaxis. I. Mitteilung: Die absoluten Schwellenwerte und die relative Wirksamkeit von Spektralfarben bei grünen und farblosen Einzelligen. Zeit. Vergl. Physiol. **14**: 68-92.

———. 1931b. II. Mitteilung: Lichtintensität und Schwimmergeschwindigkeit bei *Eudorina elegans*. *Ibid.* **15**: 652-678.

———. 1932. III. Mitteilung: Die Umkehr der Reaktionsrichtung bei starken Lichtintensitäten und ihre Bedeutung für eine allgemeine Theorie der photische Reizwirkung. *Ibid.* **16**: 204-217.

MAINX, F. 1929. Untersuchungen über den Einfluss von Aussenfaktoren auf die phototaktische Stimmung. Arch. Protist. **68**: 105-176.

———. 1931. Gametencopulation und Zygotenkeimung bei *Hydrodictyon reticulatum*. *Ibid.* **75**: 502-516. [p. 504]

———, and WOLF, H. 1940. Reactionsintensität und Stimmungsänderung in ihrer Bedeutung für eine Theorie der Phototaxis. Arch. Protist. **93**: 105-120.

MANTEN, A. 1948. Phototaxis, phototropism and photosynthesis in purple bacteria and blue-green algae. Doct. Diss. Univ. Utrecht.

MASSART, J. 1891. Recherches sur les organismes inférieurs. II. La sensibilité à la concentration chez les êtres unicellulaires marins. Acad. Roy. Belg. Bull. III. **22**: 148-167.

MAST, S. O. 1906. Light reactions in lower organisms. I. *Stentor coeruleus.* Jour. Exp. Zool. **3**: 359-399.

———. 1907. Light reactions in lower organisms. II. *Volvox globator.* Jour. Comp. Neur. & Psychol. **17**: 99-189.

———. 1910. Reactions in *Amoeba* to light. Jour. Exp. Zool. **9**: 265-277.

———. 1911. Light and the behavior of organisms. 410 pp.

———. 1916. The process of orientation in the colonial organism *Gonium pectorali* and a study of the structure and function of the eye-spot. Jour. Exp. Zool. **20**: 1-18.

———. 1917. The relation between spectral color and stimulation in the lower organisms. *Ibid.* **22**: 471-528.

———. 1918. Effects of chemicals on reversion in orientation to light in the colonial form *Spondylomorum quaternarium. Ibid.* **26**: 503-520.

———. 1919. Reversion in the sense of orientation to light in the colonial forms, *Volvox globator* and *Pandorina morum. Ibid.* **27**: 367-390.

———. 1927a. Structure and function of the eye-spot in unicellular and colonial organisms. Arch. Protist. **60**: 197-220.

———. 1927b. Reversal in photic orientation in *Volvox* and the nature of photic stimulation. Zeits. Vergl. Physiol. **5**: 730-738.

———. 1931. The nature of response to light in *Amoeba proteus. Ibid.* **15**: 139-147.

———. 1932a. The role of adaptation to light and to darkness in *Volvox globator. Ibid.* **17**: 644-658.

———. 1932b. Localized stimulation, transmission of impulses, and the nature of response in *Amoeba.* Physiol. Zool. **5**: 1-15.

———. 1936. Motor responses to light in invertebrate animals. *In:* Duggar, M. [ed.] Biological effects of radiation.

———. 1941. Motor responses in unicellular animals. *In:* Calkins, G. N. and F. M. Summers [eds.] Protozoa in biological research.

———, and GOVER, MARY. 1922. Relation between intensity of light and rate of locomotion in *Phacus pleuronectes* and *Euglena gracilis* and its bearing on orientation. Biol. Bull. **43**: 203-209.

———, and HAWK, B. 1936. Response to light in *Peranema trichophorum.* I. Relation between dark-adaptation and sensitivity to light. Biol. Bull. **70**: 408-412.

———, and HULPIEU, H. R. 1930. Variations in the response to light in *Amoeba proteus* with special reference to the effects of salt and hydrogen ion concentration. Protoplasma **11**: 412-431.

———, and JOHNSON, P. L. 1932. Orientation in light from two sources and its bearing on the function of the eyespot. Zeits. Vergl. Physiol. **16**: 252-274.

———, and STAHLER, N. 1937. The relation between luminous intensity, adaptation to light, and rate of locomotion in *Amoeba proteus* (Leidy). Bio. Bull. **73**: 126-133.

MAYER, A. M., and POLJAKOFF-MAYBER. 1957. Tactic movements in *Chlamydomonas*. Nature **180**: 927.

MEINHOLD, TH. 1911. Beiträge zur Physiologie der Diatomeen. Beitr. Biol. Pflanz. **10**: 353-378.

METZNER, P. 1919. Über die Wirkung photodynamischer Stoffe auf *Spirillum volutans* und die Beziehungen der photodynamischen Erscheinungen zur Phototaxis. Bioch. Zeit. **101**: 33-53.

———. 1921. Zur Kenntnis der photodynamischen Erscheinungen. II. Die induzierte Phototaxis bei *Paramecium caudatum*. *Ibid.* **113**: 145-173.

———. 1930. Bewegungstudien an Peridineen. Zeit. Bot. **22**: 225-265.

MILATZ, J. M. W., and MANTEN, A. 1953. The quantitative determination of the spectral distribution of phototactic sensitivity in the purple bacterium *Rhodospirillum rubrum*. Biochim. et Biophys. Acta **11**: 17-27.

MILLOT, N. 1957. Animal photosensitivity, with special reference to eyeless forms. Endeavor **16**: 19-28.

MIYAKE, K., and KUNEIDA, H. 1931. On the conjugation of the gametes and the development of the zoospores in Ulvaceae. Jour. Coll. Ag. Imp. Univ. Tokyo **11**: 341-357.

MJAALAND, G. 1956. Some laboratory experiments on the coccolithophorid *Coccolithus huxleyi* (Lohm.) Kamptner. Oikos **7**: 251-255.

MOLISCH, H. 1907. Die Purpurbacterien nach neuen Untersuchungen. 95 pp.

MOORE, S. LEM. 1888a. Studies in vegetable biology, III and IV. The influence of light upon protoplasmic movement. Part I. Jour. Linn. Soc. Bot. **24**: 200-251.

———. 1888b. (The same) Part II. *Ibid.* 351-389.

MÜHLDORF, A. 1935. Das Plasmodesmenproblem bei der Gattung *Oscillatoria* (Cyanophyceae). Bul. Grad. Bot. Muz. Univ. Cluj. **15**: 167.

———. 1938. Einige Betrachtungen zur Membranmorphologie der Blaualgen. Ber. Deut. Bot. Ges. **56**: 316-336.

MÜLLER, F. 1911. Untersuchungen über die chemotaktische Reizbarkeit der Zoosporen von Chytridiaceen und Saprolegniaceen. Jour. Wiss. Bot. **49**: 421.

MÜLLER, O. 1889. Durchbrechung der Zellwand in ihren Beziehungen zur Ortzbewegung der Bacillariaceen. Ber. Deut. Bot. Ges. **7**: 169-189.

NÄGELI, C. 1860. Ortsbewegungen der Pflanzenzellen und ihren Theile (Strömungen). Beit. Wiss. Bot. **2**: 59-108.

VANNIEL, C. B. 1944. The culture, general physiology, morphology, and classification of the non-sulfur purple and brown bacteria. Bact. Rev. **8**: 1-118.

———. 1954. The chemoautotrophic and photosynthetic bacteria. Ann. Rev. Microbiol. **8**: 105-132.

NIENBURG, W. 1916. Die Perzeption des Lichtreizes bei den Oscillarien und ihre Reaktionen auf Intensitätsschwankungen. Zeit. Bot. **8**: 161-193.

NIKILITSCHEK, A. 1934. Das Problem der Oscillatorien-Bewegung. I. Die Bewegungserscheinungen der Oscillatorien. Beih. Bot. Zentralb. (Z. Abt.) **52**: 205-257.

NORDLI, E. 1957. Experimental studies on Ceratia. Oikos **8**: 200-265.

NOTHMANN-ZUCKERKANDLE, N. 1915. Über die Erregung der Protoplasmaströmung durch verschiedene Strahlenarten. Ber. Deut. Bot. Ges. **33**: 301-313.

NULTSCH, W. 1956. Studien über die Phototaxis der Diatomeen. Arch. Protist. **101**: 1-68.

OLTMANNS, F. 1892. Über die photometrischen Bewegungen der Pflanzen. Flora **75**: 183-266.

————. 1917. Über Phototaxis. Zeit. Bot. **9**: 257-338.

PAPENFUSS, G. F. 1935. Alternation of generations in *Ectocarpus siliculosus*. Bot. Gaz. **96**: 428, 431.

————. 1955. Classification of the algae. *In:* A century of progress in the natural sciences, 1853-1953. Calif. Acad. Sci.

PASCHER, A. 1907. Studien über die Schwärmer einiger Süswasseralgen. Bib. Bot. **67**: 1-115.

PFEFFER, W. 1903. The physiology of plants. 2nd Ed. Vol. 3: 321-326. [Tr. and Ed. Ewart]

PHILLIPS, O. P. 1904. A comparative study of the cytology and movements of the Cyanophyceae. Contr. Bot. Lab. Univ. Penn. **2**: 237-355.

PIEPER, A. 1913. Die Phototaxis der Oscillarien. Ber. Deut. Bot. Ges. **31**: 594-599.

————. 1915. Die Phototaxis der Oscillarien. Doct. Diss., Berlin.

PINCUSSEN, L. 1930. Photobiologie. 543 pp.

PITTENDRIGH, C. S. 1958. Perspectives in the study of biological clocks. *In:* A. A. Buzzati-Traverso [ed.] Perspective in marine biology.

————, and BRUCE, V. G. 1957. An oscillator model for biological clocks. *In:* Rudnick, D. [ed.] Rhythmic and synthetic processes in growth. 15th Growth Symposium.

POHL, R. 1948. Tagesrhythmus in phototaktischen Verhalten der *Euglena gracilis*. Zeits. Naturf. **3b**: 367-374.

PRELL, H. 1921. Zur Theorie der sekretorischen Ortsbewegung. I. Die Bewegung der Cyanophyceen. Arch. Protist. **42**: 99-156.

PRINGSHEIM, E. G. 1912. Reizbewegungen der Pflanzen. [pp. 200-209]

————. 1937. Über das Stigma bei farblosen Flagellaten. Cytologia, Fujii Jubilee Vol. 234-255.

————, and PRINGSHEIM, OLGA. 1949. The growth requirements of *Porphyridium cruentum*. Jour. Ecol. **37**: 57-64.

PRITCHARD, A. 1861. A history of infusoria. 439 pp. [p. 6]

RALFS, J. 1848. The British desmidieae. [p. 22]

RAY, J. 1693. Historia Plantarum.

RICHTER, O. 1903. Reinkulturen von Diatomeen. Ber. Deut. Bot. Ges. **21**: 493-506.

ROTHERT, W. 1901. Beobachtungen und Betrachtungen über taktische Reizerscheinungen. Flora **88**: 371-421.

SCHAEFFER, A. A. 1917. Reactions of *Amoeba* to light and the effect of light on feeding. Biol. Bull. **32**: 45-74.

SCHENK, H. 1894. Lehrbuch der Botanik. p. 272.

SCHILLER, J. 1907. Beiträge zur Kenntnis der Entwicklung der Gattung *Ulva*. Sitz. Akad. Wiss. Wien. Math.-Nat. Kl. 1, **116**: 1691-1716.

SCHLEGEL, H. 1956. Vergleichende Untersuchungen über die Lichtempfindlichkeit einiger Purpurbakterien. Arch. Protist. **101**: 69-97. [p. 95]

SCHMID, G. 1918. Zur Kenntnis der Oscillarienbewegung. Flora **111-112**: 327-379.

————. 1921. Über Organisation und Schleimbildung bei *Oscillatoria jenensis* und das Bewegungsverhalten Künstlicher Teilstücke, etc. Jahrb. Wiss. Bot. **60**: 572-627.

————. 1923. Das Reizverhalten künstlicher Teilstücke, die Kontraktilität

und das osmotische Verhalten der *Oscillatoria jenensis*. *Ibid.* **62**: 328-419.

SCHRAMMECK, J. 1934. Untersuchung über die Phototaxis der Purpurbakterien. Beit. Biol. Pflanzen **22**: 315-380.

SCHRÖDER, B. 1902. Untersuchungen über Gallertbildung der Algen. Verh. Nat.-Med. Ver. Heidelberg, N. F. **7**: 139-196.

SCHULZ, G. 1955. Bewegungsstudien sowie electronenmikroskopische Membranuntersuchungen an Cyanophyceen. Arch. Mikrobiol. **21**: 335-370.

SCHULZE, BRUNO. 1927. Zur Kenntnis einiger Volvocales. Arch. Protist. **58**: 508-576.

SENN, G. 1908. Die Gestalts- und Lageveränderung der Pflanzen Chromatophoren.

SHETTLES, L. B. 1937. Response to light in *Peranema trichophorum* with special reference to dark adaptation and light adaptation. J. Exper. Zool. **77**: 215-249.

SMITH, G. M. 1946. The nature of sexuality in *Chlamydomonas*. Amer. Jour. Bot. **33**: 625-630.

————. 1955. Cryptogamic Botany. 2nd. Ed. Vol. 1. [pp. 201-203]

STAHL, E. 1878. Über den Einfluss des Lichtes auf die Bewegungserscheinungen der Schwärmsporen. Verh. Phys.-Med. Ges. Würzburg. Juli. [Summary in Bot. Zeit. **36**: 715]

————. 1880a. Über den Einfluss von Richtung und Stärke der Beleuchtung auf einige Bewegungserscheinungen im Pflanzenreiche. Bot. Zeit. **38**: 297-304.

————. 1880b. Über den Einfluss des Lichtes auf die Bewegungen der Desmidien. Verh. Phys.-Med. Ges. Würzburg **14**: 24-34.

STANIER, R. Y., and COHEN-BAZIRE, GERMAINE. 1957. The role of light in the microbial world: some facts and speculations. *In:* Microbial Ecology. 7th Symp. Soc. Gen. Microbiol. [pp. 56-89]

STRASBURGER, E. 1878. Wirkung des Lichtes und der Wärme auf Schwärmsporen. Jena. Zeit. Nat. **12**: 551-625.

STRZESZEWSKI, B. 1913. Zur Phototaxis des *Chromatium weissii*. Bull. Acad. Sci. Cracovie. B: 416-431.

TCHAKHOTINE, S. 1936. La fonction du stigma chez le flagellé *Euglena*, étudiée au moyen de la micropuncture ultraviolette. Compt. Rend. Soc. Biol. [Paris] **121**: 1162-1165.

THOMAS, J. B., and NIJENHUIS, L. E. 1950. On the relation between phototaxis and photosynthesis in *Rhodospirillum rubrum*. Biochim. et Biophys. Acta **6**: 317-324.

THURET, G. 1850. Recherches sur les zoospores des algues. Ann. Sci. Nat. Bot. III. **14**: 246-247.

TORREY, H. B. 1907. The method of trial and the tropism hypothesis. Science **26**: 313-323.

TREVIRANUS, L. C. 1817. Vermischte. Schriften anatomischen und physiologischen inhalts von G. R. und L. C. Treviranus Bnd. II, pp. 79-87.

TROIZKAJA, O. V. 1921. Sur la phototaxis et l'influence de la lumière sur *Oscillaria Agardhii* Gom. Jour. Soc. Bot. Russ. **6**: 121-136.

ULLRICH, H. 1926. Über die Bewegungen von *Beggiatoa mirabilis* und *Oscillatoria jenensis*. I. Planta **2**: 295-324.

————. 1929. (The same) II. *Ibid.* **9**: 144-194.

VERWORN, M. 1889. Psychophysiologische Protistenstudien. 218 pp.

————. 1894. Allgemeine Physiologie. 615 pp.

VISCHER, W. 1935. Zur Morphologie, Physiologie und Systematik der Blutalge *Porphyridium cruentum*. Verh. Naturforsch. Ges. Basel **46**. [Quoted in Geitler, 1944].

VOERKEL, H. 1934. Untersuchungen über die Phototaxis der Chloroplasten. Planta **21**: 156-205.

WAGER, H. 1900. On the eye-spot and flagellum in *Euglena viridis*. Jour. Linn. Soc. (Zool.) **27**: 463-481.

WEST, G. S., and FRITSCH, F. E. 1927. A treatise on the British freshwater algae. [p. 144]

WINOGRADSKY, S. 1887. Ueber Schwefelbacterien. Bot. Zeit. **45**: 513-423. [p. 517]

WOLKEN, J. J., and SHIN, E. 1958. Photomotion in *Euglena gracilis*. I. Photokinesis. II. Phototaxis. Jour. Protozool. **5**: 39-46.

ZUELZER, M. 1911. Über *Spirochaeta plicatilis* Ehrbg. und deren Verwandschaftsbeziehungen. Arch. Protist. **24**: 1-59. [p. 45]

ZURZYCKA, ALICJA. 1951. The influence of the wave-length of light on the movements of chloroplasts in *Lemna trisulca* L. Acta. Soc. Bot. Pol. **21**: 17-38.

————, and ZURZYCKI, JAN. 1950. The influence of temperature on the phototactic movements of chloroplasts. *Ibid.* **20**: 665-680.

————. 1951. The influence of some metallic ions on the phototactic movements of chloroplasts. *Ibid.* **21**: 113-124.

————. 1953. Badania nad ruchami fototakycznymi chloroplastow I. [Studies on the phototactic movements of chloroplasts. I.] *Ibid.* **22**: 667-678.

————. 1954. (The same) II. *Ibid.* **23**: 279-288.

ZURZYCKI, JAN. 1953. Arrangement of chloroplasts and light absorption in the cell. *Ibid.* **22**: 299-320.

————. 1955. Chloroplast arrangement as a factor in photosynthesis. *Ibid.* **24**: 27-63.

————, and ZURZYCKA, ALICJA. 1955. Influence of some catalyst poisons on phototactic movements of chloroplasts. *Ibid.* **24**: 663-674.