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Historical corner

Contributions of Theodor Wilhelm Engelmann on phototaxis, chemotaxis, and photosynthesis

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Abstract

Theodor Wilhelm Engelmann (1843–1909), who had a creative life in music, muscle physiology, and microbiology, developed a sensitive method for tracing the photosynthetic oxygen production of unicellular plants by means of bacterial aerotaxis (chemotaxis). He discovered the absorption spectrum of bacteriopurpurin (bacteriochlorophyll *a*) and the scotophobic response, photokinesis, and photosynthesis of purple bacteria.

Abbreviations: B – Bacterium; *C – Chromatium*

Introduction

The fame of people celebrated and honored during their lifetimes often dwindles shortly after their death. This holds true for the sciences and humanities as well and is a normal process if the achievements were restricted to the celebrity's time. Some are forgotten, even though their contribution to their field was comparable to the achievements of those found in bibliographies, encyclopedias, and textbooks of the present time. The reasons why some are cited as the leader and founder of their discipline while others are neglected are numerous.

The contributions of Theodor Wilhelm Engelmann, a great experimenter and formulator of theories on the contraction and excitability of muscles and heart – and a somewhat forgotten celebrity – is presented here. During a short period of his life, he made important discoveries on the influence of the quality and quantity of light on the movement of sulfur purple bacteria and on the aerotaxis of heterotrophic bacteria.

The life and work of Theodor Wilhelm Engelmann

Theodor Wilhelm Engelmann was born on November 30, 1843, as the son of well-known bibliographer and publisher Wilhelm Engelmann and his wife Christiane Therese Hasse, in Leipzig, Germany. He was raised in a stimulating atmosphere of humanities and science. At the prestigious Thomas School in Leipzig, young Engelmann developed a predilection for the cello and soon attained a professional level of competence. In addition, he was inspired by his uncle Julius Viktor Carus and the anatomist Carl C. Gegenbaur to conduct systematic observations of living organisms, particularly of the Infusoria.

Engelmann studied natural sciences and medicine at the universities in Jena, Heidelberg, Göttingen, and Leipzig. His dissertation on the cornea published in 1867, brought him to the attention of the distinguished Dutch physiologist Frans Cornelius Donders, who offered him a post as his associate. There in Utrecht, Engelmann began a very successful career. He was promoted as asso-

ciate professor and later as full professor, and became the successor of Donders.

The 30 years spent in Utrecht by Engelmann were not only a productive scientific period, but also were a personally fulfilling time in his circle of family and friends. Engelmann married Donder's only daughter Marie in 1869. Their bliss was tragically brought to an end a year later when Marie died during the birth of twins. This trauma was compounded by the demise of his brother-in-law, A. von Bezold and his brother, Paul, within two years during this time period. Engelmann's personal dilemma was assuaged when he met the pianist Emma Brandes (née Vick), whom he married in 1870. She retired from a promising career as a concert pianist to raise a family and preside over the household. Emma and Theodor Engelmann were accomplished musicians and played a pivotal role in the musical culture of Holland. Musicians such as Clara Schumann, Anton Rubinstein, Heinrich Herzogenberg, Hans von Bülow, Edward Grieg, Josef Joachim, and Johannes Brahms visited their home and admired their contribution to chamber music. Johannes Brahms dedicated his third string quartet to Engelmann (Kingreen 1972; Kamen 1986).

Engelmann's research on muscle excitation and contraction, and on cardiac physiology (myogenic theory of excitation and stimulus transduction) earned him international acclaim and distinction. He was offered professorships in Freiburg, Zürich, and Jena, but he declined them because of the good working conditions, the quiet atmosphere, and the relative absence of burdensome administrative duties in Utrecht. In 1897, he was offered the prestigious professorship for physiology in Berlin. Despite his reservations because of his poor health, his age of 54, and the excessive work that would await him, he accepted the position after the Minister for culture fulfilled all of his requests for modernization of the institute (Kingreen 1972). From 1897 to 1905, Engelmann (Figure 1) reorganized the curriculum in physiology, reformed the Institute of Physiology, published numerous research articles, and was active as the dean of the medical faculty (Kingreen 1972). He was highly respected and had a charming personality. Unfortunately, the burden of work and the fragile state of his health lead to the rapid decline of his health. He retired in 1908 and died on May 20, 1909, at the age of 65 years and 6 months.

Figure 1. Portrait of T. W. Engelmann as young Professor of Physiology in Utrecht, 1872; the figure is from Kingreen 1972.

The remainder of this article will concentrate on the period of 1881–1888, when most of his microbiological studies were published. After 1888, Engelmann greatly reduced his microscopy studies because he suffered from headaches. The contributions of Engelmann to music and to the physiology of higher organisms and his life are described in Kingreen (1972), Rothschuh (1981) and Kamen (1986).

The production of oxygen in oxygenic photosynthesis shown by the aerotaxis of bacteria

The formation of oxygen in the photosynthesis of plants and algae has been known since the investigations of Jan Ingenhousz (1730–1799) in 1796 and Théodore de Saussure (1767–1845) in 1804 and has been measured using a variety of methods (e.g., gas analysis by Ingenhousz, Saussure, and Jean Baptiste Boussingault; counting bubbles by Julius Sachs (1832–1897) and Wilhelm F.P. Pfeffer (1845–1920)). The outstanding contributions of Ingenhousz to photosynthesis have been discussed by Gest (2000). Engelmann confirmed that oxygen production is dependent on chlorophyll and a distinct quality and quantity of light (Engelmann 1881a; see Timiriazeff (1875) for an action spectrum in the red region for CO_2 fixation by leaves). Engelmann's major contributions were the measurement of oxygen production by microscopic algae and the determination of the spectral

efficiency of light on this process using a microscopic method – the aerotaxis of bacteria, i.e., the movement of oxygen-sensing bacteria in a gradient from low to higher concentrations of oxygen, in combination with a microspectral apparatus (Engelmann 1881a, 1882b, c). The microspectral apparatus (Engelmann 1889), constructed by Carl Zeiss, Jena, consisted of an illumination system (gas light or sunlight, later also electric light, directed on a slit, adjustable to 0–2 mm width and a variable length), a condenser lens, a prism, and an objective lens in order to project the image of the spectrum at the level of the specimen (Engelmann 1882b, c, 1889). The wavelength was determined using an ocular micrometer calibrated to the Fraunhofer lines of the sun spectrum.

Engelmann simultaneously observed the effect of the different parts of the spectrum on the accumulation of aerotactic active, chemotrophic bacteria in the immediate surrounding of the irradiated parts of thylakoids of unicellular algae, such as *Euglena, Cladophora,* and *Oedogonium,* or cyanobacteria, such as *Oscillatoria*. In another series of observations, Engelmann moved the sample successively through the different regions of the spectrum (Engelmann 1882b, c). For quantitative measurements, the light intensity absorbed by the sample was compared with the light intensity in a parallel slit (Engelmann 1884). Before the experiment was started, oxygen in the microscopic chamber was removed by respiration of the bacteria or by flushing with pure hydrogen. When the algae were irradiated, the bacteria swam along the oxygen gradient to the area where the maximum amount of oxygen was produced photosynthetically. The accumulation of bacteria began in the red region of the spectrum around Fraunhofer lines B and C (~650–680 nm) and continued into the orange region (Frauenhofer line D; ~590 nm) and the violet and blue regions of the spectrum (Frauenhofer line F; 480–490 nm) (Figure 2). The results differed from those of Julius Sachs and Wilhelm Pfeffer (Engelmann 1882a) because they had used whole leaves or multicellular algae. Figure 2 shows the maximum of oxygen production at the 660–680 nm region of the spectrum in *Cladophora, Pinnularia* and *Oscillatoria* measured by Engelmann, and at around 570 nm in *Elodea* measured by Pfeffer (Engelmann 1882c). Engelmann found that the lower layers of leaves have an action spectrum that differs from that of the upper layers because of different light scattering and absorption (Engelmann 1882a, b). He also surmised that besides chlorophyll, other pigments are also present in plants, algae and bacteria.

Engelmann (1884) was the first to determine an action spectrum of photosynthesis, although he could not determine the exact ratio of input of quanta to O_2 production. However, he was aware of the different intensities of light across the regions of the spectrum and the loss by scattering of light. He regulated the intensity, by using the technology of his time, which involved varying the slit width to ensure a constant level of illumination. Before illumination of the algae, the intensity of light in the slit for the sample and the parallel control slit were adjusted to be the same (Engelmann 1884). Afterwards, the difference in the intensities of light in the parallel slit and in the slit with the algae was determined and from the result, the amount of absorption (n) was calculated. The loss by scattering was determined by comparison of chlorophyll-containing and chlorophyll-free cells. $\gamma = A^{g}/A^{s}$ (A^{g} light of the gas burner, A^{s}, sunlight), Table 1. Engelmann determined the ratio between absorption (n) and energy of assimilation (A^{s}) in *Cladophora* (green alga), *Navicula* (Diatom), *Vaucheria, Euglena, Oscillaria* (blue green bacteria), *Spirogyra, Ceramium* (red alga) and *Closterium* (Figure 3, Table 2). The absorption minimum was in the far red, several maxima and minima of absorption were between Fraunhofer B and E and in several cells up to F. The absorption values increase continuously to the short wavelengths. From red to green, A and n have about the same course. In the short wave region the course of A and n differ strongly (Figure 3, 1–4). Engelmann concluded that under fixed experimental conditions (optimal illumination and presence of CO_2), the ratio of light absorption by chlorophyll/oxygen production, measured as the accumulation of bacteria, is constant over the various regions of the spectrum. 'The ratio of the absorbed light energy (E_{abs}) to the produced potential chemical energy (E_{ass}) is for all wavelengths and for all chromophylls constant, $E_{abs} = E_{ass}$' (Engelmann 1884). $E = \sqrt{A}/n$ (E, actual energy of light at the respective position of a (width of the slit necessary to result in an aerotactic accumulation of bacteria in response to O_2 production). Table 2 shows the values for different groups of algae.

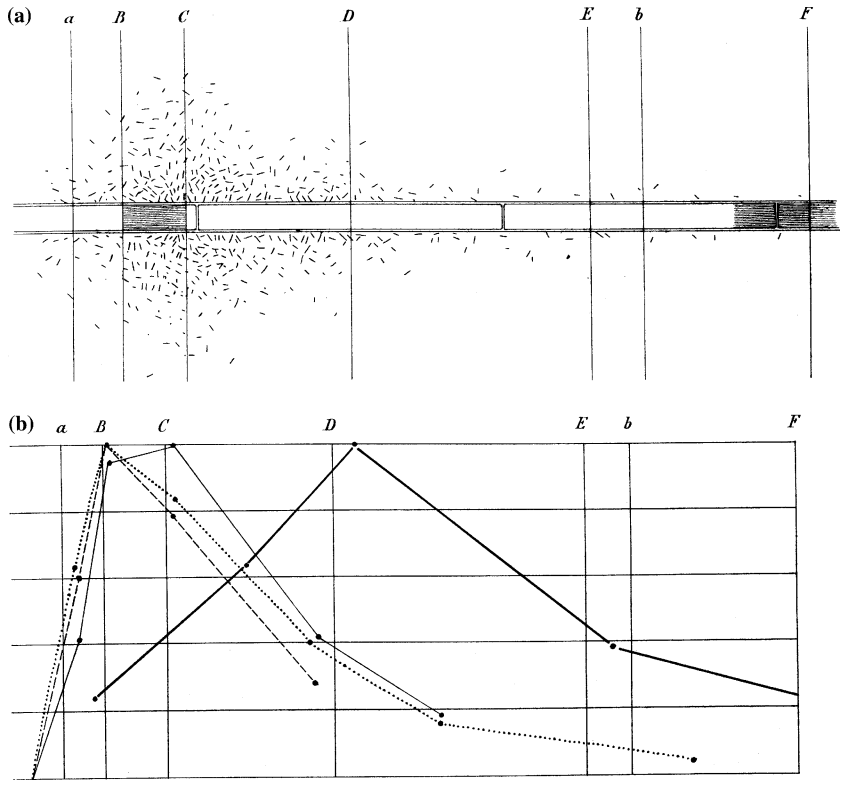

Figure 2. The photosynthetic production of oxygen in algae dependent on the quality of incident light. The oxygen production was measured by the strength of accumulation of aerotactic chemotrophic bacteria. (a) A piece of a *Cladophora* filament illuminated by light from a microspectral apparatus (see text for experimental details). The absorption bands are shown by shadowing of the filament; the maximum of oxygen production was between the Fraunhofer lines B and C (~670–680 nm). (b) 'Kurve der Assimilationsenergie', curve of energy of assimilation, measured as intensity of accumulation of aerotactic bacteria as function of the wavelength of the incident light. Full line, *Cladophora,* thickness about 0.02 mm; broken line, the same for *Pinnularia* (width 0.008 mm); dotted line, Oscillaria sp., thickness 0.005 mm. The thick line represents values for *Elodea* taken from Wilhelm Pfeffer, Pflanzenphysiologie I, Figure 29. Figure 2 is from Engelmann (1882c).

During the last decade, our knowledge of the structure and composition of the photosynthetic apparatus and the biochemistry and bioenergetics of photosynthesis has increased greatly (Govindjee 2000). But at the time of Engelmann, it was real progress to measure absorption and transduction of light energy in cells of algae in a microspectrum. The time-line of discoveries in oxygenic photosynthesis was recently presented by Govindjee and Krogmann (2004).

The influence of light and oxygen partial pressure on the mobility and movement of bacteria

The colorless, chemotrophic Bacterium termo, Cohn, Ehrenberg ('Fäulnisbakterien', putrefying bacteria), which was used by Engelmann to determine oxygen production by plants, was not from a pure clone culture, but was enriched from rotting material. The decisive criteria were aerokinesis (swimming only in the presence of oxygen)

Table 1. The relative energy of assimilation γ of gas light (A^g) to sunlight (A^s)

λ	718 nm	680 nm	622 nm	589 nm	522 nm	468 nm	431 nm	
	A	$B^1/_4C^a$	$C^1/_2D^a$	D	$E^1/_2B^a$	F	G	Fraunhofer lines
γ	1.400	1.000	0.784	0.651	0.411	0.254	0.125	

[a] Fraunhofer lines $B^1/_4C$, $C^1/_2D$, $E^1/_2$ B mean that the measuring point, indicated by the wavelength in λ, is in between the Fraunhofer lines.

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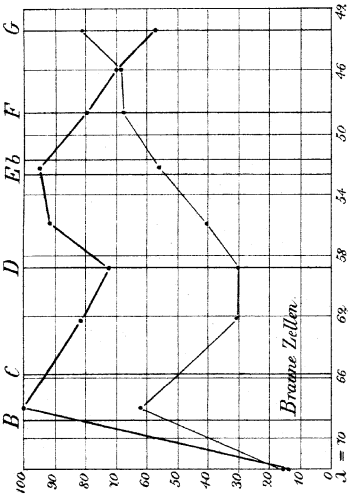


Fig. 2.

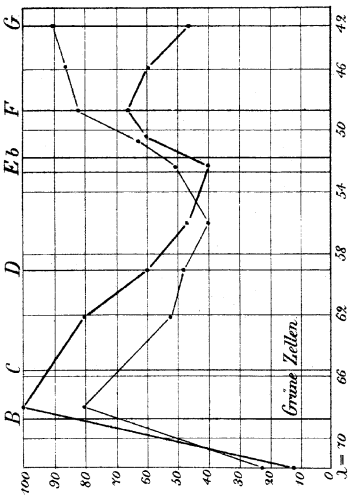
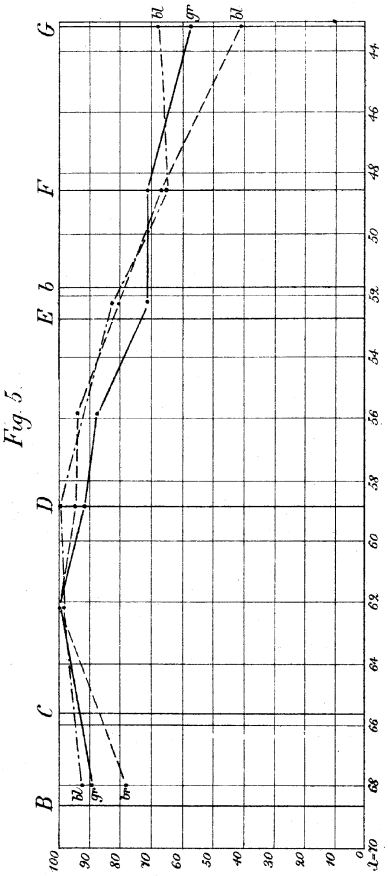


Fig. 1



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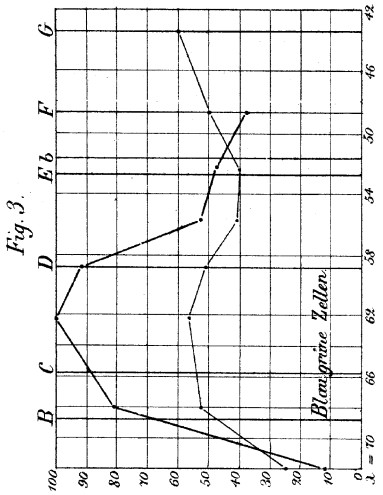

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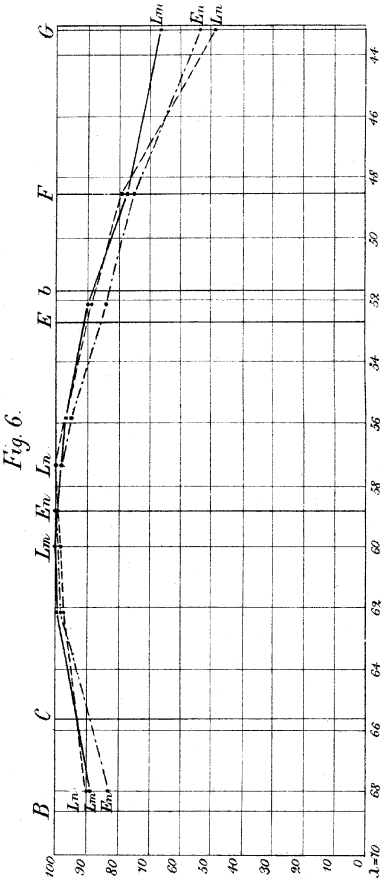

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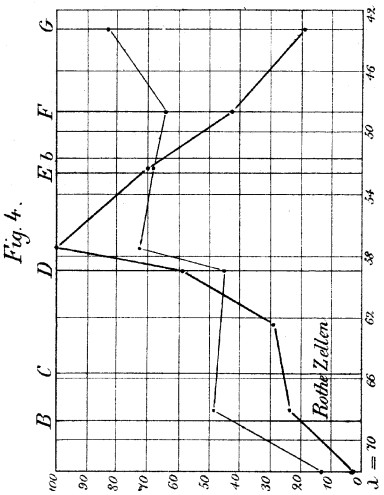

Fig. 4.

Table 2. The actual energy E of light at a specific position a in the spectrum which results in an accumulation of aerotactic bacteria

λ	718 nm	680 nm	622 nm	589 nm	522 nm	468 nm	431 nm
Green cells	57.8	89.5	100	91.9	70.8	71.8	57.4
Brown cells	54.4	77.8	100	95.3	80.4	66.9	41.0
Blue-green cells	51.6	92.4	99.5	100	82.7	64.7	67.1

The width of the slit is given by a. $E = \sqrt{A/n}$, where A is the energy of assimilation and n the absorbed energy.

and aerotaxis (swimming by flagella in the direction of an oxygen gradient). The movement of Bacterium termo was not influenced by light (Engelmann 1881b).

The influence of light on motility and scotophobic response of sulfur and non-sulfur purple bacteria

The influence of light on growth, photokinesis, and phototaxis of purple bacteria was studied with a natural enrichment taken from a side tributary of the Rhine River. The bacterium from the Rhine, designated Bacterium photometricum (Engelmann 1883), was an oval-shaped, sometimes pleomorphic, reddish-brown-colored bacterium (width 1.4–1.9 μm, length 3–4 μm) with intracellular refractile globules of sulfur, swimming at 20–40 μm s^{-1} and rotating around its long axis at about 3–6 revolutions s^{-1} with the flagellated pole in front (polar monotrichous flagellation). From this description, it seems to have been a mixed culture dominated by a *Chromatium* species.

The bacteria accumulated in a small light field projected onto the slide. A dense population was used to determine the *in vivo* absorption spectrum with the microspectral apparatus. A strong absorption band was observed at ~595 nm, and weak bands were observed at ~540 nm, ~510 nm, and in the blue-violet region. There was no absorption in the red region between 620 and 680 nm. Engelmann (1883) postulated a further, invisible absorption band in the near-infrared in later photophobotactic (scotophobic response in the present terminology, Ragatz et al. 1994) experiments. He concluded that the absorption spectrum did not correspond to the absorption spectrum of chlorophyll (no absorption between Fraunhofer lines B and C, ~680 nm) or of any other known pigment. The absorption properties were constant in presence or absence of oxygen and in cells of different age (Engelmann 1883).

The motility of B. photometricum was dependent on light, but not on oxygen. Addition of B. termo or oxygen-sensitive spirillae to the B. photometricum preparation did not initiate aerotactic movement of B. termo, even when strong illuminated dense populations of B. photometricum were used. The same result was obtained with spirilla of higher oxygen-sensitivity than B. termo. The motility of B. photometricum was independent of the oxygen partial pressure. Engelmann concluded that B. photometricum does not produce oxygen in the light, in contrast to plants containing chlorophyll. He thought that light stimulated the motility of B. photometricum but not the assimilation of CO_2. CO_2 fixation and oxygen production were strictly coupled in the opinion of Engelmann and his contemporaries. Engelmann called the light-stimulated movement of B. photometricum *photokinetic induction*, with reference to the heliotropic movement of higher plants observed by Wiesner (1878). The beginning of the movement was delayed relative to the onset of illumination and sometimes stopped after the light was turned off. The length of retardation

Figure 3. Quantitative relationship between absorption of light (n) and energy of assimilation (A) in plant cells. The oxygen production was measured by the strength of accumulation of aerotactic bacteria in a microspectrum (see text for experimental details). Reproduction of Figures. 1–6 (listed below as subfigures of this figure) from Engelmann (1884). In subfigures 1–4 the values for A are connected by thick lines (upper curves), the values for n connected by thin lines. The true values for the wavelengths between the measurement points have not been determined. The points are means of numerous measurements with several algae. Subfigure (1) Green algae, subfigure (2) brown algae, subfigure (3) blue-green cells, subfigure (4) red algae. Subfigure (5), distribution of energy in a sun spectrum measured with green (gr), brown (br) and blue-green (bl) cells. In the far red lower values for E were obtained with the method of aerotaxis of bacteria. Subfigure (6) distribution of energy in the spectrum of sunlight measured by different methods: Lm^{-1}, Lamansky measurement with a flintglas prism; Ln^{-1}, the values determined by Langley with the 'actinic balance' on the basis of the table in Annal de chimie et de physique XXV, p. 215. En, the means of all measurements of A and n by Engelmann.

was related to the preceding treatment. Strong light had an inhibitory effect on movement. The movement of B. photometricum stopped in the dark and in the presence of oxygen.

A sudden dimming or cessation of illumination resulted in the bacteria immediately reversing direction, with the back end (non-flagellated pole) first. The bacteria swim backwards with higher speed for a short distance (about the 10- to 20-fold length of the cells). Thus, the reverse movement was not a run-and-tumble movement like the chemotactic movement of *Escherichia coli*. A gradual lowering or fast or slow increase of the light intensity did not effect the 'Schreckbewegung' (frightened movement; phobophototaxis). In the present terminology, the 'movement of fright' is named *scotophobic response*, which means a fear of darkness (Ragatz et al. 1994; Gest 1995). This is in contrast to the phototactic response that is an oriented movement towards or away from a light source. (The phototactic response had been earlier named topophototaxis in order to distinguish it from another phenomenon phobophototaxis (for explanation, see Drews 1959; Hustede et al. 1989).) Since the words scotophobic and phototactic response are in common use in present time, I will use these terms in the following text. According to this behavior, a light field projected onto a dark surrounding acts as a light trap because bacteria in the light field are stimulated to return to it if they encounter a dark border. In contrast to *Euglena*, a light-sensitive area in the cells of B. photometricum was not found. Engelmann (1883) supposed that the light sensitivity and the bacteriopurpurin are distributed over the whole cell.

Engelmann then used the microspectrum as a light trap. With a wide slit he was able to sample a large number of bacteria. The accumulation started at the long-wave side of the spectrum first. During a slow narrowing of the slit and sharpening of the spectrum, the bacteria accumulated in a tight, dense band in the near-infrared region around 850 nm (Figure 4). A weaker band was observed around 590 nm, and few bacteria accumulated in the green and blue regions of the spectrum. In sunlight, with a distribution of energy different from that of a gas light, more bacteria accumulated in the short-wave region of the spectrum, in the yellow, green (~535 nm), and blue (~410 nm) regions. The scotophobic movement was also observed when the bacteria moved from yellow to red and from far-red into red parts of the microspectrum. In the non-attractive regions of the spectrum, the bacteria retreat into the dark. After the bacteria were allowed to accumulate for a while in the microspectrum, they were fixed in their position and observed under bright light. In other experiments, Engelmann determined that the action spectra of photokinesis and scotophobic response coincide with the absorption spectrum of the bacteria. The accumulation of B. photometricum was also observed in light traps illuminated by light from colored glass filters. The movement and later accumulation of organisms in the direction of the light source, which Eduard Strassburger (1878) has described as phototaxis of *Chytridium* and which Stahl (1880) observed while studying the movement of chloroplasts, was not observed with B. photometricum. *Rhodospirillum centenum,* however, exhibits a phototactic response (Gest 1995). Several cyanobacteria are able to react by a scotophobic or a phototactic response, respectively, and each response is dependent on a specific region of the spectrum (Drews 1959). The reversing direction reaction of B. photometricum was only triggered by a sudden lowering of light intensity. Buder (1915) was the first who measured the discrimination threshold, i.e. the lowest difference in light intensity between two light fields which elicit the scotophobic response (also see later papers by Buder's students: Schrammeck 1934; Schlegel 1956). These investigators and Clayton (1953) determined values of about 2%. Under optimized conditions (preculture, pH, temperature, and medium for culture) values in the range of 0.7–2.4% were obtained for several sulfur and non-sulfur purple bacteria (Hustede et al. 1989). *Chromatium vinosum* D and *Rhodospirillum rubrum* Ha were the strains recommended for further studies.

All investigators from Engelmann until Clayton agreed that the action spectrum for the scotophobic response coincides with the absorption spectra of the purple bacteria under investigation. This led to the hypothesis that a sudden decrease in photosynthetic rate triggers the scotophobic response. Armitage and Evans (1981) proposed that the proton motive force is the decisive component of the sensory transduction chain.

Engelmann did not propose a theory of scotophobic response because he realized that the

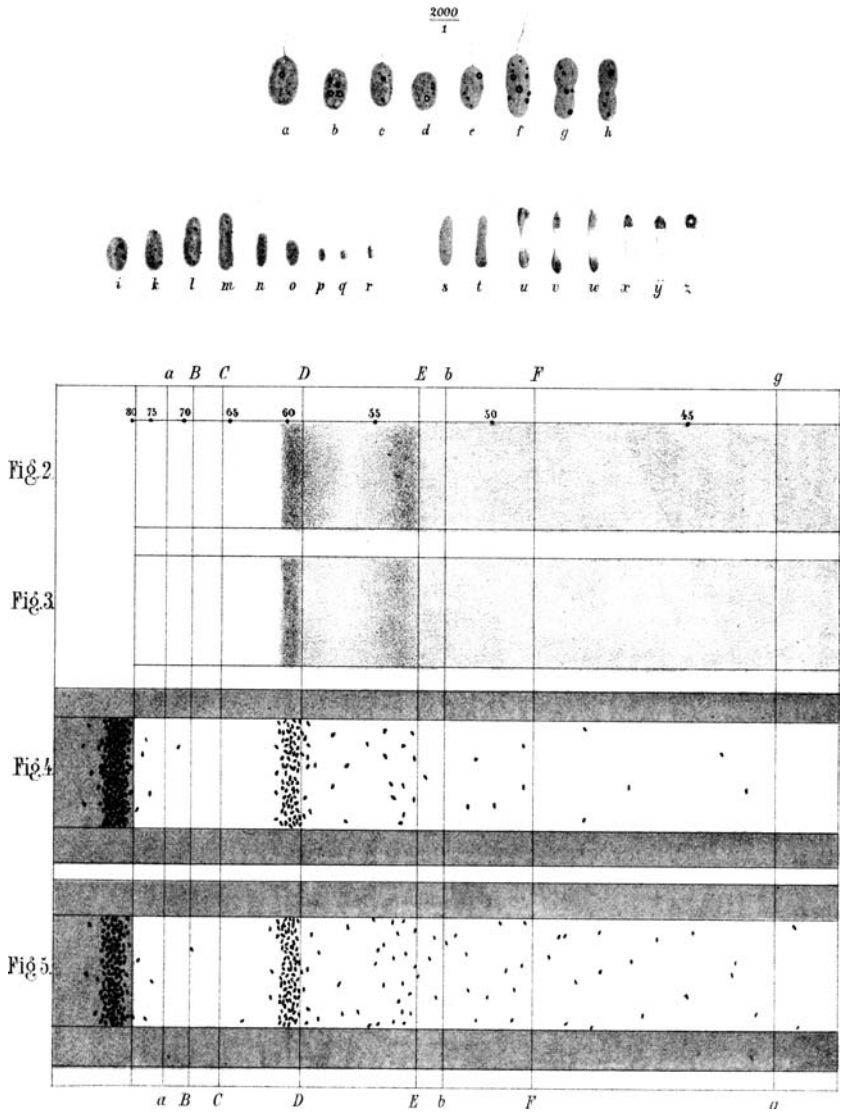

Figure. 4. Bacterium photometricum (*Chromatium* sp.). Morphology, absorption spectrum and scotophobic accumulation in a microspectrum. Reproduction of Figures. 1–5 (listed below as subfigures of this figure) from Engelmann (1883). Top (subfigure 1) a–h, typical cell form, motile; i–z, small, pleomorphic cells, motile (i–r) and resting nonmotile states (s–z). Bottom panels (subfigures 2–5): *In-vivo*-absorption spectrum (visible part) of whole cells in a 0.1-mm layer (subfigure 2), and in a 0.05-mm layer (subfigure 3), and the distribution of B. photometricum in the microspectrum with gas light (subfigure 4) and with sunlight (subfigure 5). Bacteria accumulated around 850 nm, 590 nm, and in the blue and green regions of the spectrum. B, C, D, E, F are the Fraunhofer lines of the spectrum, 80, 75, 60–45 are the wavelength in 0.1 nm. The 850-nm accumulation is outside of the visible spectrum.

mechanism is complex and that his results were insufficient to explain it (Engelmann 1883).

Bacteriopurpurin and photosynthetic growth of purple bacteria

Cultures of the sulfur purple bacteria *Thiocapsa roseopersicina, Chromatium* (*C.*) *okenii, C. vinosum, C. warmingii,* Ophidomonas saguinea (possibly *Thiospirillum jenense*), obtained from Sergej N. Winogradsky (Strassbourg), J. Eugenius B. Warming (Copenhagen), and W. Zopf (Halle), and a pure culture of *Rhodospirillum rubrum* Esmarch, obtained from Ferdinand Hueppe (Wiesbaden), were used to study the pigment bacteriopurpurin (named by Lancaster 1874) of these bacteria (Engelmann 1888a). Engelmann coined the name

purple bacteria for these organisms on the basis of their orange to purple color. All of these bacteria showed the same scotophobic and photokinetic response as described for B. photometricum. In the spectrum of gas light, sunlight, or electric light, they accumulated in the infrared region near 850 nm, in the yellow region at 590 nm, and in the green region between 520 and 550 nm. This action spectrum coincides with the *in vivo* absorption spectrum of bacteriopurpurin (bacteriochlorophyll *a*), which has maxima at 850, 590, 530, and 490 nm. Engelmann was unable to measure the absorption band at 370 nm. The major absorption region of chlorophyll between Fraunhofer lines B and C (~680 nm) is a region of minimum absorption of bacteriopurpurin. The absorption in the infrared region was studied in cooperation with his colleague W.H. Julius in the physics department, using a Langley bolometer, and the absorption in the visible part of the spectrum was measured with the microspectral photometer. Absorption maxima at 850, 590, 530, and 480 nm were measured. The growth of the purple sulfur bacteria was found to be dependent on light. Near infrared radiation (~850 nm) was most effective for growth and scotophobic response (Engelmann 1888b). Unfortunately, and in contrast to earlier publications in this area, Engelmann thought he observed photosynthetic oxygen production by the purple sulfur bacteria during growth in the light (Engelmann 1888a, b). It is hard to understand why Engelmann changed his mind and came to the wrong conclusion, although he used the same method earlier when he discovered the anoxygenic photosynthesis. For the experimental work he selected bacteria with a high sensitivity to low concentrations of oxygen. Control experiments excluded that the tactic movement was caused by compounds other than oxygen. Possibly under the influence of the general hypothesis of the time that in photosynthesis CO_2 is split and starch and oxygen are the end products, he believed that the bacteriopurpurin-containing bacteria have an oxygenic photosynthesis. However, Engelmann was the first to formulate clearly that *bacteriopurpurin is a true chromophyll insofar as it transduces the absorbed light energy into potential chemical energy*. He discriminated the bacteriopurpurin-containing and scotophobic-sensitive sulfur bacteria from the colorless sulfur bacteria studied by Sergej N. Winogradsky. The addition of H_2S delayed the cessation of motility after the light was switched off. It is interesting to note that in Engelmann's summarizing article, for the first time electric light was preferred for microscopy studies because it could be regulated easier than the sunlight or the gas light (Engelmann 1888b). Since the cultures of purple bacteria have different colors, Engelmann concluded that at least two pigments are present in all strains.

Although Engelmann was a physiologist specializing in muscles and their excitation and working with animal tissues, he discovered in a decade of his life, the flagellar movement of bacteria and the influence of the quality and quantity of light and oxygen partial pressure on the motility of chemotrophic and phototrophic bacteria as well as the scotophobic response of purple bacteria. The microscopy techniques he developed were ingenious for his time. In the early 1950s, Roderick Clayton confirmed the similarity between the photosynthetic spectrum and the photoresponse spectrum in purple bacteria (Clayton 1953, 1955). Today we know that *Rhodobacter sphaeroides,* a non-sulfur purple bacterium, contains multiple phospho-relay systems and chemoreceptors expressed under different growth conditions. Some phototrophic bacteria contain a photoactive yellow protein that undergoes a photocycle in blue light. However, the action spectrum of scotophobic response and the primary response to a step-down in light intensity on the rate of electron transfer suggest that bacteriochlorophyll has an important role in the transfer of the light stimulus to the chemosensory pathway and the reaction of flagellar movement. The photoresponse and chemoresponse of *R. sphaeroides* has been intensively studied and reviewed by Judith Armitage and coworkers (Armitage and Evans 1981; Armitage 1999; Armitage et al. 1999; Shah et al. 2000; also see Armitage and Hellingwerf 2003).

The similarity of photosensory and chemosensory perception is underscored by genetic analysis of *Rhodospirillum centenum* which has demonstrated that both processes utilize a common Che-like phospho-relay signal transduction system (Jiang et al. 1997; Jiang and Bauer 2001). In addition, a 'photorecptor' involved in the scotophobic response of *R. centenum* has been identified that has significant similarity to chemoreceptors (Jiang and Bauer 2001).

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