The characteristic movements of the filaments of the blue-green alga *Oscillatoria* have not uncommonly been held due to the activity of a superficial layer of substance, a kind of "plasma membrane," external to the cell wall (cf. Pfeffer, 1906; Schaeffer, 1920). Other theories as to the mechanism of these movements have invoked "osmotic processes" between the cells and the medium (cf. Vines, 1886), or the secretion of mucilaginous substance over all or part of the surface of the filament (cf. Correns, 1897; Gicklhorn, 1921).

This type of motility is of interest in itself, and also for the information it may perhaps be made to give as to the nature of the movements of slender protoplasmic processes. Measurements of the temperature coefficients of ameboid progression, for example, or of phagocytosis (Fenn, 1922), do not necessarily have a direct bearing on the interpretation of motion in pseudopodial projections, or in such structures as the terminal arborizations of neurones (if it be that in fully developed nervous organs these processes do indeed undergo retractions and protrusions). Some more recent notions (Schaeffer, 1920; Mast, 1923) as to the basis of ameboid creeping depend upon the activity of a "fluid outer surface layer," demonstrated by the streaming movement of adhering particles (Büttschli, 1892; Gruber, 1912), and identified by Schaeffer (1920) with the "plasma membrane." The nature of the activity of this superficial protoplasm is quite obscure (cf. Chambers, 1924). *Oscillatoria* seems a most suitable organism wherewith to investigate it.
It may be expected that the superficial streaming motion revealed by attached particles is not very dissimilar in *Oscillatoria* (Siebold and Schultze, as cited in Pfeffer, 1906; Schaeffer, 1920), in diatoms (Müller, 1889, 1897; Lauterborn, 1896), and in at least some amebae.

With a properly selected species, the rate of movement of *Oscillatoria* becomes a delicate index of the effects of temperature and of certain other agencies. Several aspects of the motility are susceptible of measurement. In some species the free trichomes swim in spiral path through the water; with other forms this type of motion is not so pronounced. Again, if one end of a filament is held in a colonial mass, the free portion may move in a conical path. Under constant conditions, the rate of this activity is very steady, as we have found. With certain species a gliding motion in contact with glass or other surface is most conspicuous. In uniform environment the rate of such translatory movement is remarkably constant. It is well known that the direction of the motion suffers periodic reversal (somewhat as in an Ascidian heart), at which times the direction of spiral streaming on the outer surface of the filament is said also to be reversed.

Neither in the particular species used for our measurements nor in two others available for observation have we been able to convince ourselves that the filament as a whole rotates during the translatory motion. Observations with ordinary microscopic equipment were supplemented by the use of dark-field illumination and an immersion objective. The pigment granules are easily followed. There is not more than a barely detectable layer of "slime" coating a filament, which itself does not visibly rotate. There is no appreciable protrusion of slime at either end of a filament during active motion, nor a detectable alteration of the surface or the ends of the filament when the direction of movement is reversed. This was verified by study of filaments in suspensions of Chinese ink. An occasional jerky movement, probably due to contact of the advancing filament with some obstacle, may rotate the filament slightly. When the filament rubs over a bit of debris there is no obvious disturbance of the surface such as might be visible if "slime" were present. The fact that the rate of movement is independent of the length of the filament would seem to argue against the theory that the
end-cell is a locomotor organ. We have observed that under dark-field illumination the protoplasts of a moving filament seem to contract rhythmically, but the significance of this fact has not been fully made out.

II.

For the present inquiry we have utilized the linear translatory movement of a species of Oscillatoria in which this sort of motion is well developed, and in which the filament as a whole does not rotate upon its long axis when in contact with glass.

Our cultures were started with "film" from the surface of a sewage-purification filter-bed, in which two species of Oscillatoria were abundantly represented. We are indebted to Dr. Margaret Hotchkiss for a supply of this material. In shallow water at the bottom of a covered crystallizing dish the plants may be maintained in good condition for a long time. All the observations were made with one species, which we have not been able to identify with certainty; the preparations were made from a single culture dish, kept in diffuse light, in which the pH remained practically constant at 7.4. The filaments of this species are 0.0034 mm. wide and in length vary between 0.1 and 1.2 mm.

The filaments were removed in small quantities from the culture dish with the aid of a wide mouth pipette and mounted under a supported cover-slip. The slide was placed in an electrically heated warm stage with thermostatic control; the objective of the microscope passed into this chamber through a flexible ring of rubber cemented to the cover. The thermometer bulb was close to the preparation. For lower temperatures a similar box was prepared large enough to accommodate a small brine coil. The whole apparatus was also enclosed within a large glass chamber cooled with ice. Illumination practically constant was obtained with a substage lamp.

A series of the readings at low temperatures was obtained through the use of a cold chamber at the New Brunswick Laboratory of E. R. Squibb and Sons. The warm stage equipment, as set up in this refrigerated room, permitted readings at temperatures down to 6°C. For courteously allowing us to use the facilities of their plant in this way we are indebted to Dr. Lloyd K. Riggs of the research department of Squibb's.
The velocity of the moving filaments was determined with a 4 mm. objective and 8 × ocular, at tube length 151 mm. Each division of the ocular micrometer then corresponded to 0.0340 mm. At higher temperatures the time required to traverse three of these divisions was obtained in each case. At room temperature this time was about 25 seconds. Thus the movement is a slow one, 0.00408 mm. per second, but about ten times as fast as that of leucocytes under normal conditions. The low velocity made it easy to secure accurate estimations. At lower temperatures, the time to cover one micrometer division was taken, as the slow rate of movement might for longer distances of travel more often lead to the upsetting of readings through chance contact with other organisms in the preparation. The end of a moving filament was easier to follow, as a rule, than a definite pigment granule in a mid-region. The readings were taken from straight filaments in unimpeded motion. The time was read with a stop-watch. The temperature was constant within 0.1°C. or better for each set of observations.

The degree of consistency in the readings is illustrated in several sets plotted in Fig. 1.

Although the method of handling the filaments was as nearly as practicable the same in each preparation, we were led to examine the possible effect of mechanical agitation upon subsequent movement. This was tested by measuring the velocity of movement of filaments which had been shaken in a small amount of culture fluid. We desired particularly to get information on this point as a means of controlling subsequent experiments with salts. In one series of tests the material was placed in a small tube strapped to the bob of an electrically driven pendulum having a period of one second. The current through the actuating coil was so increased that at the end of each complete vibration the pendulum received a definite "bump," resulting in the forcible agitation of the alga in the tube. With intervals of this agitation extending up to 30 minutes, no perceptible change was measurable in the velocity of movement. Irregular, but still gentle, agitation in a bottle for 3 minutes gave no effect at 29.6°C. Similar agitation for 6 minutes led to a slight acceleration of movement immediately after shaking (0.149 divisions per second as compared with 0.136
FIG. 1. Frequency distribution of several series of measurements giving the time, in seconds, required for different filaments of *Oscillatoria* to traverse 3 micrometer divisions (A, D) or 1 micrometer division (B, C).

The variation in these measurements is small, but too great to be explained as due to mere errors of timing. In each case the position of the mean is shown.
before); after 10 minutes shaking, the velocity observed immediately was 0.182; this acceleration is succeeded by a drop, in this case to 0.129, within 5 minutes after the shaking ceases. The extension of these experiments may give further light upon the mechanism of movement.

At least 10 minutes were allowed for each preparation to come to thermal equilibrium. This was found by test to be sufficient.

One series of measurements gave at different temperatures velocities almost exactly one-half those otherwise obtained. These figures were plotted as in Fig. 2, and the slope of the line fitting them was seen to be the same. This particular set of measurements is therefore incorporated in Fig. 2 after multiplication by a constant; if omitted altogether the line in Fig. 2 is not affected.

III.

The mean velocity of translatory movement was obtained from forty-one sets of measurements at known temperatures. These are shown plotted logarithmically against the reciprocal of the absolute temperature (Fig. 2).

In agreement with the Arrhenius (1889) equation for velocities of irreversible chemical reactions, the graph is a straight line (between 6° and 36°). The value of the critical increment, \( \mu \), in this equation,

\[
\frac{\text{velocity at } T_2}{\text{velocity at } T_1} = e^{\mu \left( \frac{1}{T_1} - \frac{1}{T_2} \right)}
\]

is 9,240. This case is a particularly instructive one, because it is not confused by “breaks” of the type frequently encountered. Above 37° destructive effects become evident; these will be studied separately.\(^1\)

The critical increment given is based upon the slope of the line fitted to the means (Fig. 2). The scattered means are closely confined (with one exceptional point known to be of doubtful

\(^1\) The maximal temperature as obtained under the conditions of these experiments agrees fairly well with that given by Velten and others for cyclosis in cells of other plants (Davenport, 1897). It is well below the “upper thermal death point,” which is above 40°C.
value) between two lines parallel to that giving the best fit. The reality of this fact is further demonstrated in Fig. 3, where the highest and the lowest readings in each set of measurements are similarly plotted. For a case in which the temperature coefficient of the latitude of variation at different temperatures is the same as the temperature coefficient of the mean, Loeb and

![Graph](image-url)

Fig. 2. The logarithm of the mean relative velocity of movement (100 times scale divisions per second) for each set of measurements is plotted against the reciprocal of the absolute temperature. The extreme variates from the best fitting line are themselves confined within two lines parallel thereto.

Chamberlain (1915) suggested that the variability might be due to the fact that in different individual organisms the effective amount of a catalyst for the process measured fluctuates within definite limits. The latitude of variation should thus be a constant fraction of the mean, over the temperature range considered. The type of graphic representation used in Figs. 2 and 3 gives a neater
method of demonstrating this point. Other similar cases might be cited (e.g. Crozier and Pilz, 1923-24).

The magnitude of the critical increment for the mean velocity of movement, and the fact that the extreme high and the extreme

![Graph]

**Fig. 3.** For each set of measurements the extreme high and low variates are plotted as in Fig. 2. The latitude of variation is not lawless, but tends to be at each temperature a constant fraction of the mean. The slope of the confining lines is the same as that fitting the means of all the series (Fig. 2).

low variates at the different temperatures yield the same value of μ, are grounds for the conclusion that the translatory motion of this species of *Oscillatoria* depends upon the velocity of a chemical process. The velocity of this reaction is governed in charac-
teristic fashion by temperature, and the specific reaction rate seems proportional to the amount of some substance (catalyst) which in different filaments of the alga varies within definite limits (perhaps also in the same filament, from time to time).

This conclusion is quite independent of the actual mechanics of the movement. It concerns merely the type of activity which controls the speed of movement. Thus, surface tension effects are not evident in the relation to temperature, whatever rôle they may actually play; it is obvious that while viscosity changes and surface tension phenomena are frequently appealed to in physiological theorizings, it must in some instances be recognized that these physical properties are altered as a resultant of chemical change, rather than that they serve as a controlling cause of activity (Crozier, 1924-25).

IV.

It has been suggested (Crozier, 1924-25) that the magnitude of the critical increment \( \mu \) may be employed to identify types of chemical reaction, especially among processes obviously catalyzed. This view is based in part upon empirical findings with varied vital activities, and upon a theory of temperature coefficients due to F. O. Rice (1923). While the very incomplete knowledge of critical increments for simple chemical systems perhaps does not permit more than the deduction of suggestive hints, it is possible from this standpoint to compare rather precisely physiological processes known or suspected to be really analogous. The critical increment for most chemical processes is above 10,000. Where diffusion is probably concerned, or some surface action analogous to that involved in the development of vapor tension, as in the action of trypsin on powdered casein or of powdered castor beans on cotton oil, the value of \( \mu \) is near 7,500. To what particular group of processes the one fundamental to the motion of Oscillatoria may be assignable is not yet clear.

In seeking other physiological processes for comparison, we may for the present consider merely some activities not unlikely to be in a measure related. Among these, the "rate of loss of water" from certain plant cells (Delf, 1916) yields \( \mu = 20,000 \) (above
26°C.), this figure is derived chiefly from measurements of the rate of shrinkage of onion leaf (Fig. 4), corresponding data for dandelion scape (Delf, 1916) being found to have a curious discontinuity in the mid-range of temperatures. However, this is a slow process, and perhaps not one very pertinent to the discussion.

A connection has been suspected between protoplasmic streaming and the movements of Oscillatoria. The rates of cyclosis in
cells of several plants yield $\mu = 4,700$ to $10,300$, in the range of "normal" temperatures. (Fig. 5, based on Velten's observations; data reduced in Davenport, 1897, and Kanitz, 1915). So far as these critical increments serve as indication there is no very definite parallelism between cyclosis and the creeping of *Oscillatoria*.

![Graph](image_url)

**Fig. 5.** The velocity of cyclosis in cells of several plants. The actual data (due to Velten; reduced in Davenport, 1897; Kanitz, 1915) have in each case been multiplied by a factor, which permits all four graphs to be shown in one figure. The measurements at higher temperatures and at very low temperatures are omitted. The lines show a definite change in thermal effect beginning somewhere near 15°C. (*A*, Chara, $\mu = 8,450$; *B*, Vallisneria, $\mu = 8,450$; *C*, Nitella, $\mu = 10,300$; *D*, Elodea, $\mu = 4,780$).
Scanty data on the rate of pulsation of the contractile vacuoles of *Infusoria* (cf. Kanitz, 1915) lead to higher values of $\mu$ in certain instances, and in one case (*Euplotes*) to a lower magnitude (7,900). Where a phenomenon (such as pulsation rate in these vacuoles) is unquestionably determined by a number of concurrent influences, it is not unreasonable to expect that in different species the controlling influence may not be the same.

A more interesting comparison is provided by measurements of the velocity of ameboid progression in human neutrophilic leucocytes (McCutcheon, 1923); $\mu$ here is 10,800 (Fig. 6).

**Fig. 6.** The velocity of ameboid progression of human neutrophilic leucocytes as function of temperature (data of McCutcheon, 1923). Between 27° and 40° the critical increment is $\mu = 10,800$.

These comparisons of course by no means involve the conclusion that the velocity of progression in leucocytes, for example, is determined by the activity of the "outer layer of protoplasm," as vaguely conceived in certain theories of ameboid movement. The critical increments indeed are in all probability significantly different. Pending more detailed investigation all that need be said is, that the velocity of cyclosis in certain cells, of creeping in leuco-

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cytes, of pulsation in the vacuoles of some ciliates, and of translatory motion of Oscillatoria filaments, are all influenced in a not very dissimilar way by the temperature, although the actual values of the several critical thermal increments seem distinct and characteristic.

SUMMARY.

In a species of Oscillatoria exhibiting movement of type suitable for exact measurement the velocity of linear translatory motion is found to be controlled by the temperature (6—36°C.) in accordance with Arrhenius' equation for irreversible reactions. The value of the critical increment (\( \mu \)) is 9,240. The extreme variates in series of measurements at different temperatures yield the same value of \( \mu \). The velocity of movement is therefore regarded as determined by the velocity of an underlying chemical process, controlled by the temperature and by the amount of a substance (? catalyst) whose effective quantity at any moment varies within definite limits in different filaments of the alga.

On the basis of its temperature characteristic the locomotion of Oscillatoria is compared with certain other processes for which this constant is calculated.

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