

ON THE CRITICAL THERMAL INCREMENT FOR THE LOCOMOTION OF A DIPLOPOD.

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I.

A good deal of attention has been paid to the temperature coefficients of vital processes. The data available up to 1914-15 are for the most part collected in Kanitz' (1915) book. The chief interest of this work has centered about the "R. G. T." (van't Hoff) rule. In common with many chemical reactions, at ordinary temperatures the velocities of a variety of protoplasmic activities are found to be about doubled or trebled by a 10° rise of temperature.

The temperature coefficient, Q_{10} , giving the ratio of velocities for an interval of 10°, is a quite imperfect means of characterizing a process. It is in any case not a *constant* quantity, but depends upon the particular temperature. Moreover, it is known that in the neighborhood of certain temperatures, varying with the process considered, abrupt changes occur in the temperature relations of many biological phenomena. A means is required of dealing with these "critical points." Such complexity of dynamical balance as must be postulated for living matter leads one to expect that by considerable change of temperature a different fundamental reaction might be brought into control of the velocity of a given phenomena.

For certain vital activities which may be taken as typical, it is found that the underlying or controlling processes may be treated as systems of "irreversible" first order reactions (Osterhout, 1914, 1922; Hecht, 1918-19, 1918-19, *a*; Osterhout and Haas, 1918-19).

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To such processes the equation of Arrhenius (1889) should be applied. Originally with the status of a useful empirical relation, the theoretical foundation for this equation seems now quite extensive (J. Rice, 1915; Rodebush, 1923; Thomson, 1924). It considers that the velocity of an irreversible reaction is proportional to the exponential of $-\frac{E}{RT}$, where R is the gas constant, T the absolute temperature, and E the gram molecular energy of activation or "critical increment" of the "active" substance (or, for a bimolecular reaction, the sum of these energies).

As ordinarily employed, this relation has the form

$$K_2 = K_1 e^{\frac{\mu}{2} \left(\frac{1}{T_1} - \frac{1}{T_2} \right)},$$

K_1 and K_2 being the velocity constants at the respective temperatures. The quantity μ ($=E$) is independent of the temperature, and independent of the actual velocity of the process. For simple chemical processes μ varies in different cases from about 4,000 to 35,000. It is therefore a more delicate, as well as being theoretically a more significant, index than the Q_{10} ratio for the characterization of a process. The quantity μ , in distinction to the "temperature coefficient," might be termed the *temperature characteristic*.

Since μ has the meaning "energy of activation," it is to be expected that processes governed by the same species of "active molecule" will yield the same value of the constant μ . Thus, various reactions determined by the same catalyst should yield a practically constant "critical increment," namely that associated with the formation of active from inactive molecules of catalyst. This view has been developed in a very suggestive recent paper by F. O. Rice (1923), with particular reference to hydrogen ion catalysis. Reactions in living matter must frequently, if not usually, be conceived as catalytically excited. A preliminary survey has shown that vital phenomena are to a large degree empirically separable into groups according to the associated values of μ .

An illustration will serve to indicate the sort of additional information obtainable by means of the temperature characteristic. In a study of the toxicity of pure salts for the colonial protozoan

Zoothamnium alternans, Koltzoff (1913) measured the time required for disorganization ("cytolytic" collapse) of the "kinoplasm" of the contractile stalk at different temperatures, in 0.5 normal solutions of NaCl and of KCl. The reciprocals of these times give a measure of the velocities of the process underlying the disorganization. The observations are plotted in Fig. 1. It is clear that the value of μ in the Arrhenius equation is the same for each set of experiments, namely 16,680. This value of μ I find associated with certain oxidative processes (as in *Arbacia* eggs; data of Loeb and

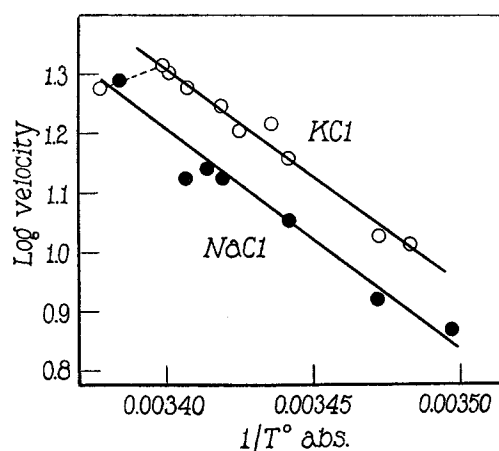


FIG. 1. The relation between temperature and the velocity of "cytolytic collapse" of the "kinoplasm" of the stalk of *Zoothamnium* in 0.5 N solutions of KCl and NaCl; data of Koltzoff (1913).

Wasteneys, 1911). The velocity with which carbon monoxide displaces oxygen from combination with hemoglobin, as given in the beautiful experiments of Hartridge and Roughton (1922-23), I find to yield $\mu = 16,525$. The same value may be demonstrated also in the measurements published by Gray (1923-24); though here (as is not infrequently the case), at temperatures greater than about 15° a second process, in this instance with μ approximately 11,000, becomes dominant (Fig. 2). Gray's data give measures both of oxygen consumption and of ciliary activity in the gill epithelium of *Mytilus*. The second process indicated by Fig. 2 may be an

alkaline catalysis (*cf.* O. F. Rice, 1923); a value of μ probably identical with this is recognizable in other cases of tissue respiration (over a portion of the temperature range), for example in the figures given by Evans (1923), plotted in Fig. 3.

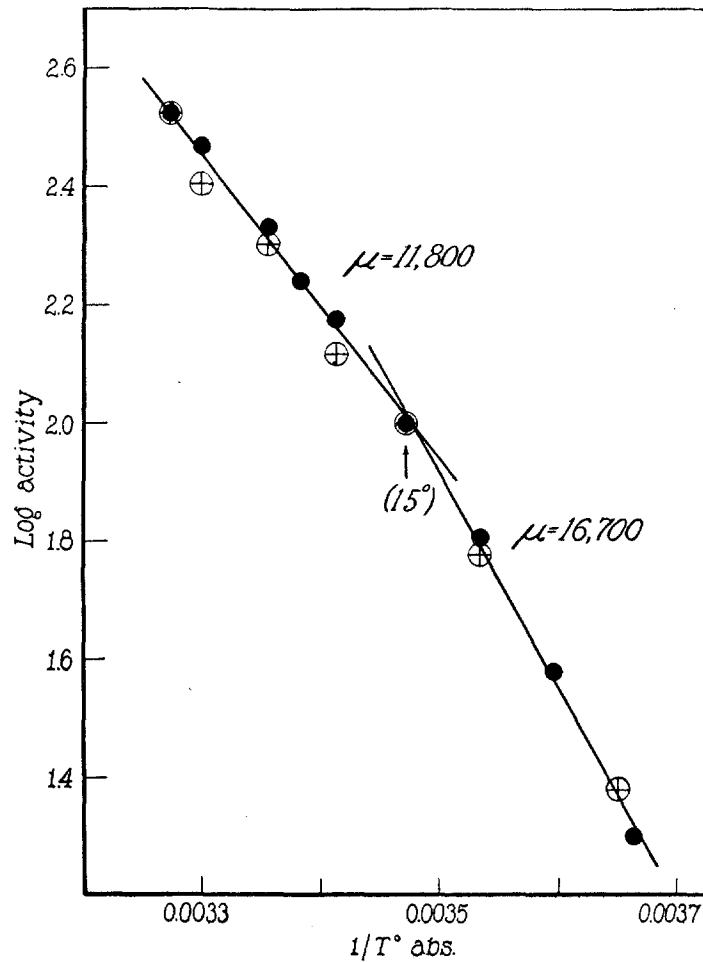


FIG. 2. Ciliary activity (black circles) and oxygen consumption (white circles) of *Mytilus* gill epithelium; data of Gray (1923). The two series of observations have been adjusted to give equal velocities at the mid-point (15°) of each set. At the higher temperatures the line for the oxygen consumptions is perhaps little lower than that for activity, but is in any case parallel thereto.

Loeb (1896) had observed that deprivation of oxygen leads to cytolytic destruction, and (1909) that the cytolysis of *Strongylocentrotus* eggs by NaCl could be suppressed by NaCN. It is known that pure salts affect the rate of respiration (Osterhout, 1919-20; Brooks, 1919-20), under conditions such that injurious action is involved. The conclusion, therefore, is consistent, that the toxic action of NaCl and KCl as observed in Koltzoff's experiments involves an effect on oxidations which determine the velocity of the toxic process as influenced by temperature.

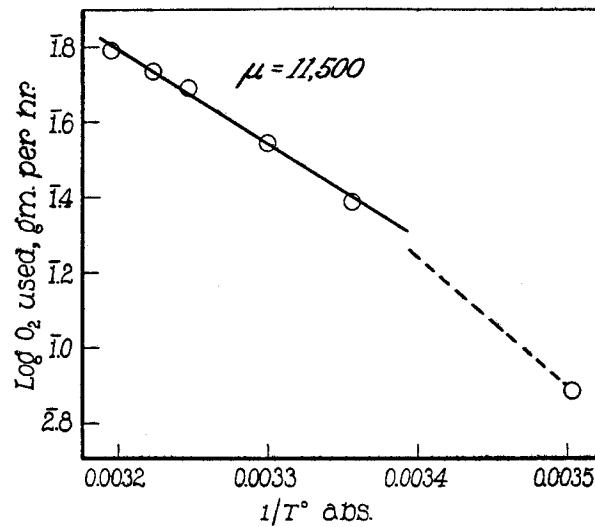


FIG. 3. Oxygen consumption of guinea pig uterus at different temperatures; data of Evans (1923). At some temperature between 25° and 12.5° the relative oxygen utilization is abruptly decreased.

Considerations of this sort may not infrequently permit decision as to whether physical alteration of the protoplasm (*e.g.* viscosity change) at particular temperatures is the *cause* of chemical disorganization, or itself a consequence of the net effect of temperature upon a system of linked reactions.

Scrutiny of much published data, and of newly investigated processes, shows that a "break" in the value of μ (such as that illustrated in Fig. 2) is not at all uncommon. Deviations at supranormal temperatures (*cf.* Hecht, 1918-19, *b*), and at very low temperatures,

are of course well known, and in favorable instances they may be analyzed. Abrupt change in the temperature relation indicates that a separate process has become the governing reaction in the complex. The occurrence of such alterations at about the "normal" temperature of an animal's environment is very important for the analysis of fluctuations in natural behavior (*cf.* Crozier and Federighi, 1923), as I shall endeavor to show in detail elsewhere. Here it is sufficient to point out that for the understanding of such complex temperature relations, observations of some precision are required at short intervals of temperature.

II.

From this standpoint the investigation of animal conduct as influenced by temperature may seek to classify the fundamental processes concerned. Such classification is empirically justified, quite apart from the possibility that at least some of these processes may then be identifiable as definite types of chemical change. It might be objected that the determination of temperature coefficients may be exposed to too many sources of uncertainty. The efficient answer is, that it is the business of physiology to discover regularities, and to employ them for constructive explanation.

An example is provided by the velocity of progression in arthropods. It is well known that insects, for instance, as a rule creep more slowly the lower the temperature. The velocity of creeping was measured with the diplopod *Parajulus pennsylvanicus* at temperatures between 6° and 30°. One series of the observations was secured by the cooperation of Mr. R. Forer and Mr. A. F. Mangelsdorf. Each animal was allowed to creep over a measured distance on a moist filter paper surface. A possible effect of light was looked for in control experiments, and found to be negligible. The size (length) of each individual (10 to 30 mm.) was recorded. The time occupied by the creeping act was measured with a stop-watch.

When the animal has recently emerged from quiescence creeping tends to be continuous and exactly in a straight line. The inner mechanism maintaining straightness of the creeping path has been discussed previously (Crozier and Moore, 1922-23). Particularly at and above a certain temperature a diplopod instead of smoothly

moving ahead may seem to "hesitate," and the rate of progression then becomes slow and uneven. This type of irregularity, when apparent, tends to become obvious at about 15°. For present purposes all such irregular creeping has been excluded. Another and quite interesting type of "irregularity" is the apparent inability of some individuals to show speedier progression than that evidenced at about 15°; for these individuals, the rate of progression is practically constant at temperatures between 15° and 30°. The records of these animals have been excluded.

The rate of creeping does not vary according to the size of the animal, within the limits of size among those employed. This probably means that the efficiency of the locomotor organs, chiefly a matter of their dimensions, is proportional to the animal's bulk; such a relation has been indicated also in the gasteropod *Limax maximus* (Crozier and Pilz, 1923-24), where a given increase in frequency of pedal waves produces at the same temperature an increase in velocity of vertical creeping which is independent of the animal's weight (except perhaps for very large animals).

The creeping act involves the rhythmic use of the approximately 58 pairs of legs, two pairs to each "segment." The opposite legs forming a morphological pair move synchronously and in phase; the phase relations of the movements of the successive pairs are such that about 6 "waves" of moving legs appear on the animal's length (*cf.* also Lankester, 1904).

The observations are collected in Fig. 4. Two series of measurements, made respectively in early spring and in June, have shown satisfactory agreement. It will be observed that in the neighborhood of 16° the observations show minor irregularity.

The velocity of uniform creeping varies with temperature according to the Arrhenius equation. The curve drawn in Fig. 4 is the curve of this equation with the critical increment put $\mu = 12,245$.

III.

The speed of creeping of ants has been measured at various temperatures by Shapley (1920). To his extensive observations Shapley fitted an empirical formula. Fig. 5 shows that over what may be considered the "normal" range (16° to 38.5°) the speed of creeping

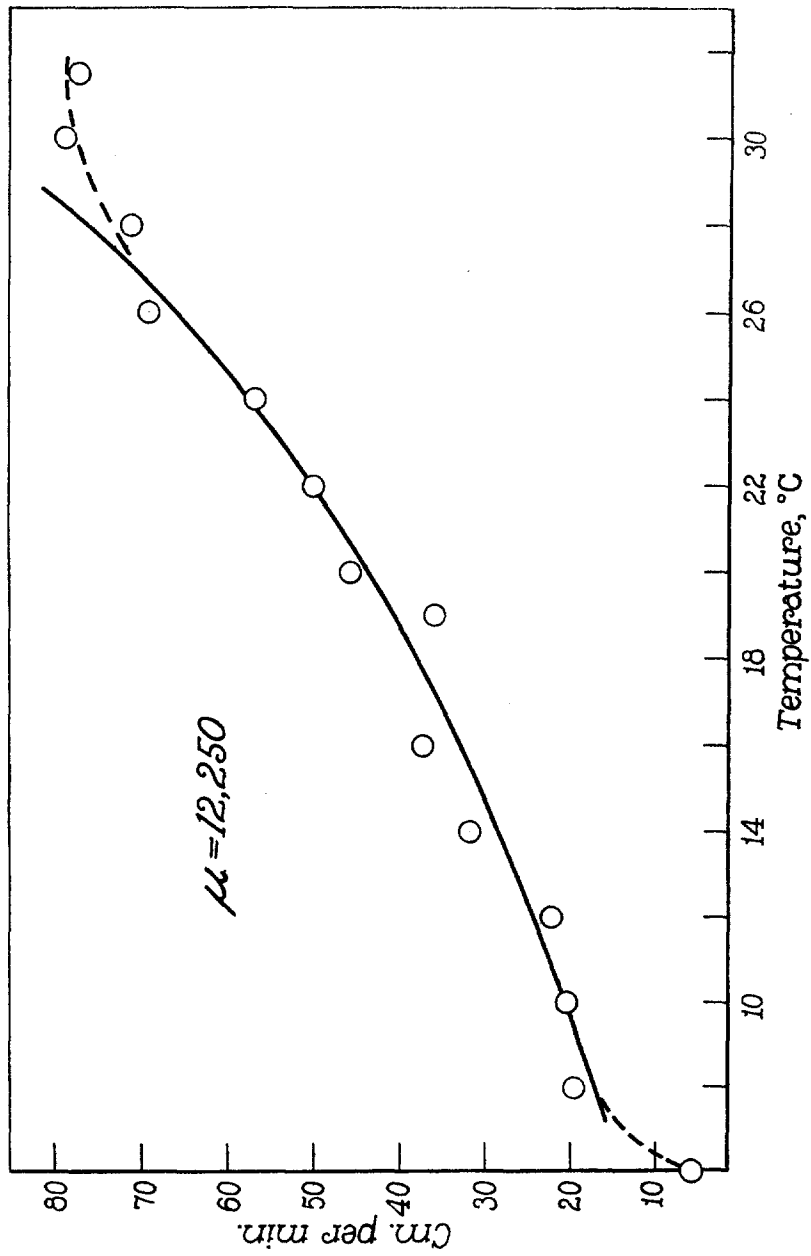


FIG. 4. The velocity of progression of *Julus* as function of temperature. The curve is the graph of the Arrhenius equation. Deviations appear below 8° and above 28°. The irregularity near 16° is commented upon in the text.

varies in logarithmic relation with the reciprocal of the absolute temperature, μ being = 12,220.

Of the various elements entering into the act of locomotion we may suspect that some central nervous phenomenon akin to "nerve center discharge" plays a controlling part. It is possible to show that nervous interconnections exist between the limbs of arthro-

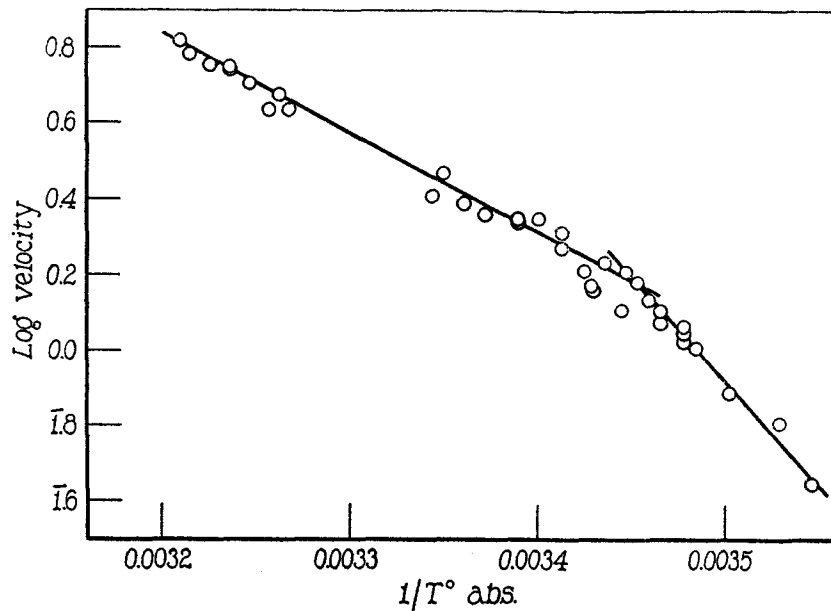


FIG. 5. The velocity of creeping of the ant *Liometopum apiculatum* is plotted logarithmically against the reciprocal of the absolute temperature (data of Shapley, 1920). Between 16° and 38.5° the value of $\mu = 12,220$; below 16°, 25,900.

pods, such as must imply "nerve center" activity in their rhythmic use. The action of atropine, in the case of caterpillars, converts protrusion of the legs and their locomotor action into retraction when the usual local stimulus to creeping is applied (Crozier, 1922). The displacement of one leg of a *Ranatra* in a state of maintained tonic immobility causes characteristic movements of its mate (Crozier, 1923).

With the supposition that the rate of movement of the legs of *Parajulus* and of ants depends upon the rate of discharge of impulses from nerve centers, we may look among arthropods for other phenomena in which the rate of central nervous activity is likely to be a governing element.

1. It has been known for some time that the frequency of "calls" by the "common cricket" (? *Æcanthus*) and by the katydid is represented rather accurately by an equation of the type

$$aT + b = N,$$

where a and b are constants, N the number of calls, and T the temperature in °F. (cited from Folsom, 1906¹). For the katydid, Hayward's observations gave

$$T = 60 \frac{N - 19}{3};$$

this yields $\mu = 12,500$. Dolbear's (1897) formula (cricket),

$$T = 50 \frac{N - 40}{4},$$

gives $\mu = 11,300$. Numerical observations are not available for more detailed analysis. This linear formula is an approximation merely, holding fairly well over the median temperatures. Fuller data are presented by Bessey and Bessey (1898), Edes (1899), and Shull (1907). These data I have averaged graphically, reducing the temperatures to °C., and the results are given in Fig. 6. It is apparent that the critical increment is in each case near 12,000. Of the several sets of observations that set by Shull is the largest and best (particularly with regard to the accuracy of the temperature measurements); the value of μ is 12,200.

2. The frequency of flashing of fireflies as a function of temperature has been considered by Snyder and Snyder (1920). From their data (Fig. 7) $\mu = 12,200$.

3. That this value of the critical increment does not reflect merely a relation between temperature and capacity of muscle fibers to

¹ Folsom (1906), p. 106.

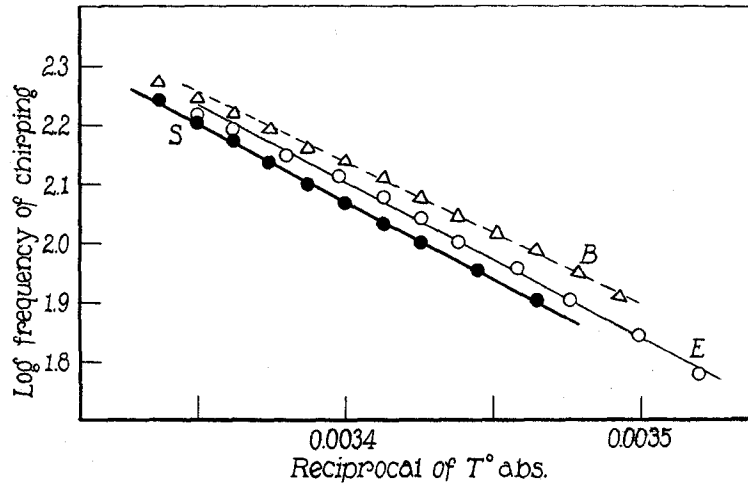


FIG. 6. The rate of chirping of the tree cricket *Ecanthus* as function of temperature; *B*, data from Bessey and Bessey (1898); *E*, data from Edes (1899); *S*, data from Shull (1907); the last series is probably the most significant. The observations were all made in the field.

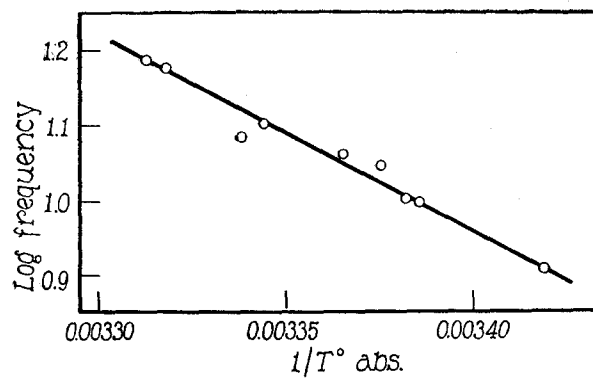


FIG. 7. The frequency of flashing of fireflies as function of temperature (Snyder and Snyder, 1920); the critical increment is $\mu = 12,200$.

respond to impulses is definitely shown by an important series of measurements due to Garrey (1920-21, *a* and *b*). These data have been plotted as in figures already given, and each set of individual observations in the original tables (Garrey) adjusted to a common scale by the use of suitable factors. The rate of the neurogenic heart beat, when the ganglion alone is subjected to different temperatures, follows the Arrhenius equation with $\mu = 12,000$, as is often true of heart beat frequencies; in all instances but one there occurs an abrupt change in the value of μ below 15° . The rates of CO_2 production by the ganglia, similarly treated, on the other hand yield $\mu = 16,700$, a magnitude rather definitely associated with oxidative processes (as already indicated earlier in the present paper). On the basis of similarities in the Q_{10} ratios, Garrey (1920-21, *a* and *b*) had argued that the rate of CO_2 production and the rate of cardiac rhythm are similarly affected by changes in temperature.

It is clear that these various processes in which the rate of activity of "nerve centers" is involved do provide closely concordant values of the critical increment. A common chemical basis of definite type may therefore be provisionally assumed for them. To what particular structural element the scene of this chemical process may be allocated is of no special consequence for the present, nor can it be definitely stated to what sort of reaction the process belongs.

It should be added that comparable phenomena in vertebrates do not necessarily yield this particular value of the constant μ (though it is not infrequently found in connection with the rate of the heart beat), nor do all rhythmic processes among insects. The rate of respiratory movements has been studied in several forms, and from series of estimations at different temperatures I find $\mu =$ approximately 16,500, for respiratory rhythm in *Libellula* larvæ (up to 15°) and (up to 30°) in *Dixippus* (data of Babák and Röcek, 1909; von Buddenbrock and von Rohr, 1922). It is of interest that a certain amount of evidence shows these rhythmic breathing movements to be to some extent governed by the oxygen tension; this point should be more thoroughly investigated.

SUMMARY.

A comprehensive theory of animal conduct must be in position to account for variability in behavior. To some degree this may be possible through the quantitative examination of alterations in behavior as determined by temperature. This idea requires for its development a means of classifying vital activities on the basis of their "temperature characteristics." Such basis is provided by the critical increment (μ) in Arrhenius' equation for the influence of temperature upon the velocity of irreversible reactions. There is also obtained in this way a method of dealing with singular points at which the relationship between temperature and activity changes; and at which behavior tends to be especially variable.

As an example of such classification, the critical thermal increments are computed for the rate of locomotion in the diplopod *Julus* and in the ant *Liometopum*. These are found to be identical, μ being respectively 12,250, and 12,220, and to agree quantitatively with the critical increments obtained for certain other types of rhythmic activity (among arthropods) in which the rate of "central nervous discharge" may be assumed to play a governing rôle.

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