

GEOTROPIC ORIENTATION IN ARTHROPODS.

II. TETRAOPES.

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I.

The geotropism of certain arthropods offers opportunity for the evaluation of descriptive equations derived from the behavior of forms already studied. If these equations, for example those for the geotropic orientation of slugs (Wolf, 1926-27) and of tent caterpillars (Crozier and Stier, 1927-28), are based upon a correct understanding of the mechanisms which essentially limit orientation, then a geotropic organism of different morphology, or with different method of progression, should be expected to obey somewhat different rules, in correlation with any obvious difference in the way in which the weight of the body can be supported upon an inclined plane. This turns out to be the case. There is thus provided a proof that the quantitative formulations previously discussed are not mathematical accidents in some way due to the averaging of observations. This kind of test has been made with the negative geotropic orientation of the milkweed beetle *Tetraopes tetraophthalmus*. The case of the fiddler crab *Uca* has been examined elsewhere (Kropp and Crozier, 1928-29), and the behavior of several other forms has also been studied in detail; the latter instances will be discussed in another place.

II.

Tetraopes was collected on milkweed plants and kept in the laboratory in terraria upon transplanted milkweeds. The animals are hardy, and submit in a satisfactory way to a variety of manipulative operations. Their geotropism is normally precise and negative. The oriented upward progress is however periodically interrupted by brief intervals of cessation of creeping, even upon a vertical surface, which

may be accompanied by more or less vague turning movements, and at times by transient but definite *positive* orientation. Here, as in other instances, there accordingly appears an important correlation between continuity of progression and precision of geotropic orientation. Moreover, the equilibrium angle of orientation, θ , also varies, within certain limits, and with fairly definite rhythm, as already mentioned for caterpillars (Crozier and Stier, 1927-28). It is notable that in the cases of geotropism with which these experiments have been concerned the assumption of a significant alignment of the axis of the organism upon the plane (as defined by the angle θ) is apparent only *during progression*. A similar relationship between orientation and creeping is evident in experiments upon a turntable. It may be taken to mean that the central nervous condition attending the rhythmic use of the appendages (or, with caterpillars, perhaps the body musculature also) in creeping permits the effect of tensions applied to the muscles to exert an influence upon orientation. This may be due, however, to the fact that *change* (increase) of tension is the effective stimulus for the tension receptors, as is true in vertebrates. Interesting questions arising from such considerations, and in connection with the intermittent failure to maintain orientation, we must put aside for the present with this bare notice of their realization.

The geotropism of *Tetraopes* is very strikingly affected as a result of mechanical stimulation such as that due to handling. In this respect there is a certain parallelism with the reversals of phototropism seen in various animals as a result of mechanical excitation. The method used to obtain geotropic trails avoided any such disturbance. As the beetle approached the upper edge of the sheet of white paper on which it was creeping upward, a small piece of paper held at one corner by the experimenter was placed in its path; when the beetle had mounted it, the paper was moved to the lower edge of the recording sheet, where, after suitable rotation of the carrier, the animal was allowed to creep back again upon the record sheet. The rotation was necessary to enable the new trail to be initiated with a path almost horizontal in direction, from which upward orientation followed. The absence of any special effect due to handling is attested by the uniformity of the results as gotten by each of the two observers.

Trails were also obtained by the method earlier described for tent

caterpillars, in which a platform 3 meters long permitted very extensive creeping. In this way it was possible to study spontaneous changes of the angle θ , and the periodic halts and other phenomena associated with such shifts.

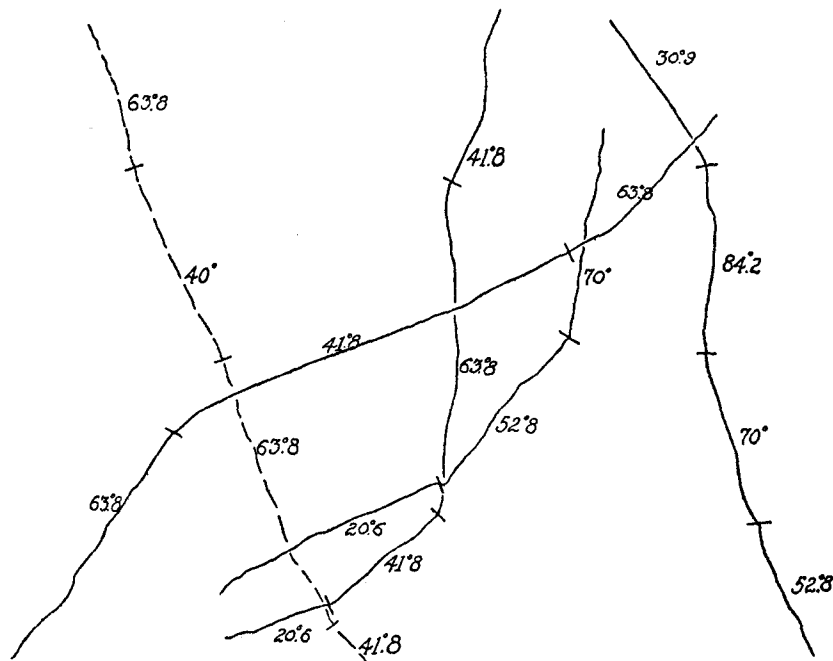


FIG. 1. Tracings of trails, selected at random, to show dependence of θ , the angle of upward orientation, upon the indicated tilt (α) of the plane upon which *Tetraopes* is creeping. Individuals temporarily asymmetric in response, *i.e.*, tending persistently to turn to right or to left, were purposely chosen for these tests in which α was altered (increased or decreased) without touching the beetles; for this reason the magnitudes of α are lower than those obtained as general averages (*cf.* Table I, Table II, and text).

It is desirable to realize that the dependence of the angle θ upon the inclination α can be demonstrated by a technic which avoids any possible consequence of immediate handling of the animals, and which is largely unaffected by spontaneous fluctuations in geotropic sensitivity. (This particular procedure, also employed by Crozier and Pincus (1927-28) in experiments with rodents, not yet described, has

the advantage that it permits a subsequent study of the latent period for geotropic response.) It consists in tilting the creeping plane at various angles, during progression of the animal upon it. The method has with some forms a certain restriction. If the inclination be *decreased*, the assumption of a new orientation may be delayed and vague, in agreement with the conception that in the field delimited by $+\theta$ and $-\theta$ orientation is not constrained. *Tetraopes'* behavior, however, allows this restriction to be circumvented. By choosing pronouncedly "asymmetric" individuals such as (for the time being) turn persistently to right or to left, the geotropic orientation is forced to work against a "brake" and thus to be expressed more delicately. Illustrative trails are copied in Fig. 1. The mean values of θ from such experiments, given in Table II, (Fig. 4) are naturally lower than with symmetrical average sensitivity (Fig. 3).

In one respect the experimental conditions differed from those required with the caterpillars. Like certain other beetles, *Tetraopes* is geotropically active consistently only in light. In darkness, creeping is usually absent, or aimless. It was shown by Moore and Cole (1920-21) that *Popillia japonica* creeps vertically (on a vertical surface) more rapidly as the illumination is increased, quite apart from any *phototropic* influence. But the photokinetic effect does not influence the *angle* of orientation on an inclined surface, in *Tetraopes*. Nor does the position of the source of light, in spite of the positive phototropism which is pronounced under other conditions (Crozier and Mangelsdorf, 1923-24). Our experiments, however, were made in a dark room with light (and diffusing screen) directly above the creeping stage, of 40 m.c. intensity. With such illuminations, light may come either from below, ahead, or from one side of the animal without modifying θ . With light of much lower intensities it is apparently possible to compound positive phototropic and negative phototropic orientations upon inclined surfaces, but the very interesting additive and threshold relationships between vectorial phototropism, geotropism, and photokinesis we have not as yet been able to examine in detail. Occasionally, good creeping was had without high light intensity. One such instance was given by beetle 16. With $\alpha = 49^\circ$, trails under white light gave $\theta = 74.48^\circ$; under weak red light, $\theta = 74.60^\circ$. In subsequent experiments with *Pyrophorus* (Kropp, 1929) observations could be made in darkness.

The absence of effective directional action by light of higher intensities in these experiments has one fortunate consequence. The use of rough white paper as a creeping surface did not introduce errors due to orientation by reflected light. This was checked by comparison with trails upon dull black cloth. It is nevertheless true that when in geotropic creeping on white paper the beetle closely approaches the boundary of a black surface upon which the paper rests, the trail suffers noticeable deflection. But it is only such contrast as between white and black areas which produces this temporary dis-

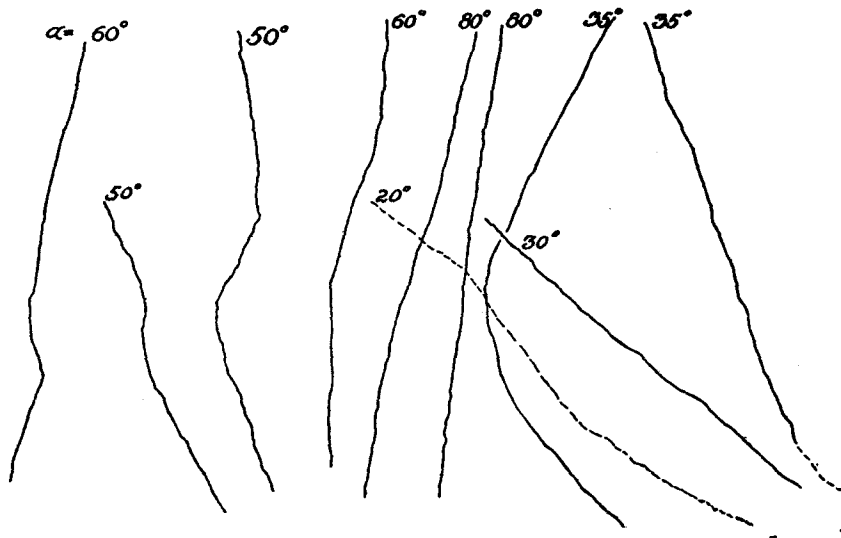


FIG. 2. Various trails, chosen at random, to illustrate properties of the records of orientation of *Tetraopes* on inclined surfaces; see text.

turbance, and even then only when the beetle is creeping slowly but not (as a rule) when moving with optimum speed.

In the field, flying of the beetles is notable on bright sunny days with high temperature. At 25° to 27° a flying beetle lighting upon a milkweed immediately creeps upward and usually flies off on reaching the top. This happens at once upon arrival at the highest point of support if there is apparent coincidence with one of the rhythmically recurrent spasms of separation of the elytra and fluttering of the wings. With higher temperatures (>27°) these periods are much

more frequent. This was also studied with beetles enclosed in a large spherical flask immersed in a thermostat at controlled temperatures. The spasms of elytral opening occur at longer intervals at 24°, although

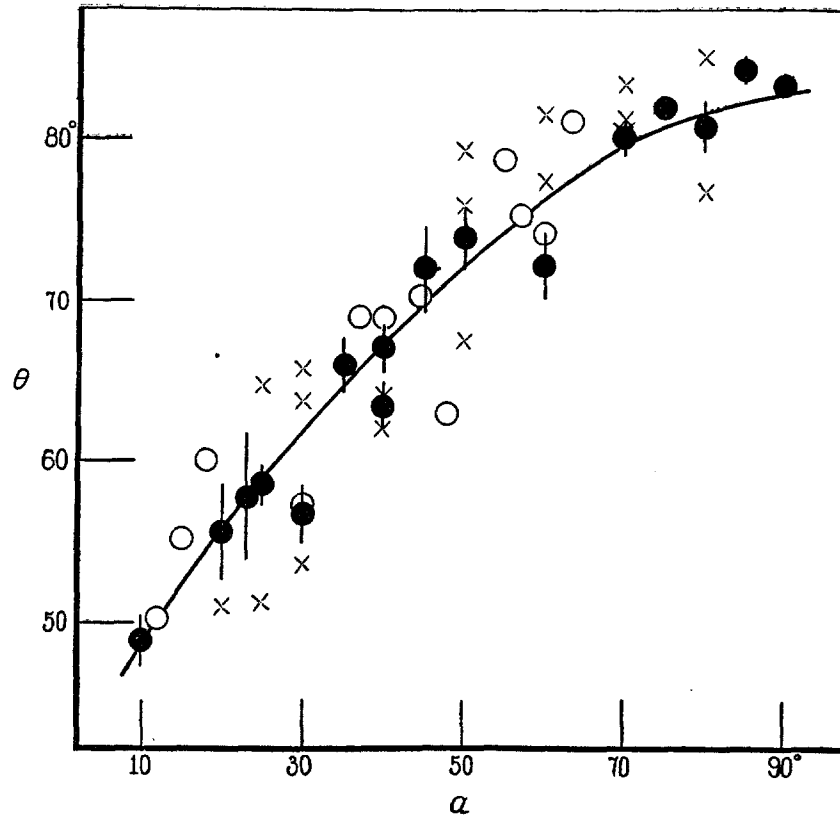


FIG. 3. Mean magnitudes of angle of orientation θ as function of the inclination of the surface α . Values which are averages from fewer than ten series of measurements are given as open circles, of ten or more as solid circles (with the probable error of the mean of the series' means indicated). There are added (crosses) mean estimates of θ from tests with a single individual (No. 15) used at a large number of inclinations. The curve is that of $\Delta \theta / \Delta \sin \alpha = \text{const.}$ (cf. Fig. 7).

even here an activity of this kind may *rarely* eventuate in flying departure from even a flat surface. To obtain creeping uninterrupted by these disturbances, the geotropism tests were made at temperatures between 23.5° and 25°.

No differences in orientation were observed which could be correlated with sex or size of individual, and the results from all have therefore been taken together. Between 10 and 20 trails were secured, at various angles of inclination of the supporting plane, with each of some 56 individuals. Not all of these were used at every inclination, some being chiefly employed for operative experiments.

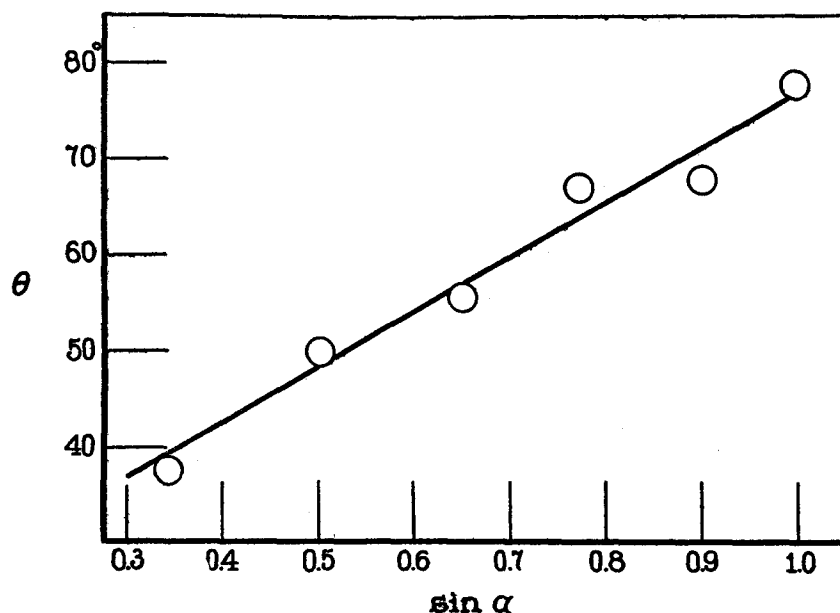


FIG. 4. Mean values of θ as a function of $\sin \alpha$, from trails with 7 markedly asymmetric individuals (*cf.* Fig. 1, and text). The values of θ (Table II) are lower than the averages at corresponding inclinations with normal (*i.e.* not asymmetric) individuals.

A total of approximately 3,400 trails form the basis of Fig. 3. The variability of θ , under these conditions, cannot be expected to show the sort of regularity discovered in other experiments with groups of selected individuals, and it is significant that the variation of the mean θ 's as tabulated cannot be reduced to any simple rule. The angles of orientation (θ) were measured upon the trails as accurately recorded with soft pencil during the progress of creeping. Illustrative details are given in Fig. 2. As with the caterpillars, there occur periods of

marked asymmetry of response. During such a period it is sometimes impossible for several hours to obtain a single trail with orientation to the right (or to the left, as the case may be) but all go to the opposite side no matter how the beetle is started creeping. Several

TABLE I.

Mean Angles (θ) of Upward Orientation of Tetraopes on a Plane Inclined at α° with the Horizontal. The Values of θ Are Not All of the Same Weight; Cf. Fig. 3.

α	θ	α	θ
<i>degrees</i>	<i>degrees</i>	<i>degrees</i>	<i>degrees</i>
10	48.89	45	71.99
12.7	50.21	46.5	63.13
15	55.25	49	74.60
18	60.02	50	73.99
20	58.04	55	78.78
23.3	62.15	57.1	75.69
25	58.96	60	72.2
28	62.92	63.3	81.17
30	61.64	70	80.17
35	66.04	75	81.95
37	68.63	80	80.77
40	63.50	85	84.35
44.3	70.3	90	83.3

TABLE II.

Mean Angles of Upward Orientation (θ) from Experiments in Which 7 Tetraopes Markedly Asymmetric in Response Were Allowed to Creep upon a Platform the Slope of Which (α) Was Subsequently Altered to the Value Noted (See Text, and Fig. 1).

α	20.6°	30.9°	41.8°	52.8°	63.8°	84.2°
θ	37.78°	50.00°	55.51°	67.08°	67.99°	77.95°

hours later, or next day, the orientation of this individual may be equally definite but to the other side. We have not attempted, in such cases, to apply the method of averaging used with the tent caterpillars, but have simply taken the values of θ , in view of the absence of any systematic divergence. Creeping is slower at higher values

of α (and of θ), but this was not studied systematically. In every case the beetles used showed a normal activity of the legs in creeping; it is *particularly* necessary to be sure that the tarsal hooks have not been torn off when the animal is removed from the milkweed, or during subsequent handling. Deficiencies of this kind, or injuries to the

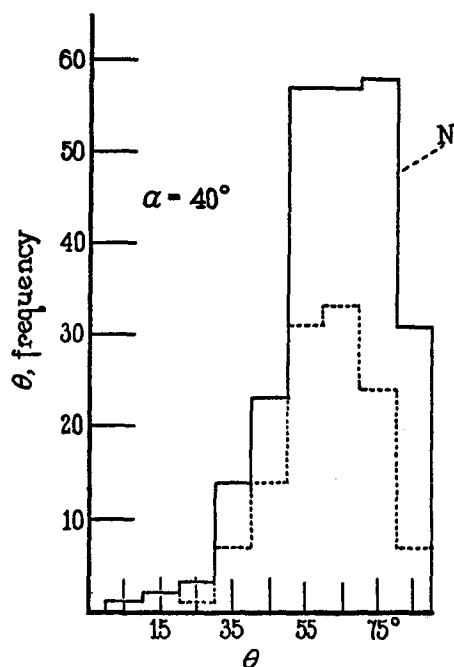


FIG. 5. Distributions of measurements of θ for all observations at $\alpha = 40^\circ$; for normal individuals (N) and for those with antennae removed.

legs, quickly reveal themselves in irregularities of orientation and in circling movements; the functional significance of the legs differs among the 3 pairs and all 6 legs are required for adequate progression, as proved by a variety of amputation tests.

III.

The average angles of upward orientation (θ) of *Tetraopes* are related to the tilt of the creeping surface as set out in Table I (Fig. 3). Each average is the mean of the averages of θ for each of a number of

individuals. The manner in which the separate readings of θ are distributed about the means is illustrated in Fig. 5. These distributions are essentially symmetrical, at inclinations below $\alpha = 60^\circ$. The proportionate scatter in such graphs is not fairly dealt with unless the size of the θ - classes is made less in proportion to $\sin \alpha$; this is due

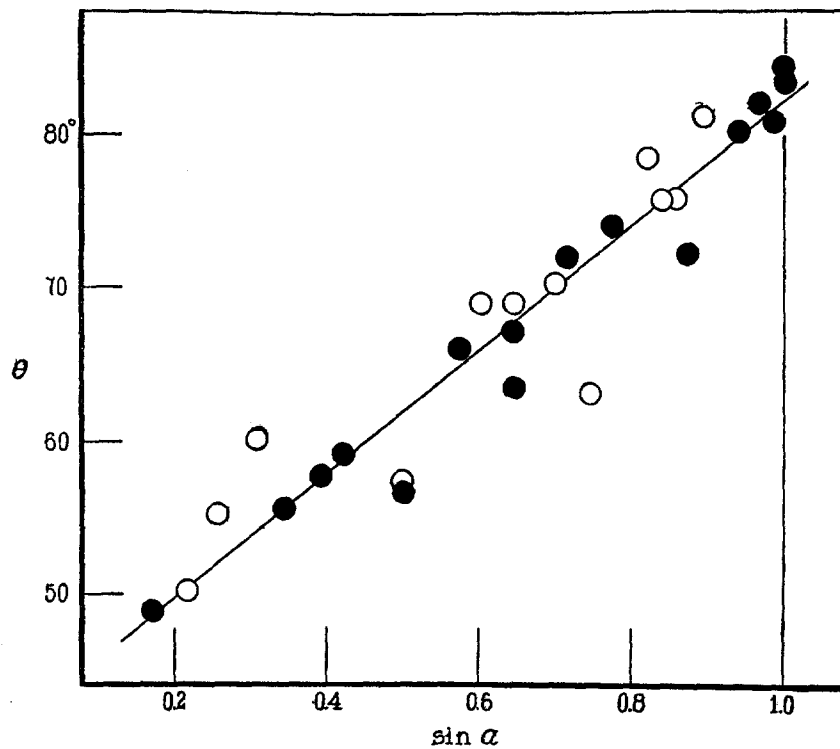


FIG. 6. The relation between θ and $\sin \alpha$ is practically linear (*cf.* Fig. 3); weighing of the points is as indicated in Fig. 3.

to the fact, brought out in earlier accounts (Crozier and Pincus, 1926-27, *a, b*), that the variability of θ is itself a function of $\sin \alpha$. Such a result provides an important test of the adequacy of the experimental procedures. At high inclinations the distribution of θ is necessarily somewhat skew, since the animal cannot very well give $\theta > 90^\circ$. The situation here as regards the distribution of θ 's is pre-

cisely that already described in our preceding paper (Crozier and Stier, 1927-28, *b*). The distribution of the mean values of θ obtained from the several individuals is also "normal." A sufficient method of weighing these means is to give the number of "runs" of observations concerned in each. In Fig. 3 the points based upon averages from fewer than 7 individuals are entered as open circlets.

Examination shows that in the case of *Tetraopes* the angle θ is linearly proportional, not to $\log \sin \alpha$ as in the earlier cases, but to $\sin \alpha$ directly. The lowest tilt at which consistent orientation is obtained is $\alpha = 15^\circ$; below this, positive and negative orientations fluctuate, or creeping is random. With some individuals the threshold is at 20° . With angles above $\alpha = 85^\circ$ creeping is slowed, and no increase in θ is to be detected. Between these limits the ratio $\Delta\theta/\Delta \sin \alpha$ is constant (Fig. 6).

IV.

Inspection of the creeping beetles at once suggests a possible origin for the difference between the descriptive formula for their orientation and that for the other forms thus far considered. The direct rather than logarithmic relationship between θ and the sine of the inclination of the surface, whatever its mechanism, is incidentally a valuable commentary on the point previously made (Crozier and Pincus, 1926-27, *a, b, c*; Crozier, 1928; and Crozier and Stier, 1927-28) regarding the "Weber-Fechner Law." In *Tetraopes*, as with certain other beetles, the center of gravity is posterior to the region of attachment of the legs (Fig. 7). This must result in a turning moment applied to the legs, in addition to the straight downward pull which they support parallel to the inclined plane. The same effect is seen in elaterids; of these, several luminous Cuban species were studied be-

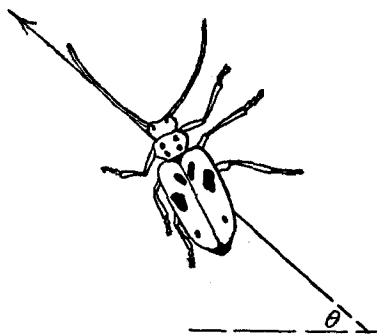


FIG. 7. The posture of *Tetraopes* upon an inclined surface. Owing to the mass of the abdomen, a twisting moment must be supported by the legs when $\theta < 90^\circ$. Diagrammatic.

cause it is possible to follow their paths in darkness. If the notion be correct that the gravitational pull supported by the legs during creeping supplies the gravitational stimulus, and also, because of a differential distribution upon the appendages of two sides, provides the limiting condition necessary to establish θ as a function of α , then the relationship should be experimentally controllable by modifying the

TABLE III.

Results of Experiments in Which the Distribution of the Weight, and the Total Load, Carried by Tetraopes during Upward Geotropic Creeping Was Varied.

1. *A small mass of colophonium cement weighing 3.8 mg. attached to the posterior dorsal surface of the elytra.*

α	θ	θ with wax attached
25°	61.1	68.4
55	80.3	84.6
75	82.0	81.93

2. *A small mass of cement attached to the dorsal surface of the thorax.*

α	θ	Attached mass	θ with wax attached
25°	61.1	3.8 mg.	57.6°
35	{ 64.5 74.04	{ 21.2 mg. 3.8	{ 35.4 (90 per cent trails +) 48.6 (30 per cent trails +)
55	80.3	3.8	63.4
75	82.0	3.8	81.2

3. *The wing covers and wings removed.*

$\alpha = 40^\circ$; mean θ for the individuals used in these tests = $67.1^\circ \pm 1.5^\circ$ before removal of wings; $\theta = 69.0^\circ \pm 2.0$ after removal.

(Removing the antennæ, also, has no detectable effect).

several components of this pull. Removal of the antennæ of *Tetraopes* has no effect on orientation (*cf.* Fig. 5). In land pulmonates (Crozier and Federighi, 1924-25; Cole, 1925-28; Crozier and Navez, 1928-29) and in young mammals (Crozier and Pincus, 1926-27, *a, b*; 1927-28; Pincus, 1926-27) control through effect on the tensions of muscles is quite clear; in certain other instances, according to a few tests made, for example, by Fraenkel (1927) with *Littorina*, and

(unpublished) by Mr. E. F. B. Fries with *Dendronotus*, the effect if any is dubious with these particular aquatic forms. The experiments with some forms are hampered by the nature of the creeping mechanism (*Dendronotus*); in the case of others it is first necessary to remove the possible influence of other sources of stimulation, and to make certain that the animal is moving with adequate speed (as has been found with *Littorina* creeping in air). In still other cases, among such pulmonates as *Limax*, for example, comparative measurements can only

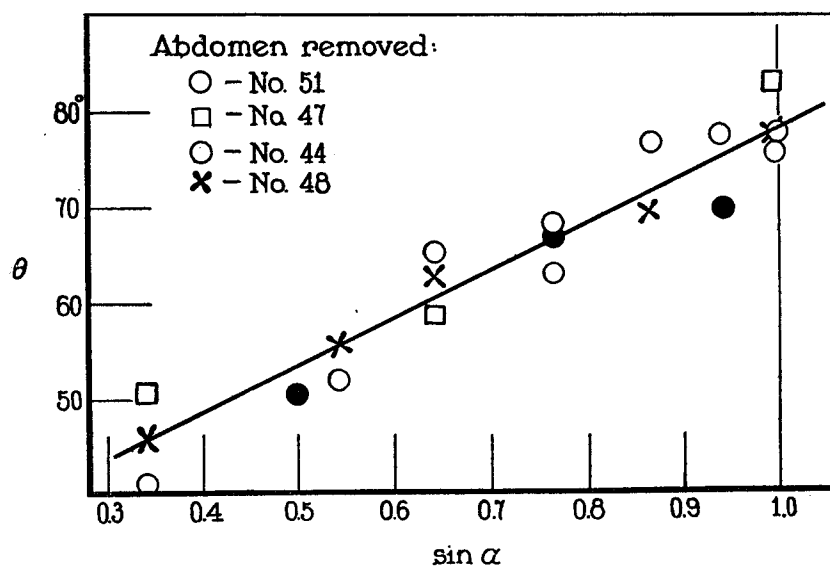


FIG. 8. Mean values of θ at various slopes (α) of the surface on which creeping takes place, for 4 individuals after amputation of the abdomen.

be obtained when the animals are creeping with comparable degrees of extension of the body, since the tonus or the degree of extension of the musculature must be supposed to influence the sensitivity of its proprioceptors to deforming pressures; this rather elementary kind of error (together with several others) has for example led Piéron (1928) distinctly astray, as our own numerous earlier experiments with *Limax maximus* suffice to demonstrate.

With *Tetraopes* it is a simple matter to perform experiments of the following kinds: 1, an additional mass (a small bit of colophonium

cement) is attached at the posterior margin of the elytra; 2, a similar addition is made to the head or at the anterior border of the thorax; 3, the wing covers and wings may be removed; 4, the whole abdomen may be cut away.

Experiments of type 1 should increase θ , slightly, at constant values of α , if α is not too large; in type 2, θ should be decreased; in 3, θ should be very little affected, but if anything decreased; in 4, it should be markedly decreased. The results obtained in a long series of trials agree with these predictions, in every particular. For most of the tests the inclination $\alpha = 40^\circ$ was chosen. The findings are summarized in Table III, which deals with the first 3 kinds of modification. The effect of adding a load anterior to the attachment of the legs being to decrease the effect of the turning moment about their lines of intersection, the fact that θ is decreased, despite the augmented total load, proves the importance of this factor.

The effect of removing the abdomen must be considered in greater detail. It is expected to do two things: first, to lessen the total downward pull; second, to remove the twisting moment on the legs. The operation is made in such a way that the legs are not directly injured, and by cutting around the chitin before cutting through the internal organs there is less extensive damage to the contents of the thorax. The cut surface is covered by a thin layer of vaseline, to prevent evaporation. Such preparations live for several days. After an interval for recovery they creep fairly well, and their orientation is definite. Mean values of θ from experiments with 4 individuals used at a number of inclinations are collected in Fig. 8; θ is consistently lower than with the intact animals (Fig. 6). In terms of the preceding suggestions, the lower values of θ resulting after amputation of the abdomen should be corrected by attachment of a substitute mass of wax. Thus in the case of *Tetraopes* No. 51:

$\alpha = 35^\circ$
 $\theta = 65.0^\circ$
 θ , abdomen removed, = 48.9°
 θ , abdomen removed = 75.6°
 but with load of
 wax (8.9 mg.) attached in its place,

If the turning moment due to the abdomen is responsible for the failure of an approximately logarithmic connection between θ and $\sin \alpha$, then

such beetles should in their orientation obey a formula different from that obtained for the normal *Tetraopes*. Experiments with several active preparations are summarized in Fig. 8. It is apparent that the relation of θ to $\sin \alpha$ is however again direct, as nearly as can be told, rather than logarithmic; the difference must arise in some other way.

These experiments give, then, an additional check upon the theory of geotropic orientation, in two particulars: (1) the different formu-

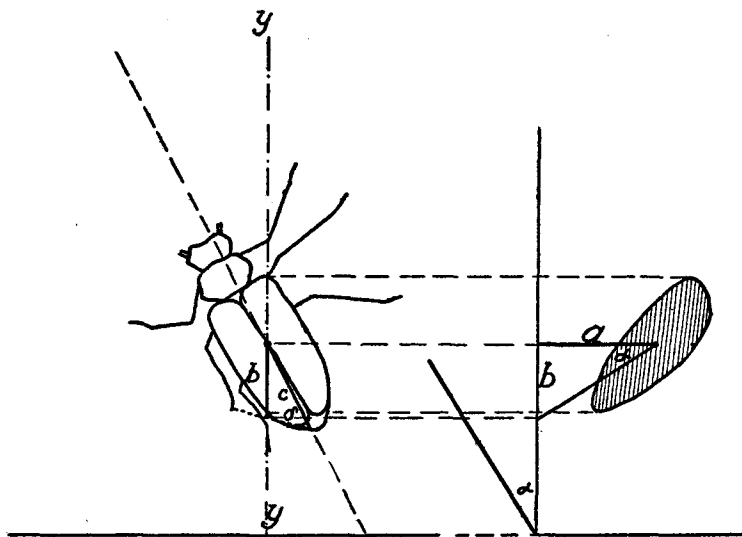


FIG. 9. Projection of a creeping *Tetraopes* upon an inclined surface (diagrammatic), and at the right a vertical section in the plane $y \dots y$. The line of gravitational pull passes downward from the center of gravity, and is assumed (as a limiting condition) to pierce the surface on the line connecting the tip of the abdomen, which is in contact with the surface, with the tip of the midmost position of the mesothoracic leg. See text.

lations required according to differences in structure, and (2) a test of the muscle tension theory when the gravitational pull can be, not merely increased as in former experiments, but also decreased as well. It remains to find a rationalization of the quantitative relations in the case of *Tetraopes*. This is done in the following way. Let it be considered that the sideward displacement of the body axis through the pull of the abdomen is for the moment ignored. Then the conditions

of progression may be diagrammed as in Fig. 7 and in Fig. 9, in which the outline of the beetle is projected normally upon the plane of creeping. But in fact the body is effectively supported at 3 points only, namely, by the legs on either side and by the posterior end of the abdomen (it is true that the mandibles are also, at each step, in brief contact with the substratum), and except at these points it is not in contact with the plane. A prime condition for stability, then, will be that the vertical line from the insect's center of gravity must pass through the plane at a point within the "base of support" defined on the downward side by the line drawn from the legs (taking the mesothoracic leg as representing the mean position) and the tip of the abdomen. A section in the vertical plane $y \dots y$ then discloses that $\tan \alpha = \frac{b}{a}$, where b is defined in Fig. 9. From the projection on the creeping plane,

$$b = \frac{x \sin (\pi - \delta)}{\sin (\pi - 90^\circ + \theta - \delta)}$$

therefore

$$\frac{a}{c} \tan \alpha = \frac{\sin (\pi - \delta)}{\sin (90^\circ + \theta - \delta)}$$

Since a and c , coordinates of the center of gravity, may be assumed constant, and likewise the structural angle δ ,

$$\begin{aligned} K \tan \alpha &= \frac{1}{\sin (90^\circ + \theta) \cos \delta - \sin \delta \cos (90^\circ + \theta)} \\ &= \frac{1}{K' \sin \theta + K'' \cos \theta} \end{aligned}$$

$$K_1 \cot \alpha = K_2 \sin \theta + \sqrt{1 - K_2^2} \cos \theta.$$

Values for the constants may be gotten by substituting pairs of values of α and θ . A plot of this relationship should show, if the interpretation be sound, a rectilinear decrease of $K_2 \sin \theta + \sqrt{1 - K_2^2} \cos \theta$ with $\cot \alpha$. The theory of this relationship assumes merely that during geotropic creeping *Tetraopes* turns upward (or downward, in case of positive geotropism) until tension on the legs such as would (unap-

posed) lead to tumbling off the surface is relieved by the attainment of a mechanically stable posture on the inclined plane. It will be brought out subsequently that this simple assumption leads to very interesting results when used to interpret the geotropic orientations of certain other forms (*e.g.*, *Uca*, *cf.* Kropp and Crozier, 1928–29) and of positively geotropic creeping. (Qualitatively, the fact was demonstrated with *Tetraopes* that *similar* changes of θ with α appear when the animal creeps on the *under* surface of a board (*cf.* also Wolf, 1926–27).)

With *Tetraopes* however, an additional feature must be considered. The downward slewing of the abdomen (Fig. 7) causes θ to be less, at a given magnitude of α , than if the axis of the body were rigidly perpendicular to the effective "axis" of the legs. This prevents obtaining a good fit of the observed θ 's by means of the foregoing equation at low values of α . It is *as if* the animal responded to the requirement of stability not merely by the upward orientation but also by turning the abdomen to one side, thus broadening on that side the base of support. A shifting of the center of gravity, by attaching bits of wax, should in the case of a backward shift cause θ to increase somewhat, as is obvious from Fig. 7, and this in spite of the inclination of the beetle's axis to the plane. A forward shift should cause the limiting value of θ to decrease, for similar reasons, since the base of support broadens up to the points of application of the legs to the substratum. These effects have already been recorded. A further difference appears at quite high values of α , since then the support at the tip of the abdomen becomes inappreciable. The simplicity of the satisfactorily direct proportionality between θ and $\sin \alpha$ (Fig. 6) therefore appears to cloak a variety of complications. In the extreme case, when the abdomen is removed, the situation is somewhat altered. We then

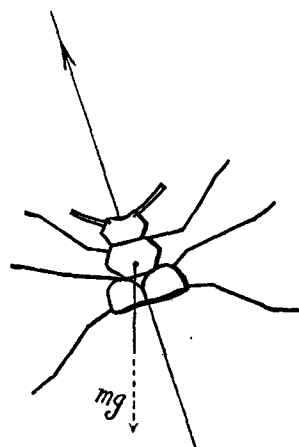


FIG. 10. Diagram of the conditions of oriented progression in *Tetraopes* with abdomen amputated.

conceive the base of support (at low inclinations of the surface) to be limited by a line connecting the points of opposition of the legs on the "down" side. At higher values of α , this condition cannot be met, and orientation must be due to the adjustment of sensibly equivalent tensions on the legs of the two sides. As indicated in connection with Fig. 10, the conditions are in fact too complex for calculation; a more significant test is indeed obtainable by measuring geotropic orientation of beetles of other species, and of ants, in which the abdomen is normally not directly in contact with the inclined substratum.

SUMMARY.

The creeping of the beetle *Tetraopes tetraophthalmus* during negatively geotropic orientation shows the angles of orientation (θ) on a surface inclined at α° to the horizontal to be proportional to $\sin \alpha$. The direction of orientation easily suffers temporary reversal to positive as result of handling. Mechanical stability during upward progression should be just possible when $K_1 \cot \alpha = K_2 \sin \theta + K_3 \cos \theta$, the weight of the body being supported on the tripod formed by the legs on either side and by the posterior tip of the abdomen. Lack of this stability produces tensions on the legs through (1) the bilaterally distributed pull of the body mass on the legs, and (2) the torque on the legs due to the weight of the abdomen. The downward gravitational displacement of the tip of the abdomen causes K_2 and K_3 in the preceding formula to be functions of α .

These relations have been tested in detail by shifting the location of the center of gravity, by attaching additional masses anteriorly and posteriorly, and by decreasing the total load through amputation of the abdomen; the latter operation changes the conditions for stability.

Different formulæ are thus obtained (*cf.* earlier papers) for the orientation of animals in which the mechanics of progression and the method of support of the body weight on an inclined surface are not the same. This demonstrates in a direct way that the respective empirical equations cannot be regarded as accidents. The results are in essence the same as that already obtained with young mammals. The diversity of equations required for the physically unlike cases merely strengthens the conception of geotropic orientation as limited

by the tensions applied to the musculature of the body (caterpillars, slugs) or of appendages (beetles, and certain other forms) when the body is supported upon an inclined surface, since equations respectively pertaining to the several instances, and satisfactorily describing the observations, are deduced on this basis.

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