

## THE GEOTROPIC RESPONSE IN ASTERINA

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### I

With various animals differing markedly in structure it has been found that the extent of geotropic orientation upon a sloping surface is a function of the inclination of the surface. Empirically, the connection between angle of oriented progression on the surface ( $\theta$ ) and the tilt ( $\alpha$ ) cannot be described by the same equations in the cases of forms for which it is clear that the sensorial equivalence of impressed muscle tensions on the two sides of the body cannot be achieved in the same ways (Crozier and Pincus, 1926, 1926-27; Crozier and Stier, 1928-29; Kropp and Crozier, 1928-29; Crozier, 1929); whereas for forms dynamically similar in this respect the same formulations do apply (*cf.* Wolf, 1926-27; Crozier and Oxnard, 1927-28; Crozier and Stier, 1927-28; Crozier, 1934-35).

It is of interest to examine from this standpoint the geotropic reactions of certain echinoderms. According to Jäger (1932) *Asterias rubens* creeps geotropically upward in such a way that  $\theta$  is a function of  $\alpha$ , although not in approximate proportion to  $\log \sin \alpha$  as had been found for certain other forms (Crozier and Pincus, 1926-27; Wolf, 1926-27; Crozier and Stier, 1927-28). At first sight it is perhaps difficult to see why, in the case of a starfish, there should be any definite relationship between  $\theta$  and  $\alpha$ ; in any case, it could not be expected to be of the general form obtaining in rats, caterpillars, slugs, and snails unless the gravitational pull upon the stomach (*cf.* Wolf, 1925; Parker, 1922) could be suitably involved; deforming pressures upon the body wall would obviously seem to be ruled out in this case, although clearly indicated for holothurians (Stier, 1933; Yamanouchi, 1929).

## II

Experiments were made with *Asterina gibbosa* of 1.0 to 2.0 cm. radius. According to Kalmus (1929) *Asterina* is negatively geotropic. This is complicated, however, by spontaneous reversals to geopositive creeping which may persist for some time. At any time it is possible to induce reversal of the predominant mode of response by mechanical stimulation, as by handling, removing briefly from the water, or by stirring of the water. Corresponding reversal to geonegative creeping can be brought about in a similar way during a "spontaneous" phase of positive geotropism. Such reversals due to handling are temporary.

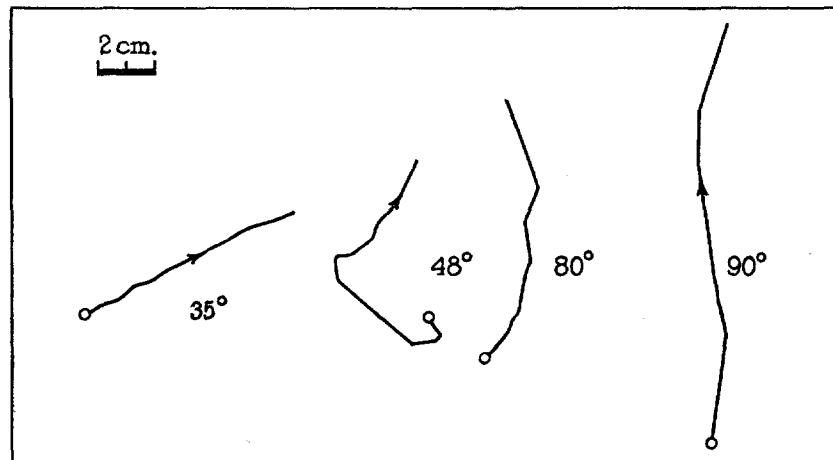


FIG. 1. Specimen trails of *Asterina* upon surfaces of different slopes ( $\alpha = 35^\circ$ ,  $48^\circ$ ,  $80^\circ$ ,  $90^\circ$ ), illustrating points discussed in the text.

A sea-star was placed upon a glass plate subsequently tilted under water to a desired slope. The under surface of the plate was ruled with a diamond point into a coordinate grid. The path followed by an *Asterina* could then be copied accurately upon ruled paper, and the angles made by the path measured. Observations were made in weak diffuse light. Kalmus (1929) says that young *Asterina* are positively phototropic, "adults" negative. The individuals used in these experiments were found not to be phototropic at all, at least after 24 hours in the laboratory; upon horizontal or vertical surfaces the direction of movement was not influenced by light. The temperature varied between  $17.8^\circ$  and  $20.5^\circ$ . Typical trails are given in Fig. 1.

Detailed measurements were made with six individuals. At two slopes of surface creeping was studied on the *under* side of the plate.

In general character the trails secured are similar to those obtained with other geotropic animals (*cf.* Crozier and Pincus, 1926–27; Crozier and Stier, 1927–28; 1928–29). Upward (or downward) turning of the path upon an inclined plane is continued until a rather definite angle of progression is attained; in some cases the turning, due in this instance perhaps to the phenomena of “persistence” or of “continued rotation of direction” seen in sea-stars, may be continued so far that, as with other forms, the path lies in a sector on the plane within which the path is not specifically oriented. This can be tested by turning the creeping-plate through  $90^\circ$ , and observing the subsequent course of orientation. There is usually a definite elongation of the body in the direction of movement. There is no detectable tendency for the tip of one ray to be in advance; usually an inter-radius lies in the direction of steady creeping. There is no evidence that the region of the madreporite tends to be ahead.

Measurements of orientation angles are collected in Table I.  $\theta$  increases with increase of  $\alpha$ . At low slopes, the scatter of  $\theta$  is greater; 10 or more paths were measured for each average. When the speed of movement is higher, at fixed  $\alpha$ ,  $\theta$  tends to be somewhat greater.

### III

The relationship between  $\theta$  and  $\alpha$  is roughly of the type encountered in tests with a number of other forms, in that the curve is convex upward. But  $\Delta\theta/\Delta \log \sin \alpha$  and  $\Delta\theta/\Delta \sin \alpha$  each increase as  $\alpha$  is made greater;  $\sin \theta$  *vs.*  $1/\sin \alpha$  is concave. None of the equations empirically justified with other forms fits the orientation data from *Asterina*. This is of interest, since the basis for a theory of the dependence of  $\theta$  upon  $\alpha$  would also appear to be quite different, and grows out of the following considerations.

The speed of progression of *Asterina* is variable, but under comparable circumstances it is also a function of the slope of the surface, increasing at higher slopes. On a horizontal surface, at  $20^\circ\text{C}$ ., creeping was at the rate of 1 cm. in  $40.0 \pm 4.1$  seconds; upon a vertical surface, 1 cm. in  $23.7 \pm 5.5$  seconds.

Kalmus (1929) made one experiment in which a cork float was attached by a thread to the dorsal side of *Asterina*. He found that in

consequence of the upward pull, the sea-star moved downward upon a vertical surface, in agreement with the effect upon a turntable. This we have repeated. A fragment of cork is attached at one end of a thread 2 or 3 inches long, the other end sewn through the dorsum of an *Asterina*. The volume of cork is adjusted to give about the maximum pull supportable, under water, by a few of the tube feet. On a surface

TABLE I

Mean orientation angles ( $\theta$ ) for *Asterina gibbosa* as a function of slope of surface (angle  $\alpha$ ).

$\alpha$	$\theta$
degrees	degrees
30	32.5 $\pm$ 1.6
	24.7 $\pm$ 4.9
35	28.3 $\pm$ 2.5
40	42.8 $\pm$ 3.6
	38.8 $\pm$ 4.1
	27.0 $\pm$ 2.7
	36.2 $\pm$ 2.2
45*	45.0 $\pm$ 2.5
46	37.3 $\pm$ 4.4
48	47.1 $\pm$ 1.4
50	42.8 $\pm$ 4.1
57	53.0 $\pm$ 2.5
60	57.8 $\pm$ 2.3
63	57.5 $\pm$ 4.0
70	60.0 $\pm$ 2.3
73	75.3 $\pm$ 2.1
75*	70.0 $\pm$ 1.5
80	72.9 $\pm$ 2.1
85	70.0 $\pm$ 2.5
90	87.0 $\pm$ 1.8
	80.6 $\pm$ 1.4

\* Creeping on *under* side of glass plate.

inclined at  $\alpha = 70^\circ$ , the animal goes slowly downward, at  $\theta = 90^\circ$ ; this is also true at  $\alpha = 30^\circ$  or lower. Repeated reversals of the inclination of the plate are followed by prompt and precise downward movement. When the upward pull is stopped, by holding the cork, movement continues downward for about 1 minute or so, but much more rapidly; then the animal orients upward through an arc, and at

an appropriate  $\theta$ ; if the upward pull is restored, downward movement is immediate. If the pull is made to act horizontally, by passing the thread over a rod, the *Asterina* creeps horizontally toward the other side. In these respects the direction of movement is controlled precisely as in the case of a gasteropod (Crozier and Navez, 1930). In relation to the question of the connection between  $\theta$  and  $\alpha$  the demonstration can be made more illuminating by using smaller cork floats, giving a lesser upward pull. Upon surfaces of intermediate slope (e.g.,  $55^\circ$ ) the *Asterina* then creeps downward, but at  $\theta < 90^\circ$ ; if the pull of the float be removed, it orients upward, but at a higher  $\theta$  than on the downward path. It was pointed out before that in downward and in upward progression on the sloping surface (without the attached cork)  $\theta$  is the same. The effect of the attached float is the same when the sea-star is creeping upon the under surface of the plate; in this case the direction of pull is in the plane of the surface.

The direction and the magnitude of the tension exerted upon the tube feet thus appear to be unquestionably responsible for the direction and for the limitation of the extent of gravitationally induced orientation under these conditions. The "spontaneous" reversals of orientation, and the reversal to positive geotropism seen after mechanical disturbance, present a problem of a different order; presumably there must be involved a central nervous reversal of sensory effects similar to that concerned in the reversal of galvanotropism (Crozier, 1930) in sea-stars and other echinoderms.

#### IV

In view of these facts it is necessary to consider that upward orientation involves movement in the direction away from a lateral pull. In Fig. 2 the gravitational component acting laterally to the *Asterina*'s path is labelled  $N$ , that in the line of movement  $M$ . We have to suppose that when the fraction of the total pull parallel to the surface ( $W \sin \alpha$ ) which corresponds to  $M$  reaches a certain value as result of orientation, the laterally acting component ( $N$ ) is without further influence; this merely corresponds to the fact that there is a threshold slope of surface for orientation. It is further to be supposed that when  $\alpha$  is varied the limiting fraction ( $M/W \sin \alpha$ ) will be a function of  $W \sin \alpha$ , and presumably directly proportional to it; since the

orientation angles are the same for *Asterina* of different sizes,  $W$ , the weight of the animal, may be ignored. It cannot be supposed that component  $N$  has merely to be reduced to a certain minimum or threshold value;  $N$  is measured by  $N = \sin \alpha \cdot \cos \theta$ , and is neither constant at orientation nor a simple function of  $\sin \alpha$ .<sup>1</sup> We then write  $\Delta (M/\sin \alpha)/\Delta \sin \alpha = \text{const.}$  as giving a reasonable statement of expectation concerning the geotropic performance of *Asterina*. Since (Fig. 2)  $M/\sin \alpha = \sin \theta$ , we have  $\frac{\Delta \sin \theta}{\Delta \sin \alpha} = \text{const.}$  as the formulation

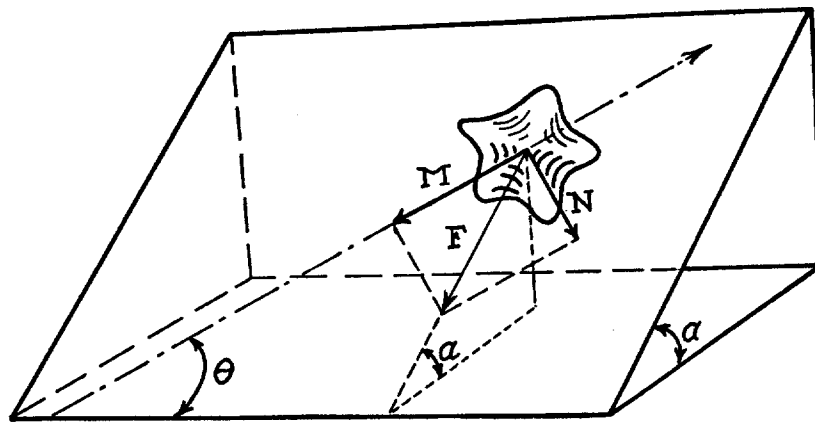


FIG. 2. The effective gravitational pull  $F$  upon an *Asterina* on a surface inclined at angle  $\alpha$  is resolvable into two components:  $M$ , in the line of progression at angle  $\theta$ , and  $N$  acting laterally to bring about further orientation until, as discussed in the text,  $M/F$  acquires a magnitude proportional to  $F$ .

it is expected should be followed. Fig. 3 shows that the equation is very nicely obeyed. At low slopes  $\theta$  is in small samples more variable (*cf.* Table I) than at high slopes, as is the general rule (Crozier and Pincus, 1926–27; Crozier, 1934–35; etc.), and the points in Fig. 3 consequently spread less and less widely as  $\sin \alpha$  increases.

In Jäger's data (1932) for *Asterias rubens* the same rule applies

<sup>1</sup> *Cf.* Crozier, 1934–35. von Buddenbrock (1931) and Jäger (1932) took  $\sin \alpha \cdot \cos \theta$  as the sine of the angle of tilt or of the transverse axis of the oriented animal. The former argued that this latter angle tended to be made constant in geotropic progression, which is not correct. Neither noticed its significance as a force vector.

accurately if one supposes, as I believe one must, that at  $\alpha = 30^\circ$  the group of  $\theta$ 's above  $65^\circ$  represents paths in the zone (*vide supra*) of no orientation (*cf.* Jäger's Fig. 22). This is shown in Fig. 4.

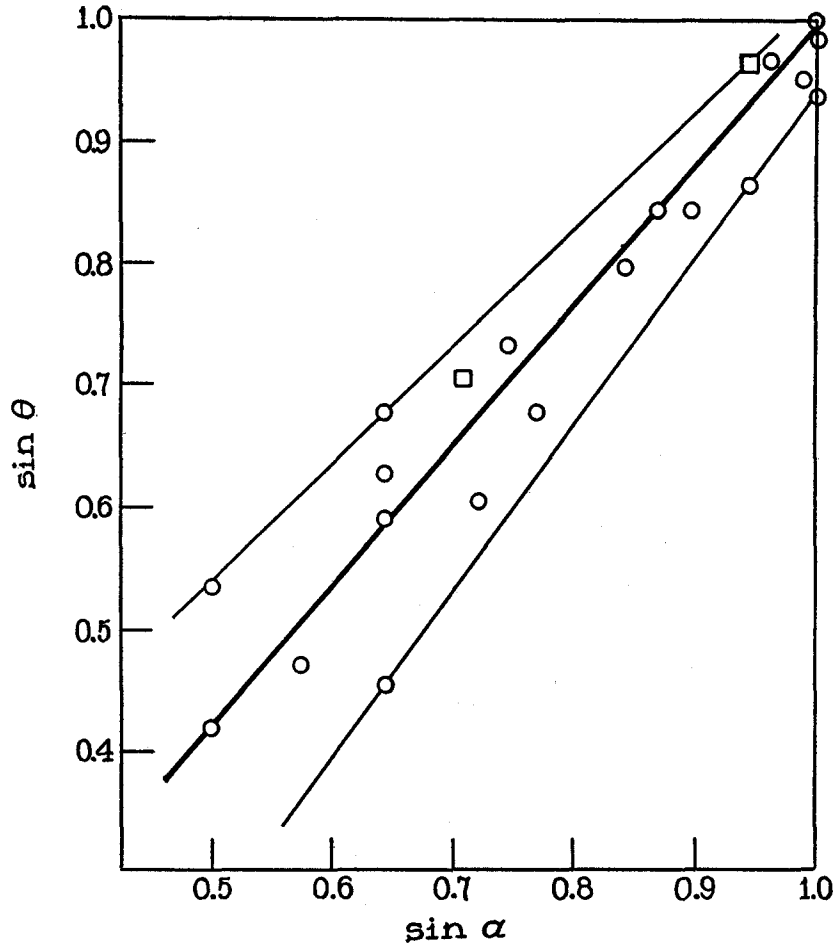


FIG. 3. Showing that  $\Delta \sin \theta / \Delta \sin \alpha$  is constant for *Asterina*. The scatter of mean  $\theta$ 's is progressively greater at lower values of  $\sin \alpha$ . Data in Table I.

This interpretation might be tested if the animal could be converted into one with bilateral symmetry. Mangold (1909) noted that single arms of *Asterina* creep upward upon an inclined surface. By cutting off four of the five rays and a strip of the disc connecting

them, one has a preparation in which most of the remaining tube feet are upon the intact ray. After a day such a preparation creeps well, all the tube feet functioning actively. It usually creeps with the tip of the ray foremost, and in the line of the axis of the ray. This is most often observed, however, if it is upon a steeply inclined surface, and is indeed then the predominant condition. After effects of handling have disappeared, it orients upward from an initially horizontal path, and creeps upward with the tip of the ray in advance; the course traced by the oral opening is in line with the axis of the ray, except for brief intervals. If the plate be reversed, orientation is reversed promptly. Orientation usually involves actual bending of the ray.

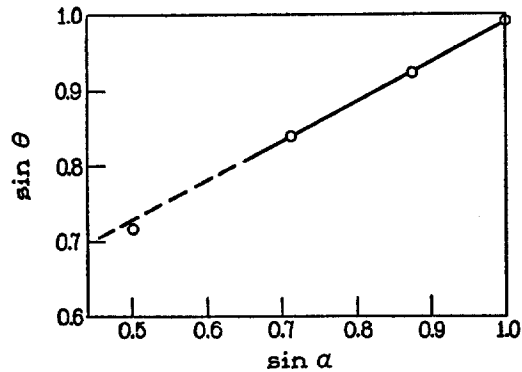


FIG. 4. A similar relationship may hold for the geotropic orientation of *Asterias*; based on the data of Jäger (1932), the measurements at  $\alpha = 30^\circ$  being corrected as explained in the text.

Occasionally the path swerves to a steeper  $\theta$ , and the rotation continues until the corresponding  $\theta$  on the other side of the vertical mid-line is reached. In positively geotropic creeping following handling the orientation of the ray is sometimes lost, but tends to be regained; the loss of director action by the ray appears when the path is at about  $\theta = 90^\circ$  and the animal is creeping rapidly. This is the mode of orientation to be expected if the axis of progression is definitely polarized and if the pull upon the tube feet is to be adjusted in the way here assumed by the attainment of a path at angle  $\theta$  which is a function of the slope of the surface. The  $\theta$ 's observed with the single-ray preparation were generally lower than with the intact *Asterina*; this may be due to a lowering of the threshold for response to tension.



## SUMMARY

Upon a surface inclined at angle  $\alpha$  *Asterina gibbosa* orients upward during negatively geotropic creeping until the average angle ( $\theta$ ) of the path is such that  $\Delta \sin \theta / \Delta \sin \alpha = \text{const.}$  This is true also in positively geotropic movement. The direction of orientation may be temporarily reversed by mechanical disturbance. The variation of  $\theta$  is greater at low slopes. Tests with directed impressed pulls, due to an attached cork float, show that the pull upon the tube feet is of primary consequence for the determination of  $\theta$ . When the component of gravitational pull in the direction of movement reaches a fraction of the total pull which is proportional to the gravitational vector parallel to the surface, the laterally acting component is ineffective. On this basis, it follows that  $\Delta \sin \theta / \Delta \sin \alpha = \text{const.}$

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