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THE LOCOMOTIONS OF SURFACE-FEEDING CATERPILLARS ARE NOT TROPISMS.

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PRELIMINARY OBSERVATIONS.

While collecting cherries from a tree a large number of apple-tent caterpillars were thrown upon the ground. Later several of these were noticed climbing the trunk of the tree. They continued onward and upward; some to the top of the tree and others to certain branches. Near the tree was a rustic chair, the top of the curved back of which was separated from the trunk by about three inches. Several caterpillars climbed the back of this chair. When they reached the top, they would elevate the front portion of the body, wave it back and forth and around for a few minutes and then proceed down the opposite side of the curved arm. Sometimes the insect would turn about and retrace its steps. These observations suggested two questions. Are these caterpillars guided by a negative geotropism? If so, why did those that had reached the top of the chair descend?

TECHNIQUE.

These experiments were performed upon a wooden vertical maze (Figs. 1, 2) and a copper horizontal one (Fig. 3); both of the open type. The former was used in the field and the latter in an out-door insectary.

The vertical maze (Figs. 1, 2) consists of a cylindrical post about four feet tall and an inch and a half in diameter, to which are attached five adjustable rectangular arms. Some of these arms are straight and unjointed; others are formed of three straight sections so articulated as to form an arm with three adjustable sections. The straight arms and the sections of the longer arms are all of the same length. The adjustments of the arms make it possible to set each and every one at any desired angle to the pull of gravitation. The lower pointed end of the post was erected in loose soil in such a manner that, by rotating the post on its axis, it was possible to vary the position of any arm with reference to either the direction of the rays of the light or the path of the wind.

The copper horizontal maze (Fig. 3), which was supported on slender glass pillars, had one of its central alleys connected with the supporting table by means of a cardboard incline two inches wide and thirty inches long. It was so located that the strongest light came from one side.

The point of view expressed in this communication was obtained by a critical study of 1,000 caterpillars of the apple-tent moth, *Malocosoma americana* Fab., 300 of the cabbage butterfly, *Pieris rapæ* Linn., fifty of the white tussock moth, *Memerocampa leucostigma* A. & S., and a few individuals of the young of each of a large number of species of butterflies and moths collected from the surfaces of a large variety of food plants. Throughout a summer practically every kind of surface-feeding caterpillar that a diligent search of the vicinity of St. Louis yielded was put to the test. Among those tested were the flat slug-like Lyncenidæ, the elongated Papilionidæ and Pyralidæ. and the fusiform Hesperiidæ; the naked Noctuidæ, the hairy Arctiidæ, and Liparidæ, and the bristly and spiny Ceratocampidæ and Nymphalidæ; the Notodontidæ with their erect anal somites and the Sphingidæ with their oblique stripes and caudal horns; the grotesque Saturniidæ and the looping Geometridæ.

Experiments with the Vertical Maze.

To facilitate description, the parts of the vertical maze were named as follows: The upright was called the post; each straight arm and each section of a jointed arm was given a distinctive letter. Thus (Fig. 1) the first arm above the ground was called *abc*, the second, *def*, the third *j*, the fourth *g* and the fifth *h*.

In the first few hundred experiments with the tent-caterpillars the arms of the maze were arranged in a variety of ways. In the latter experiments with them and in the experiments with all others the maze was arranged as in Fig. 2; but, the bands *G* and *H* were used only on special occasions. In some of the experiments the plain maze was used; in others one or two odorous bands of filter paper were attached to certain portions of the maze. In experimenting one or more caterpillars were placed on the ground at the foot of the post, or else upon the top of the post, or on some intermediate portion of the maze.

When placed on the ground at the foot of the plain maze, the tent-caterpillar almost invariably letisimulated. In the first few experiments with the tent-caterpillars, on recovering from the feint, the larva moved toward and up the post. If its initial movements were away from the post, after a few steps it turned about and moved towards the maze. This striking behavior recalled some experiments by which H. B. Weiss[1] discovered that certain water insects when turned loose several yards from their home, would immediately go directly to the pond. It looked as though these caterpillars were being mechanically led to the post. To test the matter, a series of experiments, extending over several days, were performed. In these experiments precautions were taken to see that the heads of the caterpillars pointed in a variety of directions. In some cases the majority of the larvæ moved towards the post, in others the majority moved away from the post, in yet others about as many went away from the post as toward it. Evidently the behavior noticed in the first experiments was merely a coincidence, the uniformity of which may have been due to some factor which escaped observation.

Once upon the maze, each caterpillar displayed marked individuality. It might continue all the way to the top of the post without mounting any of the arms; it might, on its way up, explore a few or all of the arms; or it might turn about before reaching the top and return to the ground. At intervals it was sure to pause and reach upward and outward with the front end of its body and move it, in a wabbly manner, from side to side. [For

[1] Notes on the Positive Hydrotropism of *Gerris marginatus* and *Dineutes assimilis*. Canad. Entom., Vol. XLVI., pp. 269–271.

brevity throughout this discussion this form of behavior is called exploring movements.] Should it reach the top, it might encircle it, pausing now and then to make exploring movements; or it might rest there for a long stretch of time. However, it would be more apt to descend the post, pausing now and then to make exploring movements. It might continue along the post

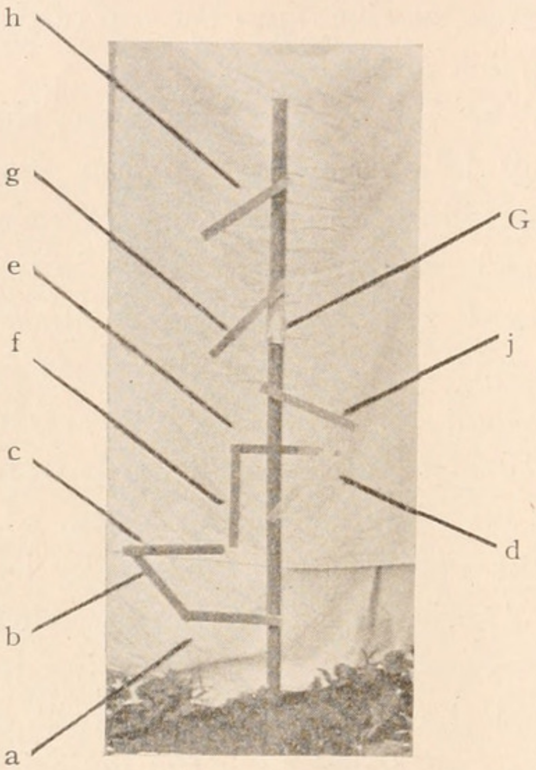

FIG. 1.

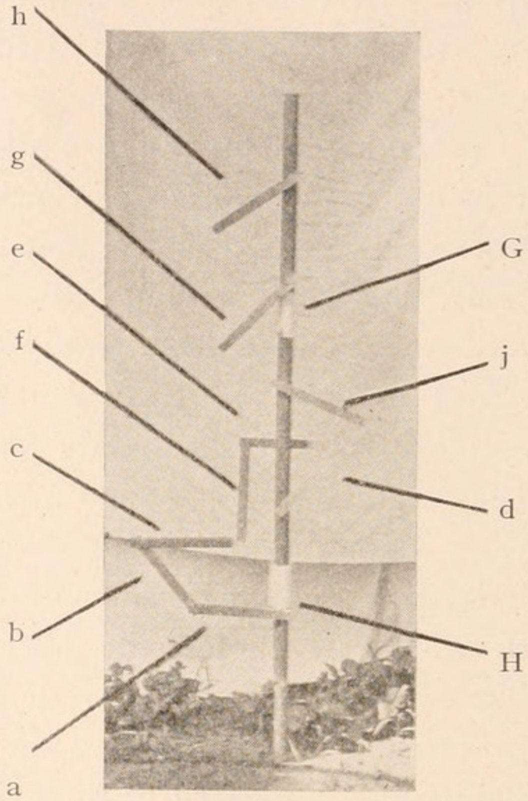

FIG. 2.

to the ground; but it would be more apt to make side trips to one or more of the arms. Often the same arm would be traversed several times. Finally it would rest for an indefinite length of time upon some part of the maze, or else reach the ground. Some caterpillars would leave the post permanently as soon as they reached the ground the first time. Others would remount the maze and explore it one or more times before leaving. The transcription of the field notes of two cases will illustrate the above description.

A tent-caterpillar about one inch long is placed on a maze arranged as in fig. 1; but without the band *G*. Ascending in a sinuous path, it passes around the bases of *a* and *d*, over the base of *j* and around the foot of *g* and *h* to the top of the post. The unhesitating manner in which it continues up and up is enough to rejoice any stanch believer in negative geotropism as the guiding power. Frequently pausing to make exploring movements,[1] it encircles the top a couple of times and then descends to *h*. It moves along *h* to its tip, makes exploring movements, returns to the post, descends to *e*, pausing several times to make exploring movements. It passes along *e* to *f*, makes exploring movements, descends *f* to its tip and makes exploring movements towards *c*. It reascends *f* to *e*, makes exploring movements, and returns to the tip of *f*. It makes exploring movements and then moves across the gap to *c*. It moves along *c* to *b*, along *b* to *a* and down *a* to the post. After making exploring movements, it encircles the post halfway, descends to the ground, moves off about three feet and rests indefinitely.

In this experiment, the subject of which is a tent-caterpillar, the arms *j*, *g*, *h* extend obliquely upward, on the left side of the post, at an angle of thirty degrees; *d* extends horizontally to the right; *e*, almost vertically upward, and *f*, almost horizontally back to the post; *a* extends obliquely upwards toward the left, at an angle of thirty degrees; *b*, horizontally towards the left; and *c*, obliquely upward, at an angle of about thirty degrees.

Following a path which is sometimes straight and sometimes spiral, the caterpillar continues upward until it reaches *g*, which it ascends to the tip. There it spends several minutes making exploring movements; then descends *g* to the post and crawls up it to the top. It goes about half way around the circumference, then crosses over to the opposite side and descends the post. Pausing occasionally to make exploring movements, it continues downward to *h*. It ascends *h* to its tip, crosses over to the opposite side and returns to the post. It continues downward an inch, rests a few minutes. Occasionally pausing to make exploring movements, it continues spirally downward to *g*, which it ascends for about four inches and upon which it rests quietly a few minutes. Returning to the post, it continues downward

[1] When a caterpillar reaches the end of branch or twig, when it encounters an angle or an obstacle, and sometimes for no visible reason, it pauses, elevates the front portion of its body, stretches it forward and upward (sometimes slightly downward) and waves it with a wabbly movement. For the sake of terseness in descriptions, this form of behavior has been called "exploring movements."

to *j*, makes exploring movements, moves up and down *j* several times and then returns to the post. In a sinuous line it continues down the post to *d*, which it mounts. Returning to the post, it continues downward to *a*, which it mounts, makes a few exploring movements and, returning to the post, continues downward to the ground. It then reascends the post a few inches and rests a few minutes. It continues upward to *d*, moves out *d* to *e* and rests thereon indefinitely.

If one may speak of types where there is so much individuality, the above descriptions may be considered typical of the many hundred of records. There were, to be sure, specific variations. Some species were sluggish and others rapid, some were vigorous, others fatigued quickly, some were persistently seeking a solution of the difficulty, others rested at frequent intervals and for long lengths of time, or else made practically no attempt to solve the problem; some letisimulated for a long period when placed at the foot of the maze, others began to climb at once. All these, however, are but minor variations, the essentials are as stated above.

When a caterpillar is placed on top of the post, either immediately or after a slight letisimulation, it moves down the post; making the same variety of random movements as are made by those caterpillars that are placed at the foot of the maze.

When a caterpillar is placed on one of the arms of the maze, either with or without a preliminary letisimulation, it soon reaches the post. There it may either descend or ascend and make the same type of random movements as is made by caterpillars placed at the foot of the maze.

As a variant, one or more bands of filter paper, saturated with oil of cloves or oil of cedar, were attached to the maze at *G* and *H*, as indicated in Figs. 1 and 2. When one scented band was used the caterpillar was placed either at the foot of the maze or on its top. Whenever the insect reached the scented band, it made exploring movements and then retreated. Otherwise its behavior was the same as that of a caterpillar on a plain vertical maze.

Where two scented bands were used (Fig. 2), the caterpillar was always placed on the maze between the two bands. The only way for the captive to escape to the ground, without crossing a scented band, was to cross the gap between *f* and *c* and proceed along *cba* to the lower portion of the post. Roaming at random to and fro over the maze, pausing from time to time to make exploring movements, retreating whenever it encountered a scented band, sooner or later the caterpillar would usually cross the gap between *f* and *c* and escape along *cba* to the lower post and thence to the ground. Occasionally a caterpillar would drop from the maze to the ground; in a few cases, after a few movements, it would rest indefinitely in one place; in less than one per cent. of the cases, the insect would escape across the scented band. In these cases the band had not lost its odor; for immediately thereafter another caterpillar, on reaching the same band, would retreat. Even the same caterpillar, on being replaced between the bands, would retreat from the band across which it had recently escaped.

A transcription of the record of one experiment will illustrate the behavior under these conditions. The specimen is a tent-caterpillar and the maze is arranged as in Fig. 2. The bands *G* and *H* are moistened with oil of cedar. It is between three and four in the afternoon and the maze is situated in the shade of trees; but, here and there, blotches of sunlight touch it. The caterpillar, which is placed near *j*, ascends the post until it reaches the band *G*. There it makes exploring movements and retreats down the post. On reaching *j*, it partly explores it, then returns to the post, and continues downward to *e*. It moves along *e* to *f*, makes a few exploring movements, descends *f* and crosses the gap to *c*. Returning to *f* it ascends *f* to *e* and then retreats to the lower end of *f*. After making exploring movements, it crosses the gap to *c*, moves along *cba* to the lower portion of the post and thence to the ground. *The caterpillar is returned to its former position between the two bands.* It descends to the band *H*, makes exploring movements and retreats up the post. It mounts *j*, and, after making exploring movements, returns to the post and descends to *H*. After making exploring movements, it encircles the post and ascends to *e*. It mounts *e*, then returns to the post and continues upward to the band *G*. After making exploring movements, it descends to *j*, makes exploring movements, returns to the post and continues downward to *e*. It moves across to *f* and back to the post. After ascending the post a short distance, it returns to *e*, passes along *e* to *f*, climbs down *f* to its end and makes exploring movements. It then ascends *f* to *e*, passes along *e* to the post and ascends it to the band *G*. After making exploring movements, it descends to *e*, passes along *e* to *f*, where it rests several minutes (in the bright sunlight). It then descends *f* to its end and reascends it to *e*. Then descending *f*, it passes across to *c*, passes along *c* to *b* and then retreats as far as *e*. It makes three trips back and forth between *e* and *f* and then passes from *e* to the post, and up it to band *G*. Avoiding the band, it encircles the post about three fourths its circumference and then falls to the ground.

With the tent-caterpillars these experiments were conducted either in the shade, or in shady places that were spotted with sunlight that had filtered through the trees. With many of the others the experiments were conducted in the bright sunlight. An accerelation of movements and an apparent tendency to climb or descend the shady side of the post were the only differences noted in the behavior of the caterpillars under these conditions.

Experiments with a Horizontal Maze.

The maze used has (Fig. 3) been fully described in Vol. XXV, pp. 348–349, of the Biological Bulletin. A cardboard incline thirty inches long and two wide connected one of the interior alleys of the maze with the supporting table. Eight inches of this incline extended above the maze (Fig. 3). This gave each caterpillar that arrived at the incline a choice of two pathways; one passing obliquely upwards, the other obliquely downwards. The maze was placed in an out-door insectary, all the light of which came through the netting covered north side. In the earliest experiments two caterpillars were used at a time, and they were so located that they would be forced to approach the incline from opposite directions. Later, when attention was focused upon the behavior of the caterpillar when coming in contact with the incline, twelve to fifteen insects were used at a time; and they were placed on various parts of the maze.

Although the insects displayed great individuality, the behavior in all cases was similar. They moved at random about the maze; roaming into blind alleys and out again, often retracing their steps when in the right pathway, and frequently pausing to make exploring movements. The rays of light were crossed

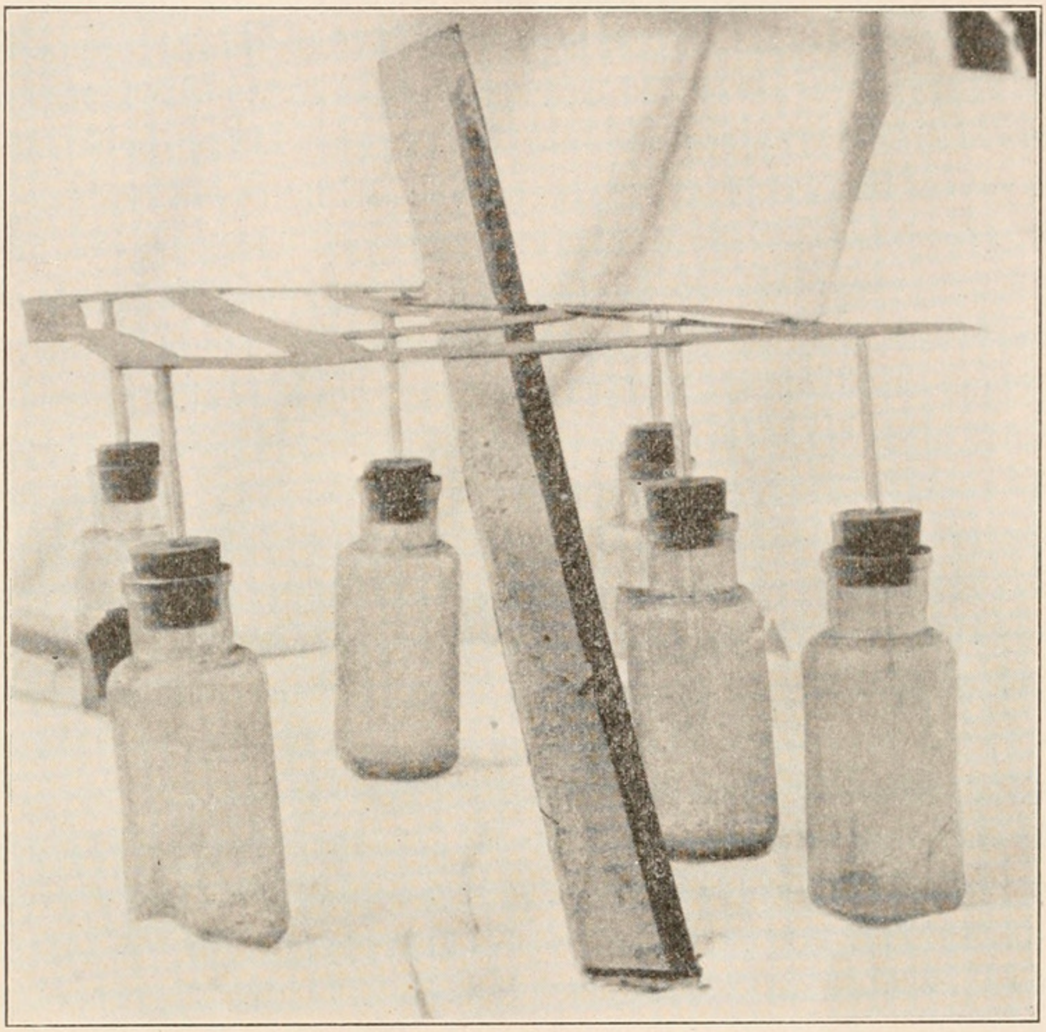

FIG. 3.

at every possible angle. When a gentle breeze was blowing, there was not the slightest indication of an anemotropism. There was one striking uniformity. Whenever a caterpillar came in contact with incline for the first time, it practically invariably ascended it.[1] This happened when the contact was made where the edges of the maze and incline came in contact, and also when the exploring movements of the insect brought it in contact with some portion of the incline that was higher than the maze. After once mounting the incline the caterpillar

[1] Only twice during the summer, did a caterpillar descend the incline upon its first contact with it.

would often return to the maze, roam around and then remount the incline. With a few exceptions, the caterpillar finally reached the table and departed. In a few cases it reascended the incline after reaching the table, and in yet fewer cases the caterpillar finally rested indefinitely upon some portion of the maze.

In spite of the individuality, there were four things common to the behavior of all of the caterpillars placed on the horizontal maze. (1) The caterpillars usually traveled along the edges of the maze, instead of along the middle of the roadway. (2) At frequent intervals the creature would stop, cling to the maze with its prolegs, stretch the front part of the body forwards and dorsalwards and wave it about in a wabbly manner. (3) On reaching the incline for the first time, it practically invariably moved upwards. (4) In all cases the locomotions were random movements. Any interpretation of the behavior on the maze must be in harmony with these four factors. The first and the third are the only ones suggesting that the reactions of these caterpillars are tropisms. The almost constant clinging to the edges of the maze suggests some form of a positive thigmotropism; the invariable ascension of the incline upon its first encounter seems to predicate a negative geotropism.

If the clinging to the edges of the maze is indicative of a positive thigmotropism, why does not the caterpillar show a pronounced tendency to linger in the many angles of the vertical maze? Why does it not rest indefinitely in the angle between the upper portion of the cardboard incline and that alley of the horizontal maze upon which it rests? Would it not be more consistent to believe that the caterpillars move along the edge because they secure a better foothold there than upon the smooth surface of the copper maze?

The fact that the incline was invariably ascended when first encountered requires critical analysis. An examination of the notes made at the time of the experiments shows that whenever the caterpillar upon the maze came in contact with the incline its head was directed towards its upper edge. A thoughtful consideration of the physical conditions of the horizontal maze used and of the normal movements of a caterpillar on the maze shows that such a condition is inevitable. Should a caterpillar be beneath the upper portion of the incline and elevate the anterior portion of its body to make the exploring movements which invariably accompany near contact with a change in its environment, it would be almost certain to touch the incline, and its head would inevitably be pointed towards the upper edge of the incline. Should the caterpillar approach the incline where one of its edges touches the maze and make the usual exploring movements what would happen? If it moved its uplifted body inwards it would come in contact with the incline and its head would be directed towards the upper edge of the incline. Should it move its body outwards, since the incline descends abruptly, the caterpillar would come in contact with nothing and would then wave its body inward. Should the sweep be sufficiently long, the caterpillar would surely come in contact with the incline and its head would be pointed towards its upper edge. This suggests that it is not necessary to predicate a negative geotropism to account for the upward movement of the caterpillar on its first contact with the maze. It simply moves off in the direction that its head happens to be pointing when it encounters the incline.

To test the soundness of this conclusion, the following simple experiment was devised. A caterpillar was placed in a long narrow test-tube; which was sufficiently wide to permit freedom of longitudinal locomotion, but which was so narrow as to make it inconvenienient for the insect to turn around or make exploring movements. This device made it possible to induce the caterpillar to come in contact with the incline with its head pointing in any desired direction. It was only necessary to wait until the caterpillar was moving freely along; and then, after first pointing the mouth of the test-tube in the desired direction, to bring it in contact with the upper surface of the incline. In more than 99 per cent. of the cases, the insect moved off in the direction its head was pointing.[1] By means of this device hundreds of caterpillars were induced to move downward, upon their first contact with the incline.

This also explains why a caterpillar approaching the vertical

[1] In the few exceptions, I had waited too long and the caterpillar had curved its head around the rim of the test-tube before I had brought it into contact with the incline.

maze from the ground always moves upwards, while one placed on the tip of the maze always moves downward. It is not necessary to postulate a negative geotropism to explain one and a positive geotropism to explain the other, and puzzle our brains to account for the reversal of the tropic response when the insect is bodily transported from one place to the other. The behavior is not a tropism. When the caterpillar nears the foot of the maze, the exploring movements which it invariably makes when it nears a change in its environment would cause it to first encounter the post with its head pointed upwards. When placed on the top of the maze, if its movements bring it in contact with the side of the post, it will inevitably be with the head of the insect pointing downward. In one case the insect ascends, in the other it descends; in neither case is the predication of a tropism necessary to explain the behavior.

Conclusion.

Evidently there is nothing about the behavior of surface-feeding caterpillars which warrants the assumption that their locomotions are tropisms. The movements made in locomotion are identical with those made by animals that learn by the trial and error method. Instinctively the caterpillars are physiologically attuned to a certain environment. Outside of that environment there is physiological unrest. To escape the unpleasantness of its environment, the creature makes random movements similar to those made by creatures that learn by the trial and error method. There is no automatic adjusting of the body so as to have it symmetrically stimulated by an external excitant. Some internal, instinctive stimulus causes it to move ahead until some sensation factor induces it to change its course. If physiological satisfaction is not obtained, it continues its random movements until fatigue causes it to rest. Evidently the locomotions of surface-feeding caterpillars need to be classified with trial and error movements rather than with tropisms.

It must be distinctly understood that nothing stated above refers to recently hatched caterpillars, nor to larvæ immediately before entering the pupa state, nor to caterpillars (like the coddling moth larva) which feed inside of plants. Their behavior is left for a future discusions.