

through some special functional state brought about by the environment, how do we know that a similar functional state was not present and responsible for the determination of the original sexual state?

(6) If allosomes have such a profound influence in the diploid condition, whether in homozygous or heterozygous association, as has recently been generally assumed, how does it come about that they are entirely impotent to influence the sexual state whether secondary or primary in the haploid cell generations following reduction, when we know that the haploid and diploid conditions do not interfere with either gametophytic or sporophytic expressions, but that either a haploid or diploid state gives a normal or nearly normal gametophyte and also a normal or nearly normal sporophyte?

(7) What is the cause or factorial mechanism if any that determines the sex of a specific region in diploid and haploid hermaphrodites and in diploid and haploid, bisporangiate sporophytes?

(8) Why are haploid unisexual gametophytes and diploid diecious sporophytes without allosomes often just as fixed in the given sexual state and just as dimorphic as similar gametophytes and sporophytes with clearly recognized allosomes?

(9) Why are organisms with allosomes often as easily sex-reversible as organisms that have no such specialized chromosomes?

(10) If in *Sphaerocarpus* the allosomes are assumed to be the direct cause (factorial hereditary cause) of maleness and femaleness in the gametophytes with which they are associated, how does it happen that when they are together no dominance is shown, but the resulting generation is completely neutral and nonsexual, when in other cases such a heteromorphic pair of chromosomes is assumed to have the one a dominant factor or group of factors and the other a recessive factor or group of factors and to be all-potent in bringing about sexual states in the diploid condition?

(11) If hereditary constitution is responsible for the sex of identical twins, how does it come about that in the diecious *Arisaema triphyllum*, while the twins are still connected by a bridge of living tissue one can nevertheless be induced to become a male and the other a female?

(12) If dieciousness in the higher plants is caused by segregating "sex chromosomes" or allosomes or by some other possible Mendelian factorial condition, how can the facts be explained that in the diecious *Acer platanoides*, for example, quite frequently one or more flowers, flower clusters or branches on a staminate tree will show sex reversal to the female condition and in the same way sex reversal will be shown on a carpellate tree to the

male condition, and that not only will the sex reversal in either case bring forth normal development of the opposite set of sporophyll on the tree but will at the same time induce reciprocal vestigial development of the sporophylls characteristic of the individual as a whole, so that in the reversed parts the carpellate tree will have vestigial gynecia and the staminate tree vestigial stamens?

(13) How can any theory of sex based on the idea of male and female determiners or chromosomes explain the fact that frequently in *Acer saccharinum*, a diecious species, certain branches will nevertheless produce first carpellate flowers, with stamen vestiges, later with further growth, staminate flowers with carpel vestiges, and still later carpellate flowers again, also with stamen vestiges?

(14) If any factorial basis is assumed to explain the dieciousness of *Morus alba*, how can the fact be explained that a staminate tree sometimes produces a branch which for years bears both carpellate and staminate catkins and in addition bisporangiate catkins, while the individual as a whole continues to be staminate, when we know that the carpellate plant is also "heterozygous for sex" and frequently produces similar branches?

(15) What convincing evidence is there to show that allosomes are not merely the results of sexuality rather than the cause of it, and that they follow the sex rather than determine and control it; and further, what definite evidence do we have to show that sex determination is not always physiological and sex stability or persistency merely a phenomenon of differentiation?

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WHY DO CILIATED ANIMALS ROTATE COUNTER-CLOCKWISE WHILE SWIMMING?

WHILE studying the development of certain proso-branch gasteropods several years ago three distinct phases of their normal swarming reactions were observed which so far as I can learn have never been recorded.

The recent work of Grave and Schmitt, Haywood, Wyman and others on the physiology of ciliary action and the histology of the cilium leads me to record these observations and other studies suggested by them in the hope that some worker in this field will interpret the phenomena.

One can not observe a group of these gasteropod larvae just before swarming begins, while they are still surrounded by the protecting jelly-like albumen in which the eggs were laid, within or without a capsule, without being impressed with the great

energy of their locomotion. Since the early gastrula stages they have been moving, a few cilia breaking out from certain epidermal cells very early, while the greater part of the yolk is present and well before the mouth appears. This motion increases hourly with the age of the veliger, but even when it has reached its greatest degree of activity in the turmoil of an egg-mass just before it finally breaks to let the veligers fare forth in the swarming of the new generation, careful study will show that the apparent complexity of it can be reduced to the same phases that marked the motion of the gastrula. These are:

- (1) A counter-clockwise rotation on the polar axis while swimming.
- (2) Swimming in clockwise circles.
- (3) Somersaulting backward; that is, toward the aboral side, while lying on the animal's left side.

Finding this behavior in all the common prosobranch veligers in the Woods Hole region the query naturally arose, "How does the behavior of snail veligers differ from that of other ciliated larvae?"

A study of ciliated and flagellate protozoa, the larvae of sponges, coelenterata, echinoderms, lamellibranch mollusks and annelids resulted in the rather surprising discovery: (1) that they all show a counter-clockwise rotation on the polar axis while swimming, (2) that in fourteen of the twenty-six forms studied swimming in clockwise circles was observed, (3) that in nine forms, somersaulting toward the aboral side was observed. No somersaulting movements were recorded for two ciliate protozoa studied—a *Paramecium* and a *Vorticella* species, nor for the seven flagellate genera, *Euglena*, *Ceratium*, *Phacus*, *Synura*, *Volvox*, *Glenodinium* and *Pandorina*; nor for the larvae of *Gonionemus* and *Hydractinia*, and the lamellibranchs, *Mytilis* and *Cumingia*; nor for the annelids *Arenicola* and *Amphitrite*. Yet of course this movement may occur in all these forms.

Likewise, none of the protozoa nor the hydrozoan larvae mentioned were observed to swim in clockwise circles, yet that behavior may occur, also.

Interesting variations of these phases of behavior are to be seen in *Nereis* and the lamellibranchs mentioned. But the simple phases are so generally found throughout this wide range of phyla that it would seem that we have here another evidence of the fact that behavior is as fixed a thing in the line of evolutionary descent as structure.

And yet the distinction implied here is a superficial one. For behavior is merely an expression of structure. This must be true throughout the whole range of living things. For the biologist, the meaning of the common expression "The Freedom of the

Will" must be limited. For the organization and hence interrelation of the nerve cells in the brain ultimately rules.

That the direction of the beat of the cilium is inherited through evolutionary descent is indicated by an observation rather frequently made during a study of the development of prosobranch gasteropods.

As one looks at the spire of a marine snail shell in polar view, the coils of the shell turn clockwise. But perhaps one shell in a thousand of any given species turns in the opposite direction. This occurred because that snail's shell-gland grew on the opposite side of its body from the normal position. A study of its anatomy would show that all its organs occupy just the opposite positions from the normal ones.

Likewise, in the study of veligers of these forms, one sees very rarely a larva which rotates clockwise on its polar axis, swims in counter-clockwise circles and lies on its right side while it somersaults toward the aboral side.

Careful study of such an individual shows that each of its asymmetrically placed organs occupies a position which is just the reverse of the normal; in short, the animal is a mirrored image of a normal animal, so far as the location of its organs is concerned. Going back one step further, students of the embryology of the prosobranchs tell us that during the earliest cleavages of the egg the first polar furrow turns to the left in cases of "inverse symmetry" instead of to the right.¹ Hence, the direction of the beat of the cilia is determined at least as early as the first cleavages of the egg.

But since the cleavage program is determined by the cytoplasmic organization of the fertilized but unsegmented egg, we must conclude that the swimming behavior of ciliated larvae is as fixed in its inheritance as for instance the polar axis of the body. This conclusion is further indicated by the fact that the protozoa which also show this typical ciliary behavior do not segment as eggs do. Hence, cytoplasmic organization must determine the distribution and the plane of vibration of cilia, and of flagella.

But Conklin in his study of Aseidian embryology found that the definite organization of the cytoplasm occurs only after the disintegration of the nuclear membrane and the consequent distribution of nuclear material throughout the cytoplasm. And since the nucleus is built up from the chromatin supplied by sperm and egg, we must go still further back to the organization of the chromosomes for the source of this inherited behavior.

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¹ Crampton, H. E., "Reversal of Cleavage in a Sinistral Gastropod," Ann. N. Y. Ac. VIII, 1894.