INHERITANCE OF DIRECTION OF COILING IN LIMNAEA

A. H. STURTEVANT

Columbia University

Sturtevant, A. H. 1923. Inheritance of direction of coiling in Limnaea. *Science*, New Series, 58: 269-270.

Electronic Scholarly Publishing Project

Foundations Series — Classical Genetics

Series Editor: Robert J. Robbins

The ESP Foundations of Classical Genetics project has received support from the ELSI component of the United States Department of Energy Human Genome Project. ESP also welcomes help from volunteers and collaborators, who recommend works for publication, provide access to original materials, and assist with technical and production work. If you are interested in volunteering, or are otherwise interested in the project, contact the series editor: *rrobbins@fhcrc.org*.

Bibliographical Note

This ESP edition, first electronically published in 2003, is a newly typeset, unabridged version, based on the 1923 original, published *Science*.

Production Credits

Scanning of originals:	ESP staff
OCRing of originals:	ESP staff
Typesetting:	ESP staff
Proofreading/Copyediting:	ESP staff
Graphics work:	ESP staff
Copyfitting/Final production:	ESP staff

INTRODUCTION

As evidence mounted for the chromosomal basis of inheritance, occasional examples were discovered that seemed to challenge the Mendelian model, as mapped to the chromosomes by T. H, Morgan and his students.

In this paper, A. H. Sturtevant (one of Morgan's students) shows that apparently aberrant patterns of inheritance can be seen to correspond to the Mendelian model, if care is taken to assign phenotype to the correct individual. The case in question is the direction of shell coiling in snails of the genus Limnaea. These shells can either coil to the right (dextral) or left (sinistral).

Coiling seemed to be an inherited trait, except that the observed patterns of inheritance were strange. Broods of offspring from sinistral snails, produced by self-fertilization (these snails are hermaphroditic) were either all sinistral or all dextral (never some of each). The same was found true if the single parent was dextral.

Complicated models had been offered to explain these results, but here Sturtevant shows that a much simpler model is equally effective:

> An analysis o£ the data presented suggests that the case is a simple Mendelian one, with the dextral character dominant, but with the nature of a given individual determined, not by its own constitution but by that of the unreduced egg from which it arose. . . . The hypothesis here suggested may be made clearer by the following elaboration, Let the recessive gene for the sinistral character be represented by *l*, and its dominant allelomorph for the dextral character by *L*. Then any heterozygote, *Ll*, will produce by self-fertilization three types of offspring — *LL*, *Ll* and *11*. Since all the eggs contained the gene *L* before reduction, all these individuals will be dextral in somatic appearance; but the *11* individuals will themselves produce only sinistral offspring. If an *11* individual of this family mates, as a female, to an *LL*, the offspring will all be sinistral (since the mother carried no *L*); but they will be *Ll* in constitution and will therefore produce only dextral offspring. Further combinations may easily be worked out.

A similar problem exists with the color of bird eggs. Chickens, for example, can produce eggs that are either brown or white, and these colors are genetically determined. However, the trait "shell color" is an attribute of the hen laying the eggs, not of the chick that hatches out of the egg. When you realize that the shell is created as a secretion in the hen's oviducts, this makes perfect sense, even though the actual egg

shell is ultimately separate from the body of the hen and is part of the egg from which the chick hatches.

The direction of shell coiling in most snails is now known to be determined very early in embryonic development, usually at the third cell division when four more-or-less equal-sized cells divide unevenly to produce four large cells (macromeres) and four small cells (micromeres). The micromeres then rotate to the right or left, so that they come to rest in the grooves between the macromeres. The direction of this early rotation ultimately determines the direction of shell coiling in the snail that develops from the embryo.

The direction of micromere rotation is controlled by specific proteins present in the cytoplasm of the egg. These proteins are produced early in egg development, prior to fertilization, and so are produced solely from genes present in the mother. Just as with the color of egg shells in chickens, the direction of shell coiling in Limnaea is really part of the phenotype of the *mother* of the snail, not of the snail actually wearing the shell.

Robert J. Robbins
Seattle, Washington 2003

Sturtevant, A. H. 1923. Inheritance of direction of coiling in Limnaea. *Science*, New Series, 58: 269-270.

INHERITANCE OF DIRECTION OF COILING IN LIMNAEA

A. H. STURTEVANT

Columbia University

A recent paper by Boycott and Diver (1923, Proc. Roy. Soc., 95 B; 207) on the inheritance of dextral and sinistral coiling in the snail Limnaea suggests that this character may give an exceptionally clear illustration of "maternal" inheritance that is nevertheless dependent upon the chromosomes.

These authors find that if a single individual of Limnaea is isolated at an early stage it will reproduce, presumably by self-fertilization. Broods produced in this way are always either wholly dextral or wholly sinistral (with the rare exceptions noted below) — but either type of parent may produce either type o£ brood. This result agrees with the findings of Mayor (1902) and Crampton (1916) on the viviparous Tahitian land-snail Partula, where a given individual contains in its brood-pouch only one type of young. A sinistral individual may have either sinistral or dextral young — but never both types at once; and the same is true for a dextral mother.

Boycott and Diver have also mated together two individuals, and have reared from such pairs mixed broods, which they report as giving 3 dextral : 1 sinistral or 1 dextral : 1 sinistral. In the absence of numerical data, and in view of thee fact that the eggs from the two parents were not separated in these experiments, one may doubt if these ratios are anything more than fortuitous ones

due to the two members of the pairs in question producing different types of offspring. If one does interpret these ratios as merely chance ones, it becomes possible to formulate a much simpler interpretation than the one suggested by these authors.

An analysis o£ the data presented suggests that the case is a simple Mendelian one, with the dextral character dominant, but with the nature of a given individual determined, not by its own constitution but by that of the unreduced egg from which it arose.

This last assumption becomes extremely plausible when it is recalled that it was shown by Crampton and by Kofoid in 1894 that dextral and sinistral snails can be distinguished at least as early as the second cleavage division (perhaps at the first), since the cleavage-pattern of one is the mirror-image of that of the other. A character that appears so early in development might well be expected to be determined by the genes present in the mother — *i.e.,* in the unreduced egg, rather than by the combination present after reduction and fertilization. Yet the results obtained by Boycott and Diver can not be accounted for unless it is supposed that the sperm does actually produce an effect, though the effect is delayed for one generation.

The hypothesis here suggested may be made clearer by the following elaboration, Let the recessive gene for the sinistral character be represented by *l*, and its dominant allelomorph for the dextral character by *L*. Then any heterozygote, *Ll*, will produce by self-fertilization three types of offspring — *LL*, *Ll* and *11*. Since all the eggs contained the gene *L* before reduction, all these individuals will be dextral in somatic appearance; but the *11* individuals will themselves produce only sinistral offspring. If an *11* individual of this family mates, as a female, to an *LL*, the offspring will all be sinistral (since the mother carried no *L*); but they will be *Ll* in constitution and will therefore produce only dextral offspring. Further combinations may easily be worked out.

It is probable that dextral snails can not mate with sinistral ones; this being the case one might expect that heterozygous individuals would quickly disappear from the colonies, in which case no such results as recorded would be obtainable. The paper under discussion gives a clue as to why the heterozygotes do not disappear. In families that were expected to be purely sinistral a dextral individual occasionally appeared. If such individuals are due to some environmental cause and are genetically sinistral, they will of necessity mate with dextrals and produce new families of heterozygotes. This interpretation is borne out by Lang's results with

Helix, where the occasional cases of reversed symmetry were found not to be inherited at all.

Further data on the case of Limnaea will be awaited with interest, for it seems likely that we shall have here a model case of the Mendelian inheritance of an extremely "fundamental" character, and a character that is impressed on the egg by the mother.