On the Inheritance of Sinistrality in Limnæa peregra.

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In 1920, one of the authors commenced breeding experiments with sinistral examples of the normally dextral species *Limnæa peregra*. The animals were kindly given him from an aquarium by Mr. J. W. Taylor, and their sinistral parents had originally come from the pond near Leeds, in which for many years sinistral individuals of this species have been known to occur along with the normal form (8). The animals are sinistral, not only in shell twist but also in the arrangement of the soft parts. The abnormality is very rare, though the species is one of the most abundant fresh-water mollusca.

Four individuals were taken young and put together in two pairs. Large glass jars were used, and in each was placed a piece of water-weed (*Elodea*) from sources known to be free from any possible connection with *Limnæa peregra*. Both pairs produced extensive broods which have now been carried down to the third, and in some few cases the fourth, filial generation.

Owing to the puzzling nature of the early results and the large size of the families, it soon became apparent that the work could not under ordinary circumstances be carried on either under one roof or by one person. Fortunately, assistance was obtained from Mr. L. E. Adams, Mr. R. J. Barker, Mrs. Bateson, Mr. T. H. Burlend, Captain G. C. C. Damant, R.N., Miss Garstang, Mr. W. H. Heathcote, Mr. A. H. Illingworth, Miss Rathbone, Mr. T. H. Riches, Mr. G. C. Robson, Mr. J. J. Simpson, Mr. E. Stainton and Dr. F. M. Turner, each of whom consented to take over both the housing and work in connection with one or more of the families. Without their valuable co-operation it would have been impossible to obtain the mass of data now at our disposal.

In spite of this the position is by no means clear ; but as an orderly system of inheritance, differing in certain important particulars from those already known, appears to be emerging from this chaotic mass, it was thought that a brief preliminary statement based on our combined results might now, with advantage, be made.

Certain special difficulties are involved in using this species for genetical enquiry. It is hermaphrodite and in nature seems usually to be cross-fertilised, though in copulation there is not a mutual exchange of spermatozoa as in

the larger land pulmonates. In captivity isolated individuals fairly readily give rise to fertile eggs. We infer that these eggs are the product of self-fertilisation, though this process has not been witnessed by us (5*a*). These separated parents are, in what follows, spoken of as isolated "singles." Owing to the nature of the characters under examination, it is extremely doubtful whether effective conjugation between individuals showing opposite characters is possible. Further, unlike many land mollusca, sexual maturity is not marked by the cessation of shell growth or the formation of a lip, and individual rates of growth differ considerably under similar conditions. With these difficulties in view it seemed advisable to proceed mainly with single individuals isolated shortly after birth and, where pairs have been used, both individuals of the pair have always shown the same character.

Up to the end of 1922 (including all four generations) 202 broods had been obtained, giving a total of over 16,000 young. Of these broods, 144 were obtained from isolated "singles" and 58 from pairs. Where a pair has been used the brood obtained, although, probably in most cases, contributed to by both individuals, has up to date been regarded as one brood. Further tests are now being made by separating the two individuals of a pair after mating has been observed.

The following types of brood have so far been observed from pairs :—

(1) When both parents have been sinistral in appearance (Sin.) :—

A.	B.	C.	D.
Sin : × Sin :	Sin : × Sin :	Sin : × Sin :	Sin : × Sin :
All dextral.	3 dextral to 1 sinistral.	1 dextral to 1 sinistral.	All sinistral.

(2) When both parents have been dextral in appearance (Dex.) :—

A.	B.	C.	D.
Dex : × Dex :	Dex : × Dex :	(Not yet obtained)	Dex : × Dex :
All dextral.	3 dextral to 1 sinistral.		All sinistral.

A fifth type of brood (type E) has also been found, at present only in (1), where all the young have the same appearance, with the exception of one or two or rarely three, which have the opposite appearance. As this type of brood

obviously constitutes a special problem, it has not been included here, but will be dealt with later.

In the broods obtained from isolated "singles" we should expect to find the same four types of broods occurring, but although 144 broods have been obtained in this way we find only two of the types represented, namely, types A and D, both of which types may be derived, as in the pairs, from either dextral or sinistral parents. (Type E referred to above is again present, but here it has been derived from dextrals and from sinistrals.)

These results show :—

I.—That, with the exception of the 1 : 1 ratio, which has not yet been obtained from a dextral pair, *pairs of either appearance give the same types of broods.*

II.—That in broods raised from isolated "singles" as well as those raised from pairs, *the appearance of the offspring may be similar or opposite to that of the parent whether this be dextral or sinistral.*

III.—That *in broods raised from isolated "singles," "mixed" broods of types* B *and* C *are entirely absent.*

IV.—That in "mixed" broods, whether the parents are both sinistral or both dextral in appearance, *dextrality in the offspring seems to behave as a simple Mendelian dominant.*

V.—That *the appearance of an individual is no guide to its genetical composition.*

The absence of the "mixed" broods in the case of the isolated "singles" indicates one of several possibilities :

(i) Parthenogenesis or some abnormal method of fertilisation.
(ii) Abnormal segregation of factors.
(iii) The presence of some additional factor or "appearance-determiner."

As a careful scrutiny of this problem has revealed no systems based upon (i) or (ii) which would be at all in accord with our results, we have fallen back on the hypothesis indicated in (iii). This hypothesis suggests the only system we have so far been able to find that is not, to say the least of it, at variance with our present data on any vital point.

As the possibility of comparing directly the proportionate occurrence of individuals of different genetic types within any brood is thus ruled out, the only method of detecting the system of inheritance here in operation seems to be by the comparison of the numerical proportions in which broods of types A and D occur in "first-cousin groups," *i.e.* in a group of broods in which all the broods are derived from a common grandparent. Unfortunately, the

importance of this method was not realised until most of the results now available had been obtained, and, therefore, many of these " first-cousin groups " are of a numerical order such that the addition of one or two more broods would materially alter the ratio.

Nevertheless, there is sufficient evidence to indicate that where the parents of such a group are all of similar *appearance* and have all been treated as isolated " singles," the following *brood ratios* may occur :—

α	β	γ	δ	ϵ
All broods dextral.	3 broods dextral to 1 sinistral.	1 brood dextral to 1 sinistral.	1 brood dextral to 3 sinistral.	All broods sinistral.

(1) Where the grandparents were a *dextral pair*, giving an *all dextral* brood, " first-cousin groups " of types α and β have been found, and it is clearly indicated that type γ may also be present.

(2) Where the grandparents were a *dextral pair*, giving an *all sinistral* brood, there is at present insufficient evidence, only one such brood having been carried far enough, and this is complicated by the occurrence of broods of type E ; but the evidence seems sufficient to indicate that it constitutes a " first-cousin group " of type δ.

(3) Where the grandparents were a *sinistral pair*, giving an *all dextral* brood, again there is insufficient evidence, only one such family having been carried on. The " first-cousin group " obtained may belong either to types α or β.

(4) Where the grandparents were a *sinistral pair*, giving an *all sinistral* brood, broods have been obtained of type ϵ, and also indications are present that broods of types γ and δ may occur. One of these groups containing eight families appears to belong to group β, but it seems doubtful whether this is really so.

(5) and (6) where the grandparent was a *dextral isolated " single,"* there is, as yet, no evidence available, as no families of this description have yet reached a second generation.

(7) Where the grandparent was a *sinistral isolated " single "* giving an *all dextral* brood, only one small group is available, but it seems to be a type γ group.

(8) Where the grandparent was a *sinistral isolated " single "* giving an *all sinistral* brood, groups of type ϵ are found and there is more or less definite indication that groups of type γ may occur.

It will be seen from these results that in not a few cases the necessary evidence is either absent or not sufficiently strong for a definite statement; but considering the means at our disposal, the nature of the original parents, and the fact that in this preliminary work it was quite impossible to determine which families or groups should be carried on, these gaps cannot altogether be regarded as positive evidence of the non-occurrence of certain types of groups in particular instances.

On the other hand, the results seem to justify the following general conclusions.

I.—That the *appearance* of the grandparents does not affect the types of first-cousin groups that occur among their grandchildren, but the appearance of their children does give an indication of what may or may not occur in these groups. That is, whether the grandparents are dextral or sinistral in appearance, if all their children are dextral in appearance the range of possible groups is from type α to type γ, whereas if they are all sinistral the range is from type γ to type ϵ.

II.—That where the grandparents were a pair three types of first-cousin groups may occur, *i.e.* α, β and γ, or γ, δ and ϵ: but where the grandparent was an isolated "single" only two types seem possible, namely, α and γ, or γ and ϵ, groups β and δ not being represented.

This leads us to the general proposition upon which the method of inheritance here in operation seems to be based.

III.—That the appearance of the individual is the result of, and is determined by, the product of the parental nuclear composition, but that this individual may carry in itself any of the possible combinations of chromosomes; this nuclear composition gives a fresh product which governs only the appearance of the next generation, within which again any nuclear composition may exist.

The position as regards the occurrence and composition of mixed broods of a Mendelian character is still far from clear. Very few of these broods have been obtained, as incidentally our hypothesis leads us to expect, and these for one reason or another do not provide sufficient evidence to show whether the appearance of the individuals is determined by their own nuclear composition or not. All that is indicated at the present time is, that when two individuals of different nuclear products or appearance-determiners mate, the resulting broods, where both dextrals and sinistrals are present, will show the dextral type behaving as a normal Mendelian dominant, whereas if the appearance-determiners are the same the whole brood will be similar in appearance.

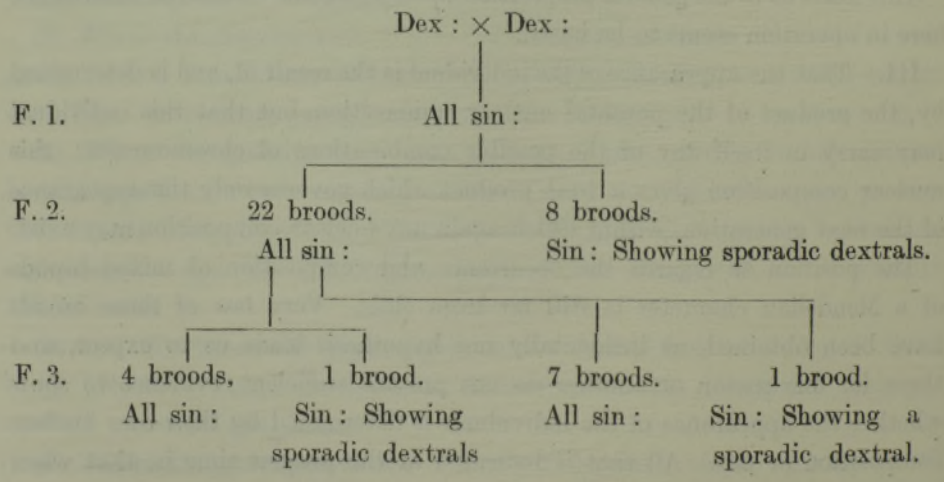
We now have to consider the special problem of type E, where all the young, with the exception of one or two, or rarely three, have the same appearance; two kinds of this type of brood are found :—

E (*a*) Where the whole brood is dextral in appearance with the exception of one or two sporadic sinistrals.

E (*b*) Where the whole brood is sinistral with the exception of one or two sporadic dextrals.

As far as E (*a*) is concerned, we have only obtained one brood of this nature in our families, and that was derived from a dextral isolated "single." Nineteen families of type E (*b*), however, have been hatched, all from sinistral parents (seven from pairs and 12 from isolated "singles"), and the proportion in which these have occurred in first-cousin groups seems to indicate clearly that such a brood occurs where, under normal circumstances, an all-dextral brood would be expected; in other words, in certain families, and in exceptional cases, either the dextral or the sinistral character in the parents seems to be sufficiently strong to inhibit the production of a brood of the opposite appearance. Beyond this at present we have been unable to go.

It is not yet clear whether a brood of type E (*a*) may be derived from a sinistral parent or *vice versa*, but a first-cousin group containing type E (*b*) broods has been derived from dextral grandparents :—



As regards the genetic behaviour of these sporadic dextrals there is at present no evidence, beyond the fact that they seem to die easily when young. In the two cases where they have succeeded in producing any offspring, their broods were restricted to one and two sinistral individuals respectively. This

aspect of the problem seems to merit, and is now receiving, special attention, and it is hoped that better results may be obtained.

Among Mollusca generally it is rare to find definite sinistral races of a normally dextral species (or *vice versa*) similar to the case under review (3, 7, 8 and 10), but sporadic sinistrals or sporadic dextrals have been found in many normally dextral or sinistral species (9). Breeding experiments have been attempted with such sporadic sinistrals (5 and 6) and the percentage of their occurrence in natural populations has been examined (1 and 9) ; but no attempt has been made to discover whether the broods containing these sporadic sinistrals occur in similar circumstances and brood-ratios as those examined by us in *L. peregra*. Where as in *Partula* (7) a definite sinistral race has been examined the position seems not dissimilar.

We do not propose at the present time to review the probable causes of inversion (2) nor the occurrence of the problem in other forms of life, beyond indicating that where figures are available for analogous variations (4) in animals or plants they seem to show an underlying similarity of system with the results we have been able to obtain.

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