The Seed-Mass and Dispersal of *Helleborus fœtidus*, Linn.

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(Plate 36.)

[Read 16th December, 1915.]

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Helleborus fœtidus, Linn., which is known as the Stinking Hellebore, the Bearsfoot, and the Setterwort, is a rare member of our native flora, and in this country is more often naturalized than wild.

Its fruit consists of three follicles, which are often slightly coherent at the base ; while the sepals, which persist throughout the fruiting period, enlarge after flowering, and by catching the wind assist the subsequent liberation of the seeds.

Long before maturity the fruit becomes pendent, so that the follicles hang almost vertically downwards. On their dehiscing, a most remarkable state of affairs is revealed and one which is, I believe, unique in our own flora ; instead of the seeds being detached singly from the placenta, they break away in one solid mass bound more or less tightly together by a thick continuous ventral strip of succulent tissue, which is of raphal origin. The mass is almost black, whereas the strip when fresh is a shining white ; sooner or later it falls out of its follicle and lies upon the ground, and its meaning and subsequent dispersal raise questions of considerable interest.

It has been stated by F. Ludwig—and no one will deny it—that the mass resembles the larva of a beetle ; he believed that the ants were deceived by the mimicry, and that they broke it into its constituent seeds, which they then carried off.

Sernander experimented with the separate seeds, and established beyond doubt that the ants take them away and that the white succulent oily tissue is the bait that attracts them : to such baits he gives the name of elaiosome, or "fat-body."

I had seen the plant fruiting on some waste ground close to the Acton Cemetery in July 1899, whence I have no doubt it had escaped, as it was at

that time to be found upon some of the graves there. I then collected a few of the seed-masses, but, although wondering mildly what their significance might be, it was not until the year 1904 that my curiosity was aroused anent their dispersal.

In that year the plant fruited in my garden at West Drayton, and I noticed the masses lying upon the ground, and was again much struck by the larva-like appearance.

It was not possible for me to make any experiments then, and my only note was to the effect that snails break up the mass by devouring the strip, and that I suspected that robins mistook it for a larva and perhaps dropped it some distance away on discovering the deception. This possibility was suggested to me by my finding the broken masses about a yard away from the parent, and by my having disturbed robins in the early morning about the plants themselves.

I have made a few isolated observations since; but I have had the misfortune to lose the whole of my botanical notes for this and some previous years, and it is not safe to quote anything more definite from memory, nor is it, fortunately, necessary to trust thereto now.

In our own country—or, at any rate, in West Drayton—the species, as a rule, ripens but little seed: in 1913 and 1914, for example, it set practically none at all; but this year (1915), owing probably to less unfavourable conditions during the pollination-period, it produced a fair crop, although a great many of the flowers failed altogether, while many others matured only one or two instead of the usual three follicles, and a good proportion of these were by no means up to the average in size or seed-contents.

However, I saw my chance at last, and I decided to make the most of it.

A word may be said here about the pollination, as illustrating the difficulties which beset the species in this country and to which I shall have occasion to refer at the close of this paper.

The plant flowers with me for the most part in January and February, sometimes in December, and occasionally it makes a start quite early in November; it continues to produce blossoms for many weeks or even months, and it secretes plenty of honey in the well-known "jars." It is a curious fact that, just as it sheds the seed-contents of each follicle in a single mass, so with its pollen the contents of each loculus form one coherent lump. Normally, no doubt, these would be carried off by the insect visitors (*Apis* and *Bombus* spp.), but in the horrible weather that we often experience in the early part of the year such visitors are conspicuous by their absence, and the pollen-masses fall out of the anther and may be seen in large numbers as small yellowish lumps upon the leaves of the parent plant. The species is markedly proterogynous, but with the usual overlap; and I fear that with me it has, in most seasons, to depend for

pollination upon purely fortuitous geitonogamy as much as, or more than, upon the insects. It is only occasionally that the conditions offer any reasonable prospect of the normal amount of crossing ; while self-pollination seems to be out of the question altogether, except as the rarest of accidents.

Things are probably different on the Continent, where, according to Sernander, the fruiting period is from the end of July until the beginning of September, whereas with me it began on June 30th and was all over by July 18th. Sernander does not mention the flowering dates, but a delay of a month or six weeks at the commencement of the year would make a considerable difference in the right direction.

But to return to the dispersal. Sernander considered the plant to be myrmecochorous, and in his Monograph, the value of which has been pointed out by Prof. Weiss, he placed it under his *Viola odorata* type ; both of these decisions are, I think, open to question, though we need concern ourselves only with the claim to myrmecochory, for if that cannot be substantiated the other ceases to be of interest.

In addition to my note on the snails and the robins, the elaiosome led me to suspect that the ants play some part in the dispersal, and I was accordingly not surprised at the results obtained by Sernander : what did surprise me was that in his valuable Monograph he makes no reference to the possible part played by birds and more especially by molluscs. I determined, therefore, to investigate these two points, so far as my material would allow, and also to confirm Ludwig's claim that the ants break up the mass by nibbling away at the strip. What follows is an account of the little that I was able to do.

I will first take the agents—Molluscs, Birds, and Ants—in that order, and then discuss the larval mimicry and the claim to myrmecochory.

Section I. Molluscs.

The first seed-mass was dropped on June 30th, and on July 3rd, at 6 P.M., I cleared the ground in front of the plants of all loose seeds and masses for a space of two square feet.

There were three whole masses with the strip still white (Nos. 1, 2, & 3, see Tables), and I shook the plant so as to dislodge any that would be likely to drop during the night. Nine fell to the ground (Nos. 4–12), and I noticed that none of them were broken by the tumble, which may have been as much as 25 inches, the height from the ground of the topmost follicles.

With one exception (see Table I., No. 15), the largest masses that came under my notice (see Pl. **36.** fig. 1) contained 14 seeds and measured, in the longest diameter, $\frac{5}{8}$ of an inch, a fair average being 11 seeds and a short $\frac{1}{2}$ inch (see Table I.). The fate of No. 15 was to be badly mutilated by the snails (see Table VII.).

The twelve masses, which I arranged in three rows of four each (see Diagram), contained altogether 133 seeds.

DIAGRAM to show the arrangement and the fate of the 19 masses.

3 July, 1915.	1 (*b*)	2 (*a*)	3 (*b*)	4 (*b*)
	5 (*b*)	6 (*b*)	7 (*d*)	8 (*b*)
	9 (*a*)	10 (*a*)	11 (*d*)	12 (*c*)
4 July, 1915.	13 (*b*)	14 (*d*)	15 (*b*)	16 (*d*)
	17 (*c*)	18 (*b*)	..	19 (*c*)

Fate.....
(*a*) = intact 3
(*b*) = broken 9
(*c*) = missing 3
(*d*) = reduced to single seeds 4
19 masses.

At 11.30 P.M. that evening one *Helix aspersa* was feeding upon the strip of one mass (No. 3 of 9 seeds) and one *Helix rufescens* upon another (No. 9 of 12 seeds), and the next morning (July 4th, at 10.30 A.M.) three of the seed-masses were broken into two portions: one of these was the one attacked by *Helix aspersa* the previous night (No. 3 of 9 seeds); the other broken ones were No. 1 of 14 seeds and No. 6 of 12 seeds, both of which had presumably been visited by the last-mentioned species. Five seed-masses had been nibbled at one end only, and had lost from one to three seeds apiece. Three were still whole: one of these was the one that had been attacked by *Helix rufescens* (No. 9 of 12 seeds in the Tables, and No. 4 in the Plate). Two others bore no traces of having been visited; they were No. 2 of 12 seeds (Pl. **36.** fig. 5) and No. 10 of 14 seeds (Pl. **36.** fig. 1).

This accounts for 11 out of the 12 masses, and the 12th was missing altogether, nor could I find it, although I searched carefully for it; it was No. 12 of 9 seeds. It should be noted that it disappeared from one end of the last row.

At 5.30 P.M. there was no change; the three conspicuous untouched masses were still in the same position.

The weather had been very dry, and by way of attracting the snails

I watered the ground gently, and shook seven more masses from the plant; these contained 76 seeds, making in all 19 masses and 209 seeds to account for. These seven masses made one more row of 4 and another of 3.

At 10.30 P.M., still on July 4th, there were three *Helix aspersa* and one *Helix rufescens* eating the strips; at midnight there were seven of the former and one of the latter, all busily feeding, and I regret that I did not notice whether the *Helix rufescens* was still on the same mass as before. There was at this time one large worm busy with a portion of a mass composed of three seeds; he was evidently either eating or trying to drag it into his burrow. I noticed this with peculiar satisfaction; for on previous occasions I have found worms feeding upon the more or less succulent capsules and seeds of the snowdrop (*Galanthus nivalis*) and the large soft berries of *Arum italicum*, and I have subsequently found the remains of the berries and the seeds of the latter plant inside the burrows.

On the morning of July 5th, at 7.45 A.M., two more masses had vanished, which, with the one missing the morning before, makes three altogether: the two newly missing ones were No. 17 of 11 seeds and No. 19 of 10 seeds. Here, again, they disappeared, whichever way we look at the diagram, from the end of an outside row; and this curious little point may be of some significance, as we shall see when we deal with the Birds. Three seed-masses were still intact; as they were the same three as were left over the morning before (Nos. 2, 9, and 10, of 12, 12, and 14 seeds respectively), probably the snails preferred the fresher ones.

At 7 P.M. the same evening the position was unchanged; the three whole masses were still *in statu quo*: they were exactly where I had placed them originally, and this is of some importance, as will be clear in the next Section.

I then proceeded to collect all the remains of the 19 masses and 209 seeds, and I have tabulated the results of these observations.

On July 6th and 7th I left the plant alone, and it dropped a few more masses which were duly broken up by snails; but I kept no further record of the numbers. In the evening and during the night of July 7th rain fell heavily, and all the seeds were washed to the edge of the border. This journey was no doubt facilitated by the slope of the ground, and the contribution of rain-runnels to short-distance dispersal is, I am sure, pretty considerable for this and innumerable other species.

It is perhaps just worth mention that here, and on subsequent occasions in a different part of the garden, where I experimented with the ants, I have seen the small black garden-slug (*Arion hortensis*) feeding upon the strip in the same manner as the snails; so that we have three distinct species of molluscs acting as disintegrating agents, but not all to the same extent.

It is true that I did not watch the snails break up the masses in the open; but I do not think that any other visitors can have done so, because when I left masses exposed for the birds, and took steps to protect them from the molluscs, they were not disturbed at all. Furthermore, as will presently appear, I proved by means of captives that *Helix aspersa* can do this work and is a very efficient disintegrating agent; that, however, is a very different thing from effecting dispersal—a point which will receive some little attention almost at once.

Tables to illustrate the work of Helix aspersa.

TABLE I.—Masses put down.

	No. of seeds.
3.7.15. No. 1	14
2	12
3	9
4	11
5	10
6	12
7	8
8	13
9	12
10	14
11	9
12	9
12 masses.	133 seeds.
4.7.15. No. 13	12
14	10
15	15
16	7
17	11
18	11
19	10
19 masses.	209 seeds.
Average ..... 11 seeds apiece.	

TABLE II.—Masses intact.

	Seeds.
No. 2	12
9	12
10	14
3 masses.	38 seeds.

TABLE III.—Masses broken.

	Seeds.
No. 1	14
3	9
4	11
5	10
6	12
8	13
13	12
15	15
18	11
9 masses.	107 seeds.

TABLE IV.—Masses missing.

No. 12	9
17	11
19	10
3 masses.	30 seeds.

TABLE V.—Masses reduced to single seeds.

No. 7	8
11	9
14	10
16	7
4 masses.	34 seeds.

TABLE VI.—Summary of Tables II., III., IV., and V.

Masses	II. Intact	3.	Seeds 38.
	III. Broken	9.	„ 107.
	IV. Missing	3.	„ 30.
	V. Reduced to single seeds	4.	„ 34.
	Masses 19, seeds 209: as in Table I.		

TABLE VII.—Reconstruction of broken masses in Table III.

	Seeds. *Cohering.*		*Single.*	
No. 1	13	0	1	= 14
3	5	2	2	= 9
4	10	0	1	= 11
5	9	0	1	= 10
6	10	2	0	= 12
8	7	3	3	= 13
13	5	3	4	= 12
15	9	4	2	= 15
18	10	0	1	= 11
9 masses.	78	+ 14	+ 15	= 107

TABLE VIII.

Loose seeds collected	41
Used for reconstruction (see Table VII.)	15
Leaving	26
Wanted for Table V.	34
Missing seeds	8

TABLE IX.—Possible fate of the missing seeds.

Probably taken by a worm	3
Possibly taken by worms or dispersed wholly or partly by *Helix aspersa*	5
Total	8

The numbers enclosed in the last column but one of Table VII. represent the seeds that I had to take from the loose ones to complete the masses, but which I could not feel sure belonged to any particular one ; after such reconstruction I ought to have had 34 seeds left over, but as a matter of fact there were only 26, so that 8 have still to be accounted for. Three of these, which possibly came from mass 8 of 13 seeds, were, I suspect, carried into its hole by the worm ; but I cannot speak definitely, because I could not find them there. The fate of the other 5 has still to be discovered or conjectured. The worms may have been responsible for them too, or, despite my search, I may have overlooked them ; but there are other possibilities, and one of them was suggested to me by a previous experience of my own.

I have noticed snails in the garden at night with seeds of the Stock sticking to the body ; but these are light, thin, and flat, and very different from the ovoid ones of the Hellebore, with which they compare favourably when one comes to the possibility of molluscan dispersal. Moreover, a single seed of the Stock could quite well finish its first flight from the siliqua by alighting on the body of a snail, whereas for *Helleborus fœtidus* this is impossible ; it would have to get there from the soil, after the disintegration of the mass. I did my best to witness an instance of its having done so in the open, but I did not succeed, and so I had to be content with experiment, and with proving the possibility of transport if it did get there.

For these purposes I employed captives. I confined a snail (*Helix aspersa*) under a glass jar on a plate ; I provided him with a leaf of a *Chrysanthemum*, which is, I know, a molluscan tit-bit, and I also gave him two seed-masses. I took care to cover the plate with earth, as I have found, when experimenting with ants and the fruitlets of *Geranium Robertianum*, that the slight irregularities of the soil, especially when it is dry, are of no small account.

The next morning (July 9th) the snail had eaten the whole of the leaf with the exception of the midrib, and had mutilated the masses, one of which was in three pieces ; as neither of them had been reduced to single seeds, there was of course no evidence of dispersal, and all I could conclude was that the snail found both the leaf and the mass palatable. The first night was therefore barren of results, so far as the evidence I was seeking is concerned.

The same evening I replaced both masses by fresh ones. Now, I know that this snail will not eat Violet-leaves except when hard up for food ; so I thought that, as I was desirous also of discovering its likes and dislikes, I would take the opportunity of seeing which of the two my captive preferred. I therefore put a single leaf of *Viola odorata* under the glass jar with the two masses.

At 10 P.M. the snail was on the top of one mass ; at 11 P.M. this was.

broken, and the foot of the snail covered most of the seeds. I watched it crawling over them, and I saw one of them which was on the edge of the snail's body dragged for a short distance before it got free from the tail end.

At midnight I looked at the snail again: he was eating the other mass, and there was one seed on the body, on the median line and close to the edge of the shell on the head side. I was unlucky in having missed the critical moment, for the seed was not there about half-an-hour previously.

By the next morning the snail had broken up both masses and had devoured a portion of the Violet-leaf: he had confined himself to one side of the midrib and had eaten about a third of the way up from the base—*i. e.*, a good half of that side; but the point of immediate interest was that one seed was sticking to the top of the glass jar $5\frac{1}{2}$ inches from the soil and an inch or more away from the now resting snail.

In the evening I removed the Violet-leaf, and left the snail with only the remains of the two masses and one additional fresh one; and at 11 P.M. it was eating the strip of the fresh mass. I hoped that if I kept it short of food it might wander about; and I was not disappointed, for at 7.40 the next morning there were, in addition to the one sticking to the top of the jar, three other seeds on its side at various levels.

Apparently my snail had been more hungry than he liked, for, whereas on the first two nights, when he could make up with *Chrysanthemum* and Violet leaves, the masses were not reduced altogether to single seeds, on the third night no two seeds remained attached to one another and all of them had been completely stripped of the elaiosome.

It looked therefore as if the snails might carry these seeds about, to the extent of a few inches at least, for I could think of no other possible explanation of those on the top and the side of the jar; but I was a little uneasy about drawing conclusions, and I still am, for it is quite possible that the side of the jar, instead of the irregularities of the soil, may have been responsible for the seeds getting upon the body of the snail. One cannot reckon upon such things in nature, although it is tempting to assume that an erect stem, or a conveniently placed stone, in the open may have taken the place of the side of the jar. I had therefore to leave this point undecided, to my regret. It still remains to be proved that the seeds get upon the snail's back without artificial assistance.

I was, however, more successful in proving the possibility of short-distance dispersal if they do get or are placed there. I made several trials with another captive, and I got so interested that I was up more than half the night of July 31st. It is sufficient to say that the creature resented a seed being put upon its tail, and very soon sloughed it off; it was equally touchy about its head and the parts thereabouts, but it seemed quite unconcerned if one were placed on the body near or against the edge of the shell on the

head side. I am, however, too ignorant of molluscan anatomy to explain the reason. Thus burdened, it crawled in a straight line for some minutes, but at last, after covering 14 inches, it had to turn ; that caused the seed to slip, and it was left behind on the newspaper on which I had the snail, having been carried a distance of 18 inches altogether ; it took the mollusc just over ten minutes to cover this distance—a somewhat slow rate compared with that registered by Sir Herbert Maxwell ; it wasted some time, however, in turning the corner.

In its wanderings it happened to pick up a fruitlet of *Geranium Robertianum* ; I did not know it was there, but I had been experimenting on the same paper with this species a few days previously. The fruitlet was caught by the threads, and the snail did not get rid of it at all. Out of curiosity, I prodded him with the point of a pencil until he retired completely into his shell, and in doing so he shed a Hellebore but not the *Geranium* seed ; it was still quite close to the edge of the shell when he began to wander again. Subsequently I set him free, and it was still on his body, where it had been for at least twenty minutes.

In dealing even with short-distance dispersal, a matter of a few inches may seem hardly worth recording at all ; but nevertheless, and I do not speak at random, it is a valuable contribution to that local dispersal with which we are now concerned. I have long ago come to the conclusion that for any given species dispersal is, as a rule, a question of several agents rather than of one ; and *Helleborus fœtidus* appears to be so little in harmony with its environment here that, when trying to understand its life-history, one cannot afford to ignore even such a trifle as this.

Six inches a year in all directions from a given point would in ten years account for a circle with a diameter of 10 feet and an area of 78·6, and ten years is but a moment in the life of a species ; if we allow the 18 inches, the distance I saw the seed carried, then the area at the end of ten years would be 707 square feet, or roughly a square 9 yards each way, allowing nothing whatever for other agents, which, with *Helleborus fœtidus*, would most certainly be a very great mistake. This is a contribution which, as such, is not to be despised, and, as a matter of fact, I have watched snails on my gravel-path travel as much as 6 yards or 18 feet in a straight line without a break in order to secure a dainty put down for the birds.

I do not for a moment imagine that one can legitimately consider the point proved ; but it is perhaps reasonable to think of *Helix aspersa* as a possible contributor to the dispersal of the seeds, in addition to being a very efficient disintegrator of the mass. Observation later on will perhaps supply the proof of what experiment suggests. Meanwhile, *Helix aspersa* goes the pace at the rate of 2 inches a minute, or a mile in 22 days, and, but for this unproved point, it certainly may be that some of the missing seeds were carried by them away from the 2-foot square area that I used.

As already hinted, the question presented itself to me whether the masses really attract the snails or are eaten merely because they come in their way, and I took the following steps in order to secure some evidence upon this point.

I cleared the snails out as far as I could—and, I believe, completely—for about a yard all round the plants, and the number I removed was astonishing, especially from an ivy-clad wall behind the Hellebores, which bounded the area in that direction. I then examined the plants themselves and found that there were three snails sheltering in them, and, what I had not noticed before, that some of the immature follicles had been nibbled through and the developing strips eaten—so I left these three, to see if I could catch them in the act. This was on July 11th. I shook three fresh masses from the plants and placed them on the ground. At 9 P.M. one snail was feeding on an unripe follicle. I cannot help admiring the strength of the molluscan stomach ; for, in handling these fruits to examine the immature elaiosome, I made my fingers so sore with the acrid juice that they smarted for three days afterwards, and the skin of my thumbs was killed and subsequently peeled off. I went out again the same evening at 9.30: the snail was still feeding, and there were two others on the ground close to the base of the plants. Believing them to be the other two which had taken shelter therein, I removed all three, so as to be sure that any later visitors must come from a greater distance. At 11 P.M. there were none, but at midnight one snail was feeding on one of the masses and there were two more on the ground a few inches off. At 7.45 the next morning two of the three masses were broken up into single seeds, but the third was intact. These snails were old ones, and I do not think that I could have overlooked them if they had been in the cleared area before dark.

By way of getting more evidence, I turned again to my captive. I already had some reason for thinking that there was not much to choose between the *Chrysanthemum*-leaf and the Hellebore's elaiosome, but that he preferred the latter to *Viola odorata*. Now, in addition to the Ivy, the plants growing in the border within the square yard are a perennial *Helianthus* (of which *Helix aspersa* is very fond), *Tropæolum majus*, *Primula vulgaris*, *Coronilla varia*, *Ribes aureum*, *Circæa lutetiana*, *Potentilla atro-sanguinea*, a perennial *Solidago*, *Bellis perennis*, and *Buxus sempervirens*. From previous experiments I know that snails will not eat Ivy, that they do not touch Primrose-leaves unless they be pretty old ones and food scarce; neither will they eat *Circæa*, perhaps on account of its raphides, nor yet the Box, even if there be nothing else.

On the first night (July 12th) I gave my captive a sample of all these plants, and I added one *Helleborus* mass. At 11.15 P.M. it had eaten part of the *Tropæolum*-leaf and part of the *Helianthus*-leaf. I watched it until midnight: it went from the *Helianthus* to the Hellebore and then back to the *Tropæolum*, and when I went to bed it was again on the seeds. The next

morning there was no *Tropæolum* left; most of the *Helianthus*-leaf had been eaten too, and the seed-mass was broken, but not into single seeds.

The next night I gave it a fresh supply of the leaves it had left untouched and another fresh seed-mass, but no *Tropæolum* or *Helianthus*. At 10.20 P.M. it was at the *Helleborus*; it then went to the Daisy, from there to the *Potentilla*, and back again to the seeds, where I left it at midnight. By the next morning it had just nibbled at the Primrose-leaf, a middle-aged one; it had taken about half an inch from the *Solidago*, and had broken up the seed-masses into single seeds.

On the 14th, as I did not want to starve it, but to discover its preferences, I gave it more Daisy, *Potentilla*, and *Solidago*, and more Hellebore seeds. It went to the seeds first, and during the night it again had a bite out of the same leaves as before, but evidently the *Potentilla* was not relished.

The next night I reduced it to *Ribes*, *Circæa*, Ivy, *Coronilla*, and Box—the things it had, so far, refused to touch,—and I added one more seed-mass. It fed upon the seeds and nothing else for four nights on end, although I kept the supply of leaves fresh. On the fifth night I relented, and gave it another seed-mass, two small *Chrysanthemum* leaves, and a young *Tropæolum* leaf. It ate the bulk of the banquet, and next morning there was nothing left on the plate but the débris of the leaves and the seeds of the Hellebore, now stripped clean of the bait.

There is, then, I think, some reason to believe that *Helix aspersa* eats the strips because it likes them, for it attacks the immature follicles and gets at them; apparently it will go for them from a distance of a yard or more, and it eats them as readily as it does other foods for which it shows a liking.

Summary of Section I.

Molluscs.—One can say almost nothing about *Helix rufescens*. This snail is comparatively rare in my garden, and I saw but one individual on the masses. The most one can conclude is that, where the two are found together, it will eat the elaiosome; but in my garden it did not apparently succeed in breaking up the mass.

For the slug, *Arion hortensis*, one may fairly come to the same conclusion, that it acts to some extent as a disintegrating agent, although in an entirely minor degree.

Helix aspersa, on the other hand, must be credited with a great deal of execution in this way. It not only can, but it does, break up the mass into single seeds; when short of food, it will strip the latter bare of the bait.

It appears that the seed-mass, or rather its elaiosome, really attracts the snails, though that is not the same thing as saying that it is an adaptation to molluscan disintegration—a point to which I shall refer later.

It also seems possible that this species may carry the seeds some little

distance away from the parent plant, although it still remains to be proved by observation that these seeds get on to the body in the open, instead of being placed there by the experimenter indoors.

Worms.—Possibly these help in burying stray seeds or small bits broken off the mass.

Section II. Birds.

My next object was, if possible, to account for the disappearance of the three whole masses. I searched in vain for them, though it is as likely as not that they were somewhere in the garden.

There is no ants'-nest in the border where my Hellebores grow, nor do I remember ever having seen an ant or a mammal thereabout, with the exception of cats and dogs, although I have kept a look-out for rats and mice; so it is difficult to avoid thinking that their disappearance is perhaps to be attributed to birds.

When the masses are fresh, the broad white strip stands out boldly against the black margin by which it is surrounded, and they frequently—I think I may say generally—fall in such a manner that the elaiosome is plainly visible from above, a point that should be noted carefully when one is dealing either with birds or ants. When the masses are stale they are not so conspicuous, for the strip turns at first a light and afterwards a darker dirty brown.

I have frequently noticed robins about the plants in the early morning and suspected that they may have been after the masses, but I have never been able to justify that suspicion.

In addition to this bird we have thrushes, blackbirds, sparrows, hedge-sparrows, starlings, wrens, and some others as occasional visitors, such as bullfinches, chaffinches, whitethroats, and very rarely a nuthatch. The thrushes are rather fond of this border, and I have disturbed them at various times of the day quite close to the Hellebores. In the early hours of July 5th one of them was on the bed in which they grow, not more than half a yard off, and I watched it to see if it would take one of the masses lying on the ground, but it went right over them, extracted a snail from the ivy on the wall, and proceeded to smash it with the usual vigour on the tiled path close by. Subsequently between the 6th and the 14th I placed perfectly fresh seed-masses in twos and threes in various parts of the garden; I laid them on the soil with the strip uppermost, and they were very conspicuous against the brown earth, but not one of them was removed.

Altogether I put down four lots of 3 each and three lots of 2 each—that is, 18 masses in seven different places. My plan was to place them in position about midnight, so as to catch the early bird, but on the first occasion I caught the late snail instead, for the first lot of three was badly mutilated by the next morning. I thought of protecting them with a ring of powder, which I know from experience neither snails nor slugs can cross, but I feared

it might have the effect of deterring the birds too, so I had to choose favourable places and clear away the molluscs first; by this means I managed all right, and the masses remained undisturbed until, when the strips had turned brown, I removed them myself, after some of them had been there for a week; they had become very fragile and some of them broke at a touch, despite my efforts and desire to keep them whole. Thus, ignoring the first three masses, which were spoilt by the snails, the remaining fifteen were left severely alone by the birds during the whole period of observation.

Summary of Section II.

In the face of this evidence, and in view of the fact that over a period of ten years or more I have never seen a seedling more than about a yard away from the parent plants, one can hardly maintain that the larva-like appearance is an adaptation or has any real dispersal value as far as my birds are concerned.

On the other hand, I admit that I am still suspicious, for it is hard to account for the disappearances except by their agency, and I am inclined to think that they may be deceived at first but soon learn their lesson.

In my own garden and neighbourhood the seed-masses must be unfamiliar objects, if not altogether unknown to the birds; there are such things as young and inexperienced birds and birds of an inquisitive nature, and, as a matter of fact, the only masses that disappeared at all, while these observations were in progress, vanished during the first two days, presumably before the birds had had time to get used to them. The curious little point that, whatever the agent, the mass was in each case taken from the end of a row lends support to the view that cautious curiosity, soon satisfied, may have had something to do with it: a glance at the diagram will show that it was not only from the end of the row, but, on both nights, from the lowest or outside row. Again, as I have already mentioned, the fall from the follicle does not break the mass, whereas those that I found some years ago were smashed, and this suggests a fall from a height greater than 25 inches.

On the whole, while denying any adaptational mimicry on the evidence adduced by me, one may, I think, admit the possibility of occasional dispersal by birds during the first few days of the fruiting-period.

Section III. Ants.

There remains the question of the part played by ants. In this matter I was unfortunately at a disadvantage in two ways—my supply of fresh masses did not hold out long enough and the fine weather broke up, rain falling on some days in torrents. The little I was able to do, however, interested me very greatly.

The ants with which Sernander experimented were three species of *Formica*, namely *rufa*, *rufa-pratensis*, and *exsecta* : none of these are, so far as I know, to be found in my small suburban garden, and for the most part I used *Donisthorpea nigra*, which abounds therein, but in a totally different quarter several yards away from the Hellebores and divided off by a fence : I also tried my luck with *Donisthorpea flava* and *Myrmica lævinodis*, and obtained results of some little interest, especially from the latter species.

I must take this opportunity of acknowledging gratefully my indebtedness to Mr. H. St. J. K. Donisthorpe, F.Z.S., F.E.S., for kindly naming my ants for me, and for giving me valuable information about their habits. I have availed myself to the full of his ready and willing assistance in these matters.

On July 9th I gave *Donisthorpea nigra* single seeds, and I found that, like the Formicas, they take them away in a very few minutes. I also saw them carry them into the nest : as the seed is considerably more bulky than the ant this is a performance worth watching, and one that is not altogether devoid of the comic element.

I then offered them a mass as well as single seeds ; they paid some little attention to the former, but soon deserted it altogether for the loose seeds. The next morning the mass was still there, and, although not broken, it was quite brittle and the strip distinctly mutilated. The border is hot and dry, and the strip had turned brown by the evening : there was no trace of its having been visited by snails, and probably the nibbling of the ants and the heat of the sun were responsible for its drying up so soon. This mass was about a foot from the entrance to the nest : the ants paid no further attention to it, and I removed it two days later, when it broke as I lifted it from the ground. I think the ants showed their sense in carrying off the single seeds instead of expending their energy upon the mass.

On July 12th I tried them again with a single mass, which I placed in the same position as the other, and I watched it for an hour between 6 and 7 in the evening, when it was fortunately sunny and the ants were out foraging. It was first attacked by a few of them, and they seemed to appreciate the fare. After, apparently, satisfying their own taste for it, they went off and presently it was receiving the attentions of a large number simultaneously—at one time I counted 14 on the strip. They nibbled away until I left them for dinner at 7 o'clock, and half an hour later they were still at it, but about 8 o'clock it began to rain and get dark and the ants deserted it. They had not broken it up when I went to bed, and I then put another mass about one inch from the entrance to the nest, without, however, having the slightest suspicion that the shorter distance would mean a fresh development.

The next morning the first mass was broken, but I cannot say whether the ants or the rain had done it. The other was a wonderful sight : there

were ants on it and under it and all round it: this was about 7.45 A.M., and at 8 o'clock I went to look at it again, but there was no trace of it to be seen—it had vanished. It had begun to rain again, and, while I attributed the disappearance of the ants, erroneously as I now believe, to the weather, I was at a loss to account for the seed-mass.

The next chance that I had was on July 18th; by this time there was only one mass left upon the plant, but I had several in reserve, and was keeping them as fresh as I could in a damp box. I put down the fresh mass and selected the one with the whitest strip from the box; both were placed about two inches from the entrance. There were only a few ants about, but in a few minutes each of them had its own visitors, and the fresh one was alive with them; about half an hour later it had completely disappeared, and I began to suspect the truth.

Just then I could not watch, so I removed the other mass and replaced it in the afternoon: it was attacked again at once, and this time I meant to see what happened, and, at last, after it had been there for the better part of an hour and I felt quite sure what the ants were about, I saw it disappear into the nest. It required some doing, but by dint of pulling and shoving, it quickly vanished, when once the ants got it into position.

After my supply of fresh masses came to an end, I tried the ants on several occasions with stale ones, fragments, and loose seeds, equally stale or staler, with the result that they will carry off the latter, but, so long as they can find any small bits or single seeds they do not trouble about moving the masses, unless they be placed close to the entrance of the nest, although they nibble away at the faded strip; it almost looks as if they make up their mind that the game is worth the candle before starting upon the onerous business of taking the mass inside. The staleness does not seem to matter, for I have seen masses which were more than a fortnight old disappear into the nest; it makes no difference whether the strip be white or brown, dirty or clean, or whether the mass be placed with it uppermost or undermost, or in any other posture.

After I had satisfied myself that *Donisthorpea nigra* will carry the mass into its nest, I amused myself in watching their performances when the conditions were favourable, and I had the opportunity. During the afternoon of July 31st, when my material was fully a fortnight old and most of it some few days older, I gave them several fragments and finally one mass, which I was careful to place just two inches from the entrance, with the idea of finding out how long it would take them to get it inside. I saw them begin to move it and then I busied myself with removing a few small weeds from the gravel-path. During the fortnight that had elapsed since the 18th the ants had had most of my fragments and loose seeds, and I found several of the latter dropped upon the path, presumably by them. As there are several nests this is merely what one would expect. My attention was,

however, attracted by a worker of *Myrmica lævinodis* carrying off one of the seeds. Up to this moment I did not know that this species was in the garden at all, but I followed her and came upon the nest a few yards away.

Returning to *Donisthorpea nigra*, I found that they got the mass into the nest in almost exactly 40 minutes from the time that they commenced operations; it was old and soil-stained, and if the larval resemblance is to be attributed to the white strip, it certainly had none at all, for the whole thing was earthy.

By this time I had only one unmutilated mass left; it, too, was old and dirty, and it happened to be a large one of 14 seeds. I first gave the Myrmicas single seeds and fragments, and they very quickly carried them inside. Finally, I gave them the mass, which I placed three inches from the entrance that they were using. It was attacked by a swarm of workers, but they moved it only with difficulty: more of them arrived and they managed to raise it bodily and get it a little nearer the hole. Then they changed their tactics, many of them went off, and those that were left worked hard at nibbling the strip. In about 25 minutes the mass broke into two and the smaller portion of five seeds was at once taken into the nest. The remainder was again divided in a very few minutes, and the whole mass was thus taken inside in three instalments and in about 32 minutes.

This is the only occasion on which I have seen a mass broken by the ants, and as I had no more left, except those that I wanted to keep for the photo, it is likely to remain the only one for some time to come.

Myrmica lævinodis is a larger ant than *Donisthorpea nigra* and presumably more powerful, and in the result it got the larger mass into its nest in about three-fourths of the time that it took the smaller species to cover only two-thirds of the distance (that is to say, it covered a distance greater by 50 per cent. in a period of time shorter by 20 per cent.), though it is not easy to decide whether it owes its greater efficiency to its superior strength, its different methods, or to both of them; one must, however, remember that the strip had become decidedly brittle by this time, whereas the fresh strip is more or less tough.

On the same afternoon I also discovered a third species in the garden, namely, *Donisthorpea flava*; it is considerably smaller than *Donisthorpea nigra*, and seemingly not nearly so energetic. Its worker simply nibbled at the bait languidly, but made no attempt to move the seed, nor was there any combined effort either for the single seeds or the fragments; in justice, however, one must again remember the staleness of the elaiosome. This species is more subterranean in its habits than the other two, and is largely dependent upon root-aphides for its food; it milks them and feeds upon the excreta, so it is not perhaps surprising that it did not display anything like the same interest—perhaps it was out of its nest merely to enjoy a sun-bath and some sleep in the open air.

Summary of Section III.

Donisthorpea nigra.—While there can be no doubt that this species disperses the single seeds when it comes across them, my evidence does not show that it disintegrates the mass, and I provided it with fresh as well as with stale ones. We have, however, the fact that when sufficiently close to an entrance-hole it can and does take the unbroken mass into the nest.

Myrmica lævinodis, on the other hand, while behaving in the same way as regards the single seeds and the fragments, will break up a bulky mass, and, in comparison with *Donisthorpea nigra*, it gets it into the nest in considerably less time.

Donisthorpea flava, the third ant, seems to be of little account or none at all so far as stale seeds and fragments are concerned.

Section IV. The Larval "Mimicry."

Presumably no one would suggest that the resemblance to a larva attracts the molluscs, and apparently it does not deceive the birds of my garden—at any rate, to an extent great enough to be of advantage to the species or to justify us in calling it adaptive so far as they are concerned. That, however, is by no means the same thing as saying that there are no birds anywhere to whom the mimicry appeals. A great deal of information and observation must be available before one can pronounce judgment on this point: we ought to know, for example, what larva or larvæ the mass resembles, whether they occur at the right time and place and in sufficient abundance in the natural haunts of the Hellebore to be really familiar to the birds of those parts, and whether the resemblance is sufficiently close to lead to mistakes often enough for one to call the mimicry an adaptation. Hence a great deal of work will have to be done to enable one to entertain an opinion worth expressing upon the interesting possibility of ornithochory.

With regard to the ants, the question whether they are or are not deceived by the resemblance is of some importance for the sake of accuracy, and lest we put *Helleborus fœtidus* into a wrong dispersal-group, although, of course, it would not be the only or even the most important point to consider.

It is notoriously difficult to prove a negative—to establish that the resemblance, when it is there, does not deceive the ants; but, on the other hand, the evidence seems to show that they are attracted all the same when it no longer exists, and that it is the elaiosome that is responsible. It is quite certain that at any rate some species go for the whole mass when it is old, stale, soil-stained, and of a uniform earth-colour—when, in other words, the resemblance has partly or completely disappeared, as far as human perception

is concerned ; neither can there be any doubt that they carry off fragments and single seeds, and also, as found by Sernander, the detached elaiosomes, as well as seeds from which the bait has been removed—attracted, no doubt, in the last instance by the oil-drops remaining upon the testa.

It is true that some ants, including *Formica* and *Donisthorpea*, carry larvæ into the nest, either whole or in bits ; but whatever one may think about the mass, one can hardly believe that they mistake the fragments or the single seeds for parts of a larva, or that they could work upon the mass itself for 32 or 40 minutes without realizing that it was not what they thought it to be.

Personally I am at one with Sernander in disagreeing with Ludwig's suggestion, and especially because it is difficult to see how it operates. One hears about mimetic resemblances so much that is fanciful or forced, if not positively foolish, that one is naturally prone to criticise them pending the production of evidence that is really pertinent and cogent. I admit I am always inclined to look askance at supposed cases, because, among other reasons, it is necessary to be on one's guard against running adaptation too hard. Organisms, as well as things inorganic, must have some form, size, and colour, whether it be of survival value or not—these are among the raw materials with which Natural Selection works, preserving, eliminating, or ignoring, as the case may be ; and it is, to my mind, not reasonable to assume that every chance resemblance, real or imaginary, must be of use to its possessor—that is a trap, about which it behoves us to be very wary indeed at all times.

Such cases as that of our Hellebore—and I know a great many of a similar nature in the world of fruits and seeds—demand a great deal of proving.

It is difficult to believe that ants, which cannot be thought of as wanting in intelligence, would be taken in more than once, unless, indeed, seed-masses and larvæ occur together in time and space and the resemblance is pretty close ; and even if they were deceived they would, one must believe, soon discover the mistake.

Again, it is not easy to decide which of the five senses is to be invoked to attract an ant from a distance, even if it be but an inch or two. Touch and taste may be ruled out at once, because neither of them operates except by actual contact. Smell and hearing are equally hopeless, until we can be sure of the emission of a larva-like odour or sound ; and so, barring the assumption of some unknown sense, which is not a very promising start in quest of a proof, we are reduced to sight, and I admit I have grave doubts whether an ant could see the strip at all until it was upon the mass, especially when it lay, as is so often the case, with the elaiosome uppermost.

Moreover, I do not believe that any additional incentive is necessary

to induce the ants to try their jaws upon a glistening white oleaginous strip whenever they come across one; they find much smaller fruits and seeds than these, possessing baits of one sort or another, that are barely or not at all visible to us.

I am of opinion, therefore, that the larval resemblance, which nobody could deny, is entirely inoperative and superfluous so far as the ants are concerned; that the idea of its deceiving them is erroneous, and that we must not look upon it as an adaptation to dispersal by them *.

Section V. The Claim to Myrmecochory.

I am, however, far from thinking, even if I am correct in the view that I have just expressed, that it disposes of the claim to myrmecochory. That claim could conceivably be maintained on other grounds, *e.g.*, the binding of the seeds into a single mass by means of a nutritious elaiosome. But if we are to consider that the mass is "adapted" in any way to dispersal by ants, we must show, in order to justify the use of that word, that the massing confers upon the species an advantage which it would otherwise be without. Personally I do not see that it is or can be so, so far as the ants are concerned, but rather the reverse.

We have seen the mass taken into the nest whole and in pieces, but I fail to recognize any advantage to the species in either event, unless the work done by the plant in binding the seeds together be undone by the ants, and the seeds subsequently ejected from the nest; and then the massing is but labour lost. The same argument would apply if it could be proved that the ants reduced the mass to single seeds, and then carried them off; it would still be a case of misspent energy on the part of the plant †.

* It is, nevertheless, possible that it may bear a negative instead of a positive interpretation; it might, for example, deter a seed-eater, of one sort or another, from attacking what looks so much more like a larva than like any other fruit or seed in our Flora. But this is, of course, an assumption pure and simple, and, moreover, is one that would have to be tested by experiment: one might, for instance, offer the same bird or other animal first the mass and subsequently the single seeds, and note the response; if the latter were taken and the former left it would suggest a deterrent of some sort, although not necessarily in the larval resemblance.

† The possibility of time being saved in dispersal by the seeds being massed, and so more easily found and carried away ten or eleven at a time, must not, however, be overlooked; but, since the seeds always, in my many trials and in my garden, lie over the whole winter, I do not consider any economy effected in this way a sufficient explanation. Normally, the mass breaks up from weathering in a very few days in the open, especially when hot sunshine alternates with heavy rain, as frequently happens in the fruiting months; and two or three days, or even a week or more, is not a large economy over a period of nine or ten months.

I cannot, therefore, avoid the conclusion that the claim of *Helleborus fœtidus* to myrmecochory is hardly a valid one *.

Final Remarks.

There are a few additional points of interest in the general subject of Myrmecochory and in the natural history of the Hellebore that came before me during this investigation.

For example, the seeds of this species, like those of *Viola odorata*, lie over the winter; and I have some evidence that, for the latter, those seeds whose caruncle has been removed or lacerated are at an advantage compared with those upon which it is left intact. They germinate earlier, which no doubt is not always desirable, but they also produce more vigorous plants, especially as regards the root-system, upon which the seedling depends for food-materials after the cotyledons have expanded. I have therefore sowed some of my snail-stripped Hellebore seeds in a separate pot, to compare the results, when the time comes round, with others from which the bait has not been removed.

Again, it appears that with the Daisy (*Bellis perennis*) the achenes carried into the nest are lost to the species unless they be subsequently ejected, while those that are dropped or abandoned after the elaiosome has been nibbled are the lucky ones. I have therefore left the ground undisturbed where I saw the masses carried in by my two species of ant, in the hopes of interesting developments next spring; for one must remember that, whereas the cotyledons of the Daisy seedling lie practically on the ground, those of the *Helleborus fœtidus* have a hypocotyl fully an inch in length, and may therefore be expected to work their way through a considerably greater depth of soil. I am not, however, at all sanguine; for ants burrow to a much greater depth than an inch, and, if one can judge by the very small percentage of seeds that germinate with me, I am afraid that they ripen imperfectly. In my borders also the snails eat the seedlings greedily; so that the species is hard put to it to hold its own against its many disadvantages, and the observer, to satisfy his curiosity, must possess his soul in patience.

I hoped to throw some little light upon the meaning of the mass—upon the question why the seeds are thus bound together; but I cannot feel that I have done anything of the kind.

Should anyone suggest that the cohesion is an adaptation to the dis-

* "Not proven" is, I feel sure, the fairest verdict that one can return so far, for, until the meaning of the mass is fully understood, the claim cannot be said to be disproved. But dispersal is such a very difficult and complicated question, and one that is so full of surprises, that this species may perhaps be retained in the group with advantage for the present, pending further research and under very grave suspicion.

integration of the mass by molluscs, and the subsequent dispersal of its components by ants, we may well ask why *Helleborus fœtidus* should, so to speak, take all this round-about trouble, whereas its brother in this country, *Helleborus viridis*, in common with many other species of different genera and families, gets dispersed by the same agency without the intervention of the strip, the snails, or the slugs. *Helleborus viridis* adopts the simpler and the usual course of dropping its seeds singly, instead of in a mass ; they are polished, black, and sculptured, and, instead of a great connecting-strip of oily tissue, each of them is provided with an inconspicuous raphal bait.

One must remember that, in this country, *Helleborus fœtidus*, whose home is in Southern and Western Europe, is at the extreme of its northern and western distribution, and it is probable that an observer at its head-quarters would find differences in the environment which would throw the needful light upon the problem that the seed-mass still presents. It is conceivable, though perhaps not very probable, that on the continent, where the Roman snail, *Helix pomatia*, is common, or in our southern and midland counties, where it is plentiful, this mollusc, with its larger body, might be a more efficient dispersal agent than our smaller garden-snail, *Helix aspersa*, which, during two nights, cannot have accounted for more than 8 seeds out of 209, or about 4 per cent. ; probably it was only 5 or less, or perhaps none at all, and that under circumstances which one cannot consider unfavourable.

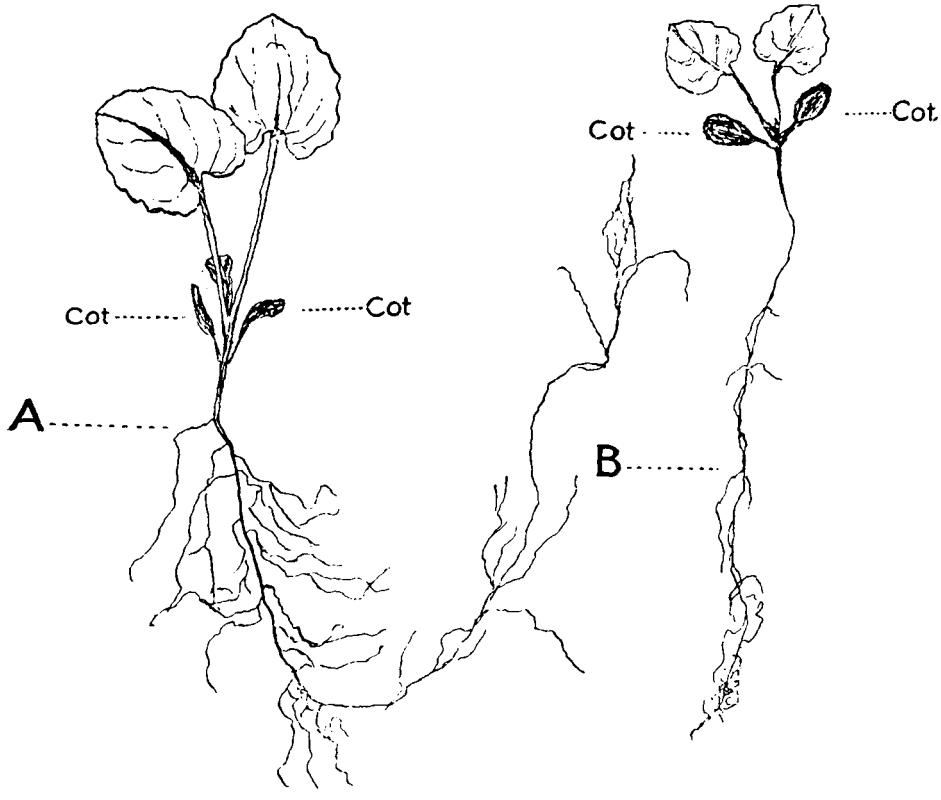
It is impossible to escape the conviction that the mass is an adaptation to some still unknown agent or agents, other than ants—perhaps to some species of bird, or possibly to some mammal or mammals that collect and store food ; and it is much to be desired that some competent naturalist may have, and may avail himself of, an opportunity of observing the dispersal of this plant where it is at home, in the sense of being fruitful and multiplying in a truly wild state. For preference, one would choose its headquarters in South-west Europe ; and until this is done, the meaning of the mass must doubtless remain a mystery.

Meanwhile, one can feel but scant satisfaction with such meagre and unconvincing results—sorry ones, indeed, for the future of *Helleborus fœtidus* in this country, especially in view of its many difficulties, and with all due allowance for rain-runnels and other well-known means of occasional help in dispersal. Probably the soundest conclusion one can draw is the wholesome and chastening one, that one should study the life-history of any given species at or near its head-quarters and in a wild state, instead of in a more or less artificial environment, on the confines of its territory.

Nevertheless, a certain interest attaches to an investigation of this sort, in that it reveals the difficulties and the fearful odds against which an organism has to struggle when at the end of its distributional tether ; if it be true that this plant is so handicapped as it appears to be in such vital matters as its



Helleborus fœtidus, Linn.



T. A. D. phot. & del.

Viola odorata, Linn.

pollination and its seed-dispersal, and if, in addition to this, I am right in thinking that the majority of the seeds do not ripen properly, while the seedlings are much more than decimated by snails, then it is not surprising that *Helleborus fœtidus* is, and is likely to remain, one of our most unfamiliar wild plants.

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EXPLANATION OF PLATE 36.

Helleborus fœtidus, Linn.

Fig. 1. Seed-mass.

2., 3., 4. The same, showing the connecting strip.

5., 6. The same, undergoing seed-disintegration.

Seedlings of *Viola odorata*, Linn.

A. Caruncle removed before sowing.

B. Caruncle not removed.