

THE GENETICS OF *ARMADILLIDIUM VULGARE* LATR.

III. DOMINANT AND RECESSIVE GENES FOR RED BODY COLOUR

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I. INTRODUCTION

One of the first genetical results obtained with the woodlouse, *Armadillidium vulgare* Latr., was that red body colour was dominant to the usual black or grey (Howard, 1938). This was quite conclusively proved (Howard, 1940, table 2) and animals homozygous for red were obtained. Also the dominant gene for red has been used in studies on sex ratios (Howard, 1939, 1942) and on the time of survival of sperms in impregnated females (Howard, 1943). It was, therefore, somewhat of a surprise when in 1945 it was found that two red females, which had been collected pregnant, appeared to be homozygous for a recessive gene for red body colour and not heterozygous for dominant red as expected (Howard, 1947). The relation between dominant red and recessive red appeared at first to be confusing, but it was found later that all results could be explained on the hypothesis that dominant red and recessive red are allelomorphic.

II. RECESSIVE RED

(1) *Descendants of female AU*

The red, type B female AU was collected on 28 May 1944 from the base of an elm tree near Four Went Ways, Abington, Cambridgeshire. She was pregnant when collected, and produced brood 185 which contained 15 red and 35 black animals. It was assumed that she was heterozygous for dominant red and had been impregnated by a black male—it must, however, be noted that 15:35 is a poor fit to a 1:1 ratio ($\chi^2=8$; for $n=1$, $P=0.01$,

$\chi^2=6.635$). However, on breeding from brood 185 animals, it was obvious that the red colour of female AU was due to her being homozygous for a recessive gene—see Table 1. The brood 185 segregation could then be explained as being due to female AU having been impregnated by two black males, one carrying recessive red and the other not (an alternative explanation of the deviation from a good 1:1 ratio is that homozygous recessive red animals have a low viability).

It can be seen from Table 1 that red brood 185 females mated with their red brothers give broods containing red animals only and that, when these same red females are mated with unrelated black males, the broods consist of black animals only. Also brood 246 from

Table 1. *Segregations in the progenies from animals of brood 185—female AU (red), collected pregnant—35 black:15 red, animals AUA to AUK*

(a) Red females × red males of same brood, i.e. brood 185			
Brood 212	♀ AUA × red brood 185 ♂	0 Black:22 Red	
Brood 213	♀ AUB × red brood 185 ♂	0 Black:30 Red	
Brood 240	♀ AUB, no male since brood 213	0 Black:51 Red	
Brood 214	♀ AUC × red brood 185 ♂	0 Black:18 Red	ABC (red ♂)*
Brood 215	♀ AUD × red brood 185 ♂	0 Black:36 Red	ACA (red ♀)
(b) Black female × black male of same brood, i.e. brood 185			
Brood 246	♀ AUJ × ♂ AUK	16 Black:8 Red	AAA to AAF
(c) Red brood 185 females × unrelated black males			
Brood 237	♀ AUC × ♂ CRA	3 Black:0 Red	
Brood 245	♀ AUD × ♂ AYA	16 Black:0 Red	
Brood 238	♀ AUE × ♂ FM	56 Black:0 Red	
(d) Black brood 185 female × unrelated black male			
Brood 253	♀ AUH × ♂ CSA	55 Black:0 Red	ADA to ADI
(e) Black brood 185 female × male heterozygous for dominant red (see Table 8)			
Brood 251	♀ AUI × ♂ CPH	20 Red:16 Black	BBA to BBG
(f) Unrelated red female × brood 185 red male (see also Table 7)			
Brood 239	♀ CU × ♂ AUF	0 Black:53 Red	CUA to CUF

* This column indicates animals bred from—thus male ABC, of brood 214, was a parent of brood 250 (see Table 4).

Table 2. *Segregations in the progenies from animals of brood 246 (for brood 246, see Table 1)*

Brood 255	♀ AAB (black) × ♂ AAA (red)	29 Black:20 Red	BCA to BCD
Brood 248	♀ AAF (black) × ♂ AAE (black)	16 Black:0 Red	AGA to AGF

black × black brood 185 animals does give the expected recessive red animals. As is indicated in the right-hand column of Table 1, some of the broods produced by brood 185 animals were also bred from. For the present we will consider the progeny of brood 246 only (see Table 2). The breeding behaviour of animals from broods 214, 215, 251 and 239 are considered later in this paper (see Tables 4 and 7–9).

It will be seen from Table 2 that some black brood 246 animals, e.g. female AAB, carry recessive red while others, either female AAF or male AAE, or both, do not. The progeny of brood 248 and brood 255 animals are considered later (see Tables 7–9).

(2) *Descendants of female GN*

The red, type D female GN was collected pregnant on 11 July 1945 from the same locality as female AU. She produced brood 223 which consisted of 95 animals, all black and no reds. There were 3 males and 92 females, 48 of the latter being type B and 44

type D (for type B and the sex-limited dominant type D, see Howard, 1940). The results of inbreeding and outbreeding from animals of brood 233 are shown in Table 3.

The results given in Table 3 show clearly that the red body colour of female GN is due to a recessive gene. The total segregation from black females of brood 223 crossed with black males of the same brood is 27 black:17 red. This is only a fair fit to a 3:1 ratio ($\chi^2=4.363$; for $n=1$, $P=0.05$, $\chi^2=3.841$; and for $P=0.02$, $\chi^2=5.412$). The deficiency is for blacks and not for the homozygous recessive reds. Consideration of animals AHA to AHC is left until later in this paper (see Table 9).

(3) Relation between recessive reds from females AU and GN

Females AU and GN were obtained in different years from the same locality and we might, therefore, expect that the recessive gene for red body colour was the same in these two animals. Such was found to be the case (see Table 4). It is unfortunate that the

Table 3. Segregations in the progenies from animals of brood 223 (brood 223—♀GN (red), pregnant when collected—95 black:0 red—animals GNA to GNH)

	(a) Black brood 223 female × black male of same brood		
Brood 254	♀ GNC (black) × ♂ GNB (black)	18 Black:11 Red	
Brood 249	♀ GNH (black) × ♂ GNG (black)	9 Black:6 Red	AHA to AHC
	(b) Black brood 223 animal × unrelated black animal		
Brood 252	♀ GNA (black) × ♂ AYB (black)	8 Black:0 Red	
Brood 256	♀ DSA (black) × ♂ GND (black)	63 Black:0 Red	

Table 4. Segregations in crosses between animals descended from females AU and GN (for origin of parents, see Tables 1–3)

Brood 250	♀ GNF (black) × ♂ ABC (red)	7 Black:10 Red	
Brood 247	♀ ACA (red) × ♂ GNG (black)	12 Black:11 Red	AEA, AEB
Brood 262	♀ AEB (black) × ♂ AEA (red)	8 Black:10 Red	BDA to BDK

crosses were red × black and not black × black. On the other hand, we know quite definitely from the results of crosses with unrelated black animals (see Table 1), that female AUC (the mother of male ABC) and female AUD (the mother of female ACA) were homozygous for recessive red and not heterozygous for dominant red.

The total for the 1:1 segregations in Table 4 is 27 black:31 red. Thus homozygous recessive red appears to be about as viable as the heterozygotes. Recessive red in *A. vulgare* may be widespread, as Vandel (1945) has found it in French animals. It must, however, be noted that the recessive red studied by Vandel was apparently not the same as found in the Cambridge material. The eyes of the recessive red animals studied by Vandel were carmine red in colour while those of the Cambridge material were black.

III. DOMINANT RED

(1) Introduction

As was pointed out in the general introduction to this paper, red body colour in *A. vulgare* of animals collected near Cambridge has usually behaved as being due to a single dominant gene. Females AU and GN were in fact bred from to obtain offspring carrying the gene for dominant red for experiments on the relative viabilities of animals homozygous for the gene for dominant red, heterozygous for this gene, and homozygous for recessive black. These experiments, however, were stopped when it was found that a recessive gene for red body colour existed, and work was then concentrated on determining the relation

between the dominant and recessive genes for red body colour. A few of the results for dominant red will, however, be considered here as they are necessary in discussing the relation between dominant and recessive red.

(2) *Descendants of the red male AZ*

The red male AZ was collected on 26 March 1944 from a fallen elm tree at the side of the Cambridge-Linton road on the Cambridge side of Babraham Park. He was mated with two black, type B females (BZ and CP), which were obtained in the same collection as himself. Both females produced two broods from the one mating and the results, together with the breeding behaviour of some of the animals from two of these broods, are given in Table 5.

Table 5. *Segregations for dominant red:black in broods from male AZ and his offspring*

(a) Broods from male AZ			
Brood 181	♀ BZ (black) × ♂ AZ (red)	7 Red: 3 Black	BZA to BZF
Brood 231	♀ BZ (black), no male since brood 181	27 Red: 21 Black	
Brood 184	♀ CP (black) × ♂ AZ (red)	11 Red: 12 Black	CPA to CPH
Brood 228	♀ CP (black), no male since brood 184	20 Red: 23 Black	
	Total	65 Red: 59 Black	
(b) Broods from red × red broods 181 and 184 animals			
Brood 194	♀ BZB (red) × ♂ BZA (red)	16 Red: 4 Black	
Brood 195	♀ BZD (red) × ♂ BZC (red)	10 Red: 3 Black	
Brood 242	♀ BZD (red), no male since brood 195	12 Red: 2 Black	
Brood 203	♀ CPB (red) × ♂ CPA (red)	6 Red: 1 Black	
Brood 204	♀ CPC (red) × ♂ CPA (red)	17 Red: 4 Black	
Brood 205	♀ CPD (red) × ♂ CPA (red)	7 Red: 1 Black	
Brood 210	♀ CPF (red) × ♂ CPE (red)	15 Red: 1 Black	
	Total	83 Red: 16 Black	
Expected 74.25:24.75; $\chi^2=4.12$; for $n=1$, $\chi^2=3.841$, $P=0.05$.			
(c) Red males from broods 181 and 184 × unrelated red (dominant?) females			
Brood 206	♀ CWA (red) × ♂ BZA (red)	37 Red: 13 Black	
Brood 207	♀ CWB (red) × ♂ BZA (red)	17 Red: 8 Black	
Brood 236	♀ CWC (red) × ♂ BZA (red)	47 Red: 20 Black	
Brood 222	♀ CVA (red) × ♂ BZC (red)	14 Red: 6 Black	
Brood 208	♀ EL (red) × ♂ CPA (red)	15 Red: 6 Black	
Brood 241	♀ EP (red) × ♂ CPA (red)	1 Red: 0 Black	
Brood 209	♀ EM (red) × ♂ CPE (red)	16 Red: 11 Black	
	Total	147 Red: 64 Black	
Expected 158.25:52.75, $\chi^2=3.20$; for $n=1$, $\chi^2=3.841$, $P=0.05$.			
(d) Miscellaneous results			
Brood 217	♀ EN (black) × ♂ CPA (red)	21 Red: 18 Black	
Brood 219	♀ EO (black) × ♂ CPG (red)	10 Red: 8 Black	
Brood 251	♀ AUI (black) × ♂ CPH (red)	20 Red: 16 Black	BBA to BBG
Brood 196	♀ BZE (black) × ♂ BZC (red)	7 Red: 8 Black	
Brood 216	♀ DY (red) × ♂ BZF (black)	17 Red: 13 Black	
	Total	75 Red: 63 Black	

It can be seen from Table 5 that good fits to 3:1 ratios are obtained both when broods 181 and 184 red animals are inbred and when they are mated with unrelated red animals suspected of being heterozygous for dominant red.

The localities from which the various red animals came were the University Farm and the same fallen elm tree from which AZ, BZ and CP were collected. Thus the red females CWA, CWB and CWC came from brood 191 of which the female parent was the red animal CW collected pregnant on the University Farm. The red female CVA was also the daughter of a red female (CV) collected pregnant on the University Farm. The red females EL and EM and the black females EN and EO all belong to brood 179 which came from the cross black

female FGB \times red male AS (see below for red male AS collected on the University Farm). The red female EP came from the same fallen elm tree as animals AZ, BZ and CP.

(3) *Descendants of male AS*

The red male AS was collected on the University Farm. He was mated with the red female AT (also collected on the University Farm) and with three black females, all from the same all black brood. Segregations in the progenies from male AS and in progenies from his offspring are given in Table 6. It can be seen that 3:1 ratios are obtained from red \times red, 1:1 ratios from red \times black and 0:1 ratios from black \times black as would be expected if the red body colour of male AS was due to a single dominant gene. The red male CX of Table 6 was also obtained from the University Farm and also appears to be heterozygous for dominant red.

Table 6. *Segregations in broods from male AS and in broods from his offspring*

(a) Broods from male AS			
Brood 180	♀ AT (red) \times ♂ AS (red)	2 Red: 3 Black	ATA to ATE
Brood 189	♀ FGA (black) \times ♂ AS (red)	0 Red: 1 Black	
Brood 179	♀ FGB (black) \times ♂ AS (red)	17 Red: 18 Black	EL to EO
Brood 178	♀ FGC (black) \times ♂ AS (red)	4 Red: 3 Black	DO, DP and DY
Brood 226	♀ FGC (black), no male since brood 178	20 Red: 12 Black	
	Total (broods 189-226)	41 Red: 34 Black	(Exp. 37.50:37.50)
(b) Broods from brood 178 and 180 animals			
Brood 201	♀ ATA (red) \times ♂ CX (red)	47 Red: 13 Black	
Brood 220	♀ ATA (red), no male since brood 201	77 Red: 25 Black	
Brood 199	♀ ATB (red) \times ♂ CX (red)	65 Red: 32 Black	
	Total	189 Red: 70 Black	(Exp. 194.25:64.75)
Brood 200	♀ ATC (black) \times ♂ CX (red)	34 Red: 24 Black	
Brood 221	♀ ATC (black), no male since brood 200	34 Red: 24 Black	
Brood 202	♀ ATD (black) \times ♂ CX (red)	37 Red: 42 Black	
Brood 218	♀ ATE (black) \times ♂ CX (red)	11 Red: 9 Black	
	Total	116 Red: 99 Black	(Exp. 107.50:107.50)
Brood 232	♀ DP (black) \times ♂ DO (black)	0 Red: 69 Black	

IV. RELATION BETWEEN RECESSIVE RED AND DOMINANT RED

(1) *Descendants of female CU*

The red female CU was collected pregnant on the University Farm and she produced broods 187 and 230 in 1944 and 1945 respectively. These showed segregations of 15 red: 19 black and 33 red: 52 black. Since all other red animals from the University Farm, e.g. CW, CV, AS, AT and CX in this paper, have been heterozygous for the dominant gene for red body colour, it was assumed that female CU was heterozygous for dominant red and had mated with a black male (the total segregation of 48 red: 71 black is, however, not a very good fit to a 1:1 ratio, P being between 0.05 and 0.02). However, when female CU was mated with the recessive red male AUF in 1946 (see Table 1)—she produced brood 239, which consisted of 55 red animals and no blacks. This suggests that female CU is homozygous for recessive red and not heterozygous for dominant red. Animals from brood 239 have been bred from and the results are given in Table 7.

Broods 263, 268 and 293 are useless for deciding whether female CU is heterozygous for dominant red as well as homozygous for recessive red, since the black males AGA and AGG may carry recessive red (see Tables 2 and 1). Brood 267 would appear to show that CUD (a daughter of female CU) is homozygous for recessive red, since male AEA (see

Table 4 and Pt. II, § 3, of this paper) is known to be homozygous for recessive red. Brood 295 needs careful consideration.

The male parent of brood 295 is the red animal BBG which came from brood 251 (see Table 1, § *e*). Brood 251 was obtained from the cross female AUI (black, but must carry recessive red since her mother was female AU) × male CPH (heterozygous for dominant red, having been obtained in brood 184 (see Table 5, § *a*)). The red male BBG must, there-

Table 7. *Segregations in broods from brood 239 females (brood 239, ♀ CU (red) × ♂ AUF (recessive red), 53 red:0 black, animals CUA to CUF)*

Brood 263	♀ CUA (red) × ♂ AGA (black)	11 Black:21 Red
Brood 293	♀ CUA (red) × ♂ AGG (black)	11 Black:11 Red
Brood 267	♀ CUD (red) × ♂ AEA (rec. red)	0 Black:12 Red
Brood 268	♀ CUF (red) × ♂ AGA (black)	18 Black:20 Red
Brood 295	♀ CUC (red) × ♂ BBG (red)	0 Black:44 Red

fore, be heterozygous for dominant red and may also carry recessive red. The female parent of brood 295 is the red female CUC which is probably homozygous for recessive red. There is, however, no segregation for red and black in brood 295 which consisted of 44 red and no black animals. The simplest explanation of this result is that there is a multiple allelo-morphic series:

dominant red (**R**), black (+), recessive red (**r**). The mating CUC × BBG would then be **rr** × **Rr** and will give red animals only.

(2) *Crosses involving brood 251 animals*

One of the animals of brood 251, the red male, BBG, has been considered in the previous section. Further results from breeding from brood 251 animals are given in Table 8. Two broods, 269 and 286, are of interest. The male parent of brood 269 is the red male BCA which came from brood 248 (see Table 2), and which is therefore homozygous for recessive red. The female parent BBA (cf. male BBG) must be heterozygous for dominant red and may carry recessive red. In brood 269 there were 20 red animals and 0 black—this can be

Table 8. *Segregations in broods from crosses involving brood 251 animals (brood 251, AUI (black, carrying recessive red) × CPH (dominant red), 16 black:20 red, animals BBA to BBG)*

(a) From brood 251 females		
Brood 269	♀ BBA (red) × ♂ BCA (rec. red)	20 Red: 0 Black
Brood 275	♀ BBC (black) × ♂ BBB (red)	7 Red: 7 Black
Brood 300	♀ BBF (black) × ♂ BBE (red)	1 Red: 7 Black
(b) From brood 251 males		
Brood 276	♀ BDA (black) × ♂ BBB (red)	2 Red: 3 Black
Brood 277	♀ BDB (red) × ♂ BBB (red)	18 Red:23 Black
Brood 288	♀ BDH (red) × ♂ BBB (red)	19 Red:25 Black
Brood 285	♀ BDE (black) × ♂ BBE (red)	1 Red: 4 Black
Brood 286	♀ BDF (red) × ♂ BBE (red)	9 Red: 0 Black
Brood 287	♀ BDG (red) × ♂ BBE (red)	2 Red: 0 Black

explained as in the previous section of the paper. Similarly, for brood 286, female BDF is known to be homozygous for recessive red, having come from brood 262. The recessive nature of the red of brood 262 was also proved in the two crosses: female BDI (red) × male ADB (black) gave brood 289, 25 black:0 red; and female BDJ (red) × male ADB (black) gave brood 290, 60 black:0 red. The black male ADB came from brood 253 (see Table 1, § *d*). Thus BBA and BBE, like BBG, appear to be of the constitution **Rr**. On the other

hand, male BBB must be **R+** since broods from him and recessive red females (BDB and BDH) give 1:1 ratios, i.e. broods 277 and 288.

(3) *Descendants of male EV and brood 249 females*

The red male EV was collected on the University Farm. Mated with two recessive red females and one black female of brood 249 (see Table 3, § a), he produced broods 271, 272 and 273 in which a segregation for red *v.* black occurred (see Table 9). Thus male EV is heterozygous for dominant red.

Table 9. *Segregations in broods from male EV and brood 249 females and from their descendants*

(a) Broods from male EV			
Brood 271	♀ AHA (rec. red) × ♂ EV (red)	4 Red: 5 Black	EXA to EXF
Brood 272	♀ AHB (rec. red) × ♂ EV (red)	5 Red: 6 Black	EVA to EVG
Brood 273	♀ AHC (black) × ♂ EV (red)	13 Red:20 Black	
	Total	22 Red:31 Black	(Exp. 26:50:26:50)
(b) Broods from brood 272 red females			
Brood 282	♀ EVB (red) × ♂ BCD (red)	15 Red:0 Black	
Brood 283	♀ EVC (red) × ♂ BCD (red)	14 Red:0 Black	
Brood 298	♀ EVE (red) × ♂ BCD (red)	32 Red:0 Black	
Brood 307	♀ EVG (red) × ♂ BCD (red)	27 Red:0 Black	
	Total	88 Red:0 Black	
(c) Broods from brood 272 black females			
Brood 279	♀ EVA (black) × ♂ BBD (red)	14 Red:14 Black	
Brood 303	♀ EVD (black) × ♂ BBD (red)	0 Red: 2 Black	
Brood 306	♀ EVF (black) × ♂ BBD (red)	6 Red:15 Black	
	Total	20 Red:31 Black	(Exp. 25:50:25:50)
(d) Broods from brood 271 animals			
Brood 280	♀ EXB (black) × ♂ EXA (black)	7 Black:5 Red	
Brood 281	♀ EXC (black) × ♂ EXA (black)	1 Black:0 Red	
Brood 296	♀ EXD (black) × ♂ EXA (black)	6 Black:3 Red	
	Total	14 Black:8 Red	(Exp. 16:50:5:50)

The four red females of brood 272, EVB, EVC, EVE and EVG, must be heterozygous for both dominant and recessive red. Mated with the recessive red male BCD (from brood 255, see Tables 2 and 1), they produced broods containing only red animals and no blacks, as is only to be expected if the genes for dominant and recessive red are allelomorphic.

The broods from the three black females of brood 272 × male BBD show a 1:1 segregation. This should mean that the red male BBD has the constitution **R+** and not **Rr**, since the black females EVA, EVD and EVF are **+r**. The cross **Rr** × **+r** would give a segregation of 3 red:1 black. Actually such a segregation from red × black has not yet been observed.

V. CONSTITUTION OF THE BLACK AND RED PIGMENTS

Both the black and red pigments occur as small granules in the cells of the hypodermis (i.e. the layer immediately below the transparent, hard cuticle). It may also be noted that black and red body colours are not due to different amounts of the same pigment as animals with a small amount of the black pigment are greyish brown and not red. Thus, in the development of black animals from their pure white stage when born, they pass through a brown stage but not a red one. These young brown animals can be separated quite easily from young red ones.

It also seems that the black and red pigments have a common source and are related. The genetical evidence for suggesting that they are related is given from the action of the sex-limited dominant gene for type D (see Howard, 1940, p. 93, and fig. D of plate IV). Type D females have the black and grey-brown pigments restricted to certain areas. Red animals which carry the gene for type D have the red pigment restricted to the same areas as the black in black type D animals.

Both the black and red pigments, the latter from both heterozygous dominant and homozygous recessive red animals, are insoluble in water, ammonia, hydrochloric acid, ethyl alcohol, ether, acetic acid, acetone and benzene. The insolubility of the red pigment in chloroform, ether and benzene suggests that it is not a carotinoid. Both black and red pigments appear to be soluble in dioxan (diethylene dioxide) + hydrochloric acid to give a yellow solution, the animal going yellow and then white.

The insolubility of the pigments and the fact that they occur as small granules suggest that they are melanins. Vandel (1945, p. 35) has also suggested that the pigments in woodlice belong to the melanin group. It has also been found by de Lattin (1939) that the white woodlouse, *Platyarthrus hoffmannseggi*, which is found in ants' nests, can be made brownish black by treating it with the *Tenebrio* enzyme—which suggests that the chromogen for melanin production is present but the enzyme for its formation absent. In *Armadillidium vulgare*, Howard (1942, p. 153) obtained 9:7 ratios for black:white in one family, suggesting that there may be two recessive genes for white—one type not having the chromogen and another lacking the enzyme.

Tests for melanin are not easy. Sections of the heads of black, heterozygous dominant red and homozygous recessive red animals have been stained by the ammoniacal silver nitrate method described by Lison (1936, p. 148, but omitting the use of gold chloride). The red granules became brownish black after 24 hr. in the ammoniacal silver nitrate and the intensity of the black colour is higher after 48 hr. The red pigment thus reduces silver nitrate as do typical melanins.

Both black and red melanin type pigments are found in vertebrates, e.g. in human hair (Arnou, 1938) and in fowl feathers (Nickerson, 1946). It seems in these two cases that the black and red pigments are not directly related but are formed from the same substrate by somewhat different reactions. Such may very well be true also for *Armadillidium*—at least for dominant red.

One further point needs some discussion. The eyes and mandibles in all animals—black, dominant red, recessive red and white—are jet black and this black colour of the mandibles is not removed by dioxan + hydrochloric acid. The black colour of the mandibles is probably due to a process concerned with their hardening—cf. Pryor (1940) for the hardening of the cuticle in insects. The cuticle of the rest of the animal is hardened by impregnation with calcium carbonate. This is easily shown by treating animals with hydrochloric acid. It also explains why Kalmus (information sent me in a letter dated 30 June 1941) did not find any differences in the resistance to desiccation of different coloured types of *Armadillidium* in contrast to the situation in *Drosophila* (Kalmus, 1941) where the pigments occur in the cuticle and where dark-coloured animals are more resistant to desiccation than light-coloured ones.

heterozygous for dominant red or homozygous for recessive red. It can, however, be said that most red animals from the University Farm have the dominant gene. The gene for recessive red does, however, exist in this population. If all red animals in the Four Went Ways population were due to the recessive gene and none to the dominant gene, it would mean that 35 % of the population were blacks carrying recessive red. This is a very high figure and seems unlikely. However, female AU had mated with a black carrying recessive red—which suggests that such animals are not rare. It is intended to carry out a further investigation with this population.

VII. DISCUSSION

It has been shown that red animals of *Armadillidium vulgare* may be homozygous for a dominant gene (**R**), heterozygous for this gene, or homozygous for a recessive gene (**r**). So far it has not been possible to notice any difference in the phenotype of these three classes of animals and, although different types of red do occur, they appear to be connected not with differences in the genotypes **RR**, **Rr** and **rr** but with differences in age of animal, in sex and possibly in other genes. Similar differences in intensity of colour are in fact found in the black series (cf. Howard, 1940, pp. 88–9 and 94). It should, however, be emphasized that there has never been any difficulty in scoring for red *v.* black.

It has also been suggested that the dominant gene for red body colour and the recessive gene for the same character are allelomorphic. This has not, of course, been proved conclusively since it is impossible to distinguish between the two genes being allelomorphic or being very closely linked in the repulsion phase. So far 141 red animals and no blacks have been obtained from crosses of type **Rr** × **rr**.

There is also reason to believe that the black and red pigments are both melanins and are formed from a common source. It is not, however, known what is the chemical relation between the black and the red melanins. Also it has not been proved that the red pigment in heterozygous dominant red animals and homozygous recessive reds is the same.

Populations contain from 5 to 8 % of red animals, but it is not known what proportions of the red animals are due to the dominant and recessive genes respectively. In one population most red animals have the dominant gene but it may be that in another population the recessive gene is very common.

Dominant and recessive genes producing the same or a similar phenotype have long been known, e.g. dominant and recessive white in poultry. The *Armadillidium* case described in this paper is of particular interest because: first, the dominant and recessive genes are probably allelomorphic; secondly, both dominant and recessive red animals occur in quite a high frequency in natural populations; and thirdly, the red type does not appear to be just a loss mutation from the commoner black type. It would seem that the nature of the original mutations has determined whether the genes for red would be dominant or recessive, and that there has not been any selection for dominance of wild type in *Armadillidium* which is a polymorphic species. It may be that in this species any animals which are heterozygous for a gene, be it recessive or dominant, are slightly fitter than homozygous animals.

VIII. SUMMARY

1. The common colour in the woodlouse, *Armadillidium vulgare*, is black or grey.
2. Red animals occur at a frequency of from 5 to 8 % in many populations.
3. Red body colour may be due to animals being homozygous or heterozygous for a dominant gene **R**, or to animals being homozygous for a recessive gene **r**.
4. Animals homozygous for the recessive gene **r** and homozygous or heterozygous for the dominant gene **R** cannot be distinguished.
5. **R** and **r** are allelomorphic, the series being **R** (dominant red), + (black), **r** (recessive red).
6. The black and red pigments are melanins.
7. It is suggested that in *A. vulgare*, which is a polymorphic species, the nature of the original mutations has determined whether the genes for red body colour should be dominant or recessive.

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APPENDIX

Since this paper was sent to the press, Prof. S. C. Harland has informed me that dominant and recessive genes for the same character and which are allelomorphic, have also been found in *Zea*, *Gossypium* and *Verbena* (see Beale, G. H. 1940, *J. Genet.* **40**, 337-58).