

THE GENETICS OF *ARMADILLIDIUM VULGARE* Latr. V. FACTORS FOR BODY COLOUR

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I. INTRODUCTION

Like several other woodlouse species, *Armadillidium vulgare* is polymorphic for body colour: thus in Great Britain Collinge has described fourteen varieties (list and references in Edney, 1953). The genetics of a number of colour types have been studied by Howard (1940; 1953) and by Vandel (1939; 1940; 1945). In this paper, which is the final one of the series, further results are given on the inheritance of body colours, and the significance of polymorphism in woodlice is briefly considered.

II. BODY COLOUR TYPES

1. *The common type*

Most adult males of *Armadillidium vulgare* are a leaden black colour (var. *plumbeus*), whereas females are greyish black with a series of small white or cream markings (var. *variegatus*, see Fig. 4 of Howard, 1940). Young males resemble females in having the white markings, but the markings are lost as the males mature. Some big, old females may also show only a few markings (Vandel, 1939), and thus resemble males. Parasitised males tend to resemble females in their colour and so do male intersexes (Legrand, 1941). The male type of colour was described as type A and the female as type B by Howard (1940)—see also the coloured plate of the different types at the end of that paper.

2. *Black, grey, brown and marbled*

There is little or no variation in the colour of black males, but "black" females vary from blackish grey to light grey or a brownish grey. The genetics of these different types of female colour have not been thoroughly investigated. Results (Table 1) recorded in studying the inheritance of sex ratios (Howard, 1942 and 1958) suggest that the darker grey black, which is the commonest colour, is recessive to the rarer light grey and brown grey. Another rare type of female, which may be called marbled, has a black background colour with numerous flecks of brown upon it. This type also appears to be dominant to the common dark grey black. How many factors are involved, and whether they are independent or members of a multiple allelomorphic series, is not known. As with type C and type D (see below), they are apparently sex-limited, males carrying the factors without showing the characters.

3. *Red*

Brownish red animals, in which, however, the eyes and mandibles are black, are fairly common, their frequency being about five per cent in many populations near

Table 1. *Examples of broods showing segregations for black, brown, grey and marbled.*

Brood No.	Female parents, all type B	Male parents	Segregations
20	H (black)	G (black, carrying brown ?)	23♂♂ : 29♀♀ ♀♀—15 black : 14 brown
38	KA (brown)	AN (black)	1♂ : 24♀♀ ♀♀—15 black : 9 brown
51	FB (black)	SF (black, carrying grey ?)	94♂♂ : 111♀♀ ♀♀—54 black : 57 grey
55	EB (marbled)	SE (black)	21♂♂ : 42♀♀ ♀♀—23 black : 19 marbled

Cambridge (Howard, 1940 and 1953, and Table 4 of this paper). Usually red body colour is due to a dominant gene, **R**, which is neither sex-linked nor sex-limited. In some populations, however, it is due to a recessive gene, **r**, which is allelomorphic with the dominant gene for red. Since the results in Howard (1953) in which 141 red animals and no blacks were obtained from crosses of the type **Rr** × **rr**, there have been found a further 169 red animals and no blacks from such crosses. Dominant and recessive red thus still appear to be allelomorphic rather than two closely linked genes in the repulsion phase.

Another type of red animals occurs rarely in populations near Toulouse, France (Vandel, 1945). In this type the eyes are red, not black, and the red colour is due to a simple recessive factor (Table 7).

4. *Variety collingei*

Vandel (1939) described the genetics of a colour type which was common near Toulouse and which he thought was similar to the variety *cooperi* of Collinge. Later, however, Vandel (1945) decided that it was not var. *cooperi*, and he renamed it as variety *collingei*. In animals of the variety *collingei*, which is due to a single dominant gene and is not sex-limited, the ground colour of the body is yellow but there is black or brown pigment on the head and along the median line (see Fig. D of plate IV in Howard, 1940). Some var. *collingei* animals bred in the laboratory from animals given to me by Professor Vandel were very similar to English type D females (see below). Vandel's genetical results for var. *collingei* are summarised in Table 6.

5. *Type C and type D*

These two colour types were distinguished first by Howard (1940). They are both sex-limited, being found in adult females but not in adult males. In some populations near Cambridge (Table 4) type C and type D females are fairly common, the highest frequency found being 7.7 per cent for type C and 9.4 per cent for type D. They are both due to dominant factors. Although they are sex-limited in adult animals to females, young males can resemble type C or type D females. As is shown in Table 2, such males do carry the factors for type C or type D.

Table 2. *Genetics of type C and type D*

- (a) Type C—Brood 35 from ♀CD (black, type B) × ♂AL (black, type A, but carrying type C) contained 64♂♂: 0♀. When young, the males were scored as 30 type B: 34 type C, but they were all type A when mature. Type B and type C young males were separated after scoring. Those used in breeding were numbered CDA to CDG.

Brood No.	Female parent	Male parent	Segregation Type C : Type B	Ratio expected
120	CCA (type B)	CDA (type B when young)	0:36	0:1
102	CGD (type C)	" " " " "	47:38	1:1
103	CCG (type B)	CDB (type B when young)	0:28	0:1
117	CCH (type C)	" " " " "	13:18	1:1
87	CBA (type B)	GDE (type B when young)	0:41	0:1
116	CBB (type C)	" " " " "	16:22	1:1
97	CCC (type C)	CDC (type C when young)	16:6	3:1
89	CCJ (type C)	" " " " "	21:5	3:1
115	CCF (type C)	CDD (type C when young)	17:10	3:1
105	CCK (type B)	" " " " "	8:9	1:1
107	CBG (type B)	CDF (type C when young)	14:13	1:1
88	CBJ (type B)	CDG (type C when young)	15:19	1:1

- (b) Type D—Brood 23 from ♀DB (black, type D) × ♂SC (black) contained 17♂♂: 50♀♀. When young, the males were scored as 7 type B: 10 type D; and the females as 25 type B: 25 type D. Two type D males, DBA and DBB, were kept for breeding, both were type A when mature.

Brood No.	Female parent	Male parent	Segregation Type D : Type B	Ratio expected
81	DAA (type B)	DBA (type D when young)	7:6	1:1
125	DAH (type B)	" " " " "	17:12	1:1
108	DAB (type D)	" " " " "	60:21	3:1
91	DAC (type D)	" " " " "	19:12	3:1
126	DAD (type B)	DBB (type D when young)	33:23	1:1
92	DAE (type D)	" " " " "	16:5	3:1
74	DAF (type D)	" " " " "	33:11	3:1
98	DAG (type D)	" " " " "	26:8	3:1

- (c) Type C × type D. Brood 93 was from ♀CBC (type C) × ♂GB (type A, but type D when young). There were 38♂♂: 76♀♀. They were scored when young as 26 type B: 50 type C: 38 type D, but the separation between type C and type D was difficult.

- (d) Broods showing lack of linkage between type C or type D and dominant red. Other similar broods have been scored.

Brood No.	Female parent	Male parent	Red Type B : Type C or D	Black Type B : Type C or D
71	KM (red, type C)	KL (black, type A)	16:14	15:13
202	ATE [♀] (black, type B)	CX (red, carrying type D)	15:16	18:21

The distinction between type C and type D females is in nearly every case clear (see Figs. E and F of plate IV in Howard, 1940). On the other hand females classified as type D in collections have varied considerably in the amount and shade of the brown pigmented areas. A few progenies have been studied from crosses of type C females with males known to carry the factor for type D and of reciprocal crosses. Difficulty was found in classifying the animals in such progenies into types C and D, and it is possible that the same major factor might be responsible for both type C and type D, and that the difference between type C and type D might be due to minor genes. As can be seen from plate IV of Howard (1940), the areas of lighter pigment in both types C and D have a similar distribution.

6. *Variety marginatus*

The description of variety *marginatus* given by Collinge was "ground colour of dorsum a dark-grey, with lighter lateral patches and broken median line; pleural plates light yellow." The results of Vandiel (1945) suggest that the variety is recessive to the common type and more or less sex-limited to females (see also Table 7).

7. *White*

White animals, but which have black eyes, have been found in a few progenies (Howard, 1942), and they are recorded as having been found wild by Collinge. They have not, however, been found in any collections made near Cambridge. White is due to either one or two recessive genes, see Table 3.

Table 3. *Broods in which white animals were found*

Brood No.	Female parent	Male parent	Segregation black : white	
73	EAF (black)	EAE (black)	20 : 1	(♀AP)
134	AP (white)	CJ (black)	32 : 24	
139	FBF (black)	FBC (black)	0 : 2	
140	FBG (black)	FBA (black)	13 : 6	
141	FBH (black)	FBA (black)	9 : 6	
330	QBB (red)	QBA (red)	22 : 10	
340	QBC (red)	QBA (red)	15 : 5	

N.B.—(1) EAF and EAE, sister and brother; AP and CJ also related, CJ coming from brood 83, parents of which were EAH (black) and EAE, sister and brother.

(2) FBA to FBH, all from brood 63 (42 black : 0 white).

(3) QBA to QBC, line being kept true for recessive red, animals all from brood 315. Segregations in broods 330 and 340, were for red : white, and not for black : white.

In two progenies from recessive red animals there were also found a number of animals which had large white patches on them. In one of these animals the front half was red and the hind end white. As they occurred in theygienic broods containing no males,

it was impossible to inbreed, and, when crossed with unrelated males, the character was lost.

8. Summary

Among the colour types of *Armadillidium vulgare* which have been studied genetically, there have been found one type (var. *collingei*) which is dominant to the common black type, another type (red with black eyes) which may be due to either a dominant or a recessive gene which are allelomorphic, two (types C and D) which are dominant but sex-limited in adults to the female sex, one (var. *marginatus*) which is recessive and more or less limited to females, and finally one type (red with red eyes) which is due to a simple recessive. In addition wild animals may be heterozygous for a recessive gene or genes for white. There is no evidence for linkage between any of these genes. Thus Vandell (1945) found that var. *collingei* and recessive red with red eyes were independent, and dominant red is not linked with the sex-limited types C and D (see Table 2).

III. FREQUENCIES OF THE DIFFERENT TYPES

Table 4 gives a summary of results obtained from the collections of wild animals made in the vicinity of Cambridge. The sex ratio is in three places markedly different from 1 : 1, and the excess of females is undoubtedly due to the frequent occurrence of thelygenic females (Howard, 1940, 1942 and 1958).

Table 4. Collections from localities near Cambridge

Collection from	Total animals	Percentage females	Percentage red males/ total males	Percentage red females/ total females	Percentage type C females/ total females	Percentage type D females/ total females	Percentage red type D females/total females	Females, percentages red + type C + type D
University Farm	1,111	68.4	6.0	9.3	2.4	0.8	—	12.5
Four Went Ways	2,475	71.8	5.0	5.0	1.9	4.8	0.7	12.4
Gog Magog Hills	328	71.3	2.1	0.0	7.7	9.4	—	17.1
Babraham	578	54.8	4.2	6.3	1.3	3.5	—	11.1
Various places	1,025	57.4	3.3	4.2	5.0	3.0	—	12.2

With the exception of the collection from the Gog Magog Hills red animals comprise at least five per cent of each population, and formed in the University Farm population no less than 9.3 per cent of the total females. The Gog Magog Hills population on the

other hand contained no less than 17.1 per cent of total females of types C and D. The percentage of total females either red, type C or type D ranged from 11.1 to 17.1 per cent. This is an under-estimation of the total amount of polymorphism because no account has been taken of the light grey or brown grey females which have been grouped with the common grey black type.

Of the 55 females collected from wild populations and bred from (this number is higher than the total given in Table 5 because not all broods were scored for sex), only one homozygote for a dominant colour type (i.e. either red, or type C, or type D) was found. This animal, a black type C female collected from the Gog Magog Hills, produced a brood in which there was one male and 62 females, all the females being black type C. A female, which was both dominant red and type D, was also collected wild and bred from, and also a female which was both recessive red and type D (female GN of Howard, 1953). Of the thirteen red type B females pregnant when collected, nine had mated with black males and four with red males. The latter number is much higher than would be expected because in no population (Table 4) do red males occur with a frequency higher than six per cent. Of the four recessive red females, two had mated with black males heterozygous for recessive red and two with homozygous black males.

Table 5. *Females collected wild and whose broods were scored for sex. F=strong thelygenic, (F)=weak thelygenic, and A=amphogenic.*

Colour type	Pregnant when collected			Not pregnant when collected			Total		
	A	(F)	F	A	(F)	F	A	(F)	F
Black, type B	1	0	1	13	0	5	14	0	6
Dominant red, type B	1	2	4	2	0	3	3	2	7
Recessive red, type B	1	0	1	0	0	0	1	0	1
Black, type C	0	0	2	1	0	1	1	0	3
Black, type D	0	0	0	3	2	2	3	2	2
Dominant red, type D	0	0	0	0	0	1	0	0	1
Recessive red, type D	0	0	1	0	0	0	0	0	1
Totals	3	2	9	19	2	12	22	4	21

One black type B female not included—♀FD, amphogenic brood in first year, thelygenic brood in second year.

2×2 contingency table—black type B: remainder and A:F

(a) 4 weak thelygenics counted as amphogenics, $\chi^2=3.04$; $P=0.07$

(b) 4 weak thelygenics omitted, $\chi^2=5.31$; $P=0.021$

(c) 4 weak thelygenics counted as thelygenics, $\chi^2=7.52$; $P=0.064$

Of the 47 wild females bred from and whose broods were scored for sex, 22 were amphogenics, 4 weak thelygenics and 21 strong thelygenics (Table 5). If the weak

thelygenics are grouped with the amphogenics, there is no strong indication that red, type C or type D females are more likely to be thelygenics than are black type B females. If, however, the weak thelygenics are either omitted or grouped with the strong thelygenics, a different result is obtained; and this suggests that red, type C, or type D females are more likely to be thelygenics than are black type B females. If this is so, then the proportion of thelygenic females is lower than is suggested by the figures in Table 5 because the wild females bred from have been selected to include a higher frequency of red, type C and type D females than occurs in natural populations.

IV. RELATIVE VIABILITIES

The occurrence of monogenic females (i.e. thelygenics and arrhenogenics) in woodlice is a means of restricting inbreeding and encouraging outbreeding (Howard, 1942), and it might therefore be that the polymorphism of populations is maintained by the heterozygotes for the dominant colour types being more viable than the homozygous black type A or type B animals. As is shown in Table 6, there is some evidence that under laboratory conditions heterozygous dominant red animals are more viable than blacks, and, if we omit the figures for sib matings, that the homozygous red animals are less

Table 6. *Genes dominant to the common type*

		χ^2	P	
A. Dominant red				
1. Heterozygous red \times black				
(a)	Females pregnant when collected	446 red : 408 black	1.70	0.20
(b)	Red animals from collections	431 red : 394 black	1.66	0.20
(c)	Lab. bred animals, non-sib matings	674 red : 628 black	1.62	0.20
(d)	Lab. bred animals, sib matings	111 red : 101 black	0.47	0.50
	Total	1,662 red : 1,531 black	5.37	0.02
2. Heterozygous red \times heterozygous red				
(a)	Females pregnant when collected	119 red : 46 black	0.73	0.40
(b)	Animals from collections	60 red : 30 black	3.33	0.07
(c)	Lab. bred animals, non-sib matings	311 red : 125 black	3.13	0.07
(d)	Lab. bred animals, sib matings	176 red : 53 black	0.42	0.50
	Total	666 red : 254 black	3.34	0.07
	Total [omit (d)]	490 red : 201 black	6.16	0.01
B. Types C and D				
1. Heterozygous \times type B (or A)				
(a)	Type C	419 type C : 431 type B	0.17	0.70
(b)	Type D	489 type D : 478 type B	0.13	0.70
2. Heterozygous \times heterozygous				
(a)	Type C	121 type C : 55 type B	3.67	0.07
(b)	Type D	115 type D : 37 type B	0.04	0.80
(c)	Type C \times Type D	148 types C+D : 47 type B	0.08	0.80
C. var. <i>collingei</i>				
1. Heterozygous \times type B (or A)				
	Vandel (1945)	4,256 <i>collingei</i> : 4,184 type B	0.61	0.40
2. Heterozygous \times heterozygous				
	Vandel ¹⁹ (1945)	920 <i>collingei</i> : 325 type B	0.81	0.35

viable than the heterozygotes. No differences in viability are, on the other hand, shown by the results for type C and type D, and for var. *collingei* studied by Vandel (1945). It should, however, be noted that most of the broods scored by Vandel were from sib matings which would probably be extremely rare in wild populations. The greater fitness of heterozygous animals could, however, occur at a different stage from that studied under the laboratory conditions. The heterozygotes might, for example, breed for a year longer, or they might produce a higher number of eggs than homozygotes. The latter is possible as there are big differences in the numbers of eggs produced, the number depending to a very high degree on the size of a female.

The feature of the results for recessive genes, Table 7, is the good viability under laboratory conditions of the homozygous recessive types, but there is some suggestion that they are not quite as viable as the heterozygotes and that the dominant homozygotes are not as viable as the heterozygotes. The number of animals scored is, however, much too small for any definite conclusions to be drawn.

Table 7. *Genes recessive to the common type*

		χ^2	P	
1. Heterozygote \times homozygote				
(a)	recessive red	131 black : 118 red	0.68	0.40
(b)	var. <i>rubra</i> (Vandel, 1945)	188 grey : 144 red	5.83	0.02
(c)	var. <i>marginatus</i> (Vandel, 1945)	no results	—	—
(d)	white	32 black : 24 white	1.14	0.30
Total		351 : 286	6.63	0.01
2. Heterozygote \times heterozygote				
(a)	recessive red	117 black : 43 red	0.30	0.55
(b)	var. <i>rubra</i> (Vandel, 1945)	103 grey : 34 red	0.002	0.95
(c)	var. <i>marginatus</i> (Vandel, 1945)*	206 grey : 79 <i>marginatus</i>	1.12	0.30
(d)	white**	37 red : 15 white	0.41	0.50
Total		463 : 171	1.32	0.25

*var. *marginatus*, females only as variety more or less sex-limited.

**not including brood 63 animals where black \times black appeared to give a 9 : 7 ratio (see Table 3). Segregation for red : white in a line being kept for recessive red.

V. INFLUENCE OF PREDATORS

Woodlice are eaten to some extent by birds. Thus Fisher (1951 and 1955) records them in the food of the Pheasant (*Phasianus colchicus*), of the Great Spotted Woodpecker (*Dendrocopos major*) and of the Redstart (*Phoenicurus phoenicurus*). Woodlice are also presumably the crustaceans mentioned by Fisher as being part of the food of the Little Owl (*Athene noctua*), of the Starling (*Sturnus vulgaris*) and of the Redwing (*Turdus musicus*). Witherby et al. (1943) mention woodlice as part of the food of the Jackdaw (*Corvus monedula*), of the Starling, of the Tree Creeper (*Certhia familiaris*), of the Grasshopper Warbler (*Locustella naevia*), of the Hoopoe (*Upupa epops*), of the Wryneck (*Jynx torquilla*), of the Little Owl, of the Common Snipe (*Capella gallinago*), of the Redshank (*Tringa*

tolanus), and of the Lapwing (*Vanellus vanellus*). The present author has seen domestic hens eating *Armadillidium vulgare*. On being disturbed *Armadillidium vulgare* rolls up into a ball and remains motionless for at least a minute. It thus relies on not being recognised by any predator as being edible. It may be therefore, as was pointed out by Haldane (1955) for polymorphism in insects, that the uncommon colour types may possess a certain advantage in that they are not taken in as high a frequency by predators as are the common type. It is also interesting to note that one human collector did confuse in beech leaf litter for a short time type D females when rolled up with the hard inner core of hawthorn (*Crataegus*) berries. In addition it may be significant that *Armadillidium vulgare*, a species which is more often found in exposed places and in loose leaf litter than some of the flatter species of woodlice which lurk under bark or stones, is the British woodlouse species showing the greatest amount of polymorphism for body colour.

VI. GENERAL DISCUSSION

Although the genetics of *Armadillidium vulgare* and other woodlice have now been studied for over twenty years, it is evident that the results obtained are still only of a preliminary nature. There are a number of interesting points raised by the results found so far, but only much more intensive work than that done by Vandel and myself will enable definite answers to be given. In my opinion there is little point in further investigations on the inheritance of sex ratios because there are no recognisable sex chromosomes and so far no sex-linked characters have been found. On the other hand extensive work on the colour types might supplement and extend our knowledge of polymorphism and how it is maintained in wild populations.

VII. SUMMARY

1. The woodlouse, *Armadillidium vulgare*, is polymorphic for body colours.
2. The rarer types of body colour may be due to either dominant or recessive factors. Some types are sex-limited to females.
3. Populations near Cambridge were scored for different colour types. About 12 per cent of the females were of the rarer types.
4. There was evidence in the case of the dominant factor for red body colour that heterozygotes were more viable than homozygotes.
5. Woodlice are eaten by birds, and this could be a cause maintaining the polymorphic structure of populations.

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