THE GENETICS OF *ARMADILLIDIUM VULGARE* LATR.

II. STUDIES ON THE INHERITANCE OF MONOGENY AND AMPHOGENY

By H. W. HOWARD

School of Agriculture, Cambridge

CONTENTS

		PAGE
I.	Introduction	143
II.	General considerations of monogeny	144
	(1) Vandel's theory to account for monogenic broods	144
	(2) Genetical segregations in monogenic and amphogenic broods	144
	(3) Variations in the sex ratios of different broods from the same females	145
III.	The inheritance of monogeny and amphogeny	147
	(1) Descendants of thelygenic female A	148
	(2) Descendants of thelygenic females CB and CC	148
	(3) Descendants of thelygenic female DA	150
	(4) Descendants of arrhenogenic female AB	150
	(5) Descendants of amphogenic female EA	151
	(6) Descendants of amphogenic female FB	152
	(7) Summary and discussion	152
IV.	The effect of monogeny on the composition of natural populations	153
	(1) Monogeny as an outbreeding mechanism	153
	(2) The effect of monogeny on sex ratios in natural populations	154
	(3) Possible stable types of populations	155
	(4) *Armadillidium* populations	156
V.	Summary	158
	References	159

I. Introduction

Vandel (1939) and Howard (1940) have reported the occurrence of three types of female in the woodlouse *Armadillidium vulgare*—amphogenic females which produce broods consisting of about 50% males plus 50% females, thelygenic females which produce broods consisting almost entirely of females, and arrhenogenic females which produce broods consisting almost entirely of males. Both thelygenics and arrhenogenics are described as monogenics.

Vandel (1938) has also described in some detail the inheritance of monogeny in the woodlouse *Trichoniscus provisorius*. He concluded that the monogenic condition was inherited cytoplasmically through the eggs —thus monogenic females produce only monogenic daughters and amphogenic females only amphogenic daughters. Vandel also found that, while many of the daughters of a thelygenic female were thelygenics, others were arrhenogenics. Preliminary results for *Armadillidium vulgare* (Howard, 1940) suggested that in this woodlouse the inheritance of amphogeny and monogeny was not cytoplasmic. The further results given in the present paper do indicate that monogeny and amphogeny

may be inherited cytoplasmically in *Armadillidium*. It appears, however, to be a rather irregular type of cytoplasmic inheritance in many cases, and it must also be pointed out that it is very difficult to distinguish in woodlice, where the female is probably the heterozygous sex, between cytoplasmic inheritance and inheritance by factors in the *Y*-chromosome, since every daughter receives her *Y*-chromosome as well as her cytoplasm from her mother.

II. General considerations of monogeny

(1) *Vandel's theory to account for monogenic broods*

Vandel (1938) found that in the woodlouse *Trichoniscus* monogenic broods were as large as amphogenic broods. The absence of one sex in monogenic broods is therefore not due to animals of this sex dying before they are scored, or at some stage before birth. Vandel also states that he has never observed any cases of sex reversal nor any intersexes in woodlice. It therefore seems unlikely that one-half of the males in arrhenogenic broods and one-half of the females in thelygenic broods have the sex-chromosome constitutions of the opposite sex. It has also been shown (see Table X in Howard, 1940, and male AL in Table 6 of this paper) that the male parent has no effect on the sex ratio of a brood; for the same male can be the parent of an arrhenogenic brood from one female and of a thelygenic brood from another, or of an amphogenic brood from one female and of a thelygenic brood from another.

Vandel's theory (see Vandel, 1938, 1941) to account for monogenic broods is simple. He suggests that in woodlice the female is the heterozygous sex (chromosomes *XY*), and that in monogenic females the cytoplasm directs the segregation of the sex chromosomes. Thus in thelygenic females every egg receives a *Y*-chromosome and the *X*-chromosome always goes into the first polar body, while in arrhenogenic females every egg receives an *X*-chromosome and the *Y*-chromosome always goes into the first polar body.

It has, however, been pointed out (Howard, 1940) that the actual mechanism by which every animal in a thelygenic brood has a sex chromosome constitution of *XY* and every animal in an arrhenogenic brood a constitution of *XX* may be different from that suggested by Vandel, and it has also been suggested in the introduction to this paper that the factors responsible for monogeny may be carried in the *Y*-chromosome and not in the cytoplasm.

(2) *Genetical segregations in monogenic and amphogenic broods*

Genetical results show that the segregation of the autosomes takes place normally in the eggs of both amphogenic and monogenic females (see Table 1), and also that the eggs of both amphogenic and monogenic females are fertilized and do not develop parthenogenetically (see Table 2). The examples given in the two tables are for the dominant

factor red. Similar results have been obtained for the two dominant factors for the sex-limited types C and D. The two results in Table 2 which suggest that some eggs might develop parthenogenetically are almost certainly to be explained by the fact that sperms can be stored in females for at least a year. Evidence for such storage of sperms is also given in Table 1 of Howard (1940).

Table 1. *Normal segregations for red v. black in the eggs of females heterozygous for the dominant factor for red*

Female parent (red)	Male parent (black)	No. of brood	Constitution of brood: Males Red : Black	Constitution of brood: Females Red : Black
BC	G	27	17 : 19	7 : 10
BD	G	28	8 : 8	15 : 19
BN	SA	34	20 : 18	6 : 8
BO	SA	39	10 : 12	8 : 6
JD	?	45	20 : 20	32 : 22
JB	SG	46	57 : 48	69 : 79
KO	HB	64	8 : 3	11 : 4
JD	(No male since brood 45)	65	9 : 10	8 : 10
KM	KL	71	0 : 0	5 : 10
KH	KF	77	7 : 4	0 : 0
BD	(No male since brood 28)	90	15 : 7	15 : 18
BF	CA	94	11 : 12	2 : 1
BQ	AL	99	0 : 6	10 : 15
BP	AL	109	5 : 8	8 : 7
BN	(No male since brood 34)	127	9 : 13	9 : 12
JB	BA	128	14 : 6	17 : 8
KJ	KF	133	7 : 7	0 : 0

Table 2. *Segregations for red v. black in broods from black females × heterozygous red males*

Female parent (black)	Male parent (red)	No. of brood	Constitution of brood: Males Red : Black	Constitution of brood: Females Red : Black
AB	B	8	9 : 13	6 : 3
GA	JA	37	0 : 0	6 : 7
CE	(Red male of same brood)	43	3 : 1	25 : 14
CD*	CG	82	5 : 21	0 : 0
DB	CH	95	19 : 32	0 : 0
FG†	CG	114	2 : 11	4 : 28
EF	JDA	148	0 : 0	3 : 3
FL	JDC	149	8 : 7	4 : 1
GG	JDB	154	2 : 0	9 : 6
EG	JDB	155	1 : 2	23 : 24
GF	JDD	160	0 : 0	4 : 3
FG†	(No male since brood 114)	163	0 : 9	1 : 11
GH	JDD	166	10 : 12	14 : 8

* Brood 82—there is a significant deficiency of reds in this brood. Female CD was mated with a black male the previous year. Sperms have probably survived from this previous mating (cf. Table I of Howard (1940)).

† Broods 114 and 163. Female FG was collected during the breeding season and may have been already impregnated by a black male before being placed with male CG.

(3) *Variations in the sex ratios of different broods from the same females*

Vandel (1939) found that the sex ratios in the three broods per year produced by *Armadillidium* under French conditions varied greatly from brood to brood (some of Vandel's results are given in Table VIII of Howard, 1940). Thus female A 2 produced a first brood containing

24·5% of males, a second containing 78% of males and a third containing 92% of males.

Under Cambridge laboratory conditions a few females produce two broods per year. In Table 3 results are given for seven pairs of broods

Table 3. *Sex ratios in first and second broods of the same year*

Name of female parent	No. of first brood	Composition of first brood ♂♂ : ♀♀	% ♀♀	No. of second brood	Composition of second brood ♂♂ : ♀♀	% ♀♀
AJ	26	6 : 50	89	44	2 : 7	78
BG	31	2 : 4	67	32	5 : 7	58
CBB	116	12 : 26	68	130	4 : 25	86
CCD	102	1 : 85	99	132	0 : 4	100
CCH	117	14 : 17	55	129	24 : 27	53
FB	51	94 : 101	52	61	34 : 32	48
HC*	111	48 : 24	33	78	60 : 9	13

* HC was a French female.

produced by the same females in one year. Unfortunately, several of the broods are very small ones. The results for females CBB, CCH and FB do, however, suggest that there are no big changes in sex ratios of successive broods from the same female. It is also interesting to note that the French female HC (given to me by Prof. Vandel) does show a change in the same direction as that found by Vandel.

In Table 4 are given data for the sex ratios of broods from the same females in two successive years. Of the twenty-two females, about fifteen

Table 4. *Sex ratios in broods from same females in different years*

Name of female parent	Brood in first year No.	Composition ♂♂ : ♀♀	% ♀♀	Brood in second year No.	Composition ♂♂ : ♀♀	% ♀♀
AB	8	20 : 9	31	25*	40 : 1	2
AF	10	4 : 3	43	49	43 : 15	26
AJ	26 + 44	8 : 57	88	69	9 : 0	0
BD	28	16 : 34	68	90	22 : 33	60
BG	31 + 32	9 : 9	50	122	7 : 11	61
BK	33	45 : 0	0	118	5 : 0	0
BN	34	38 : 14	27	127	22 : 21	49
CBJ	88	2 : 32	94	167	1 : 7	88
CD	35	64 : 0	0	82	26 : 0	0
DB	23	17 : 50	75	95†	51 : 0	0
DE	54	17 : 35	67	68	23 : 27	54
EAH	83	7 : 2	22	158	7 : 0	0
FA	22	0 : 49	100	66	0 : 38	100
FB	51 + 61	128 : 133	51	63	8 : 12	60
FC	56	9 : 129	94	72	0 : 45	100
FD	53	9 : 7	44	112	0 : 53	100
FF	59	8 : 72	90	67	0 : 25	100
FG	114	13 : 32	71	163	9 : 12	57
JB	46	105 : 148	58	128	20 : 25	56
JD	45	40 : 54	57	65	19 : 18	49
KA	38	1 : 24	96	80	0 : 20	100
U	17	0 : 12	100	48	0 : 56	100

* Brood 25—error in Howard (1940).

† Brood 95—female DB?

produced broods with similar sex ratios in both years. Of these fifteen females, six were amphogenics—females BD, BG, FB, FG, JB and JD; three were arrhenogenics—females BK, CD and EAH; and six were

thelygenics—females CBJ, FA, FC, FF, KA and U. Females AF and DE also probably show no changes. Five females, however, do appear to have broods in the second year which have different sex ratios from those found in the first year. In one case—female DB—there is a small possibility of a clerical mistake in recording whether brood 95 did come from this female. Female AJ produced broods containing 88 and 0% of females in the first and second years respectively, and female AB (a sister of female AJ) broods containing 31 and 2% of females in first and second years respectively. It is interesting to note that the change is for a female to become more arrhenogenic as she grows older (cf. Vandel's results). Female BN, however, appears to be more thelygenic in her second year than in her first, and female FD also changes from an amphogenic in her first year to a thelygenic in her second. Thus the results in Table 4 suggest that, while most females do not change with age in the types of broods which they produce, there are others which have broods with different sex ratios in successive years.

In *Trichoniscus* Vandel (1938) found females which produced some broods showing thelygenic characteristics and other broods showing arrhenogenic characteristics. Such females are called allelogenics by Vandel.

III. THE INHERITANCE OF MONOGENY AND AMPHOGENY

As has been previously stated, the male parent does not appear to have any effect on the constitution of a brood. In giving the results in this part of the present paper, therefore, the male parent of the various broods is not given in the tables. The male parent might, however, affect the type of daughters produced. The data on the inheritance of monogeny and amphogeny so far obtained are of no use for considering this suggestion. In discussing the results it is convenient to classify broods in the way shown below:

Constitution of brood		Type of female
More than 85% females;	less than 15% males	Strong thelygenic
85–60% females;	15–40% males	Weak thelygenic
60–40% females;	40–60% males	Amphogenic
40–15% females;	60–85% males	Weak arrhenogenic
Less than 15% females;	more than 85% males	Strong arrhenogenic

In the tables the following nomenclature is used: *F* for strong thelygenic, (*F*) for weak thelygenic, *A* for amphogenic, (*M*) for weak arrhenogenic and *M* for strong arrhenogenic.

It must also be remembered that the percentage of one sex in a brood as given in the tables has a large standard error; thus the standard error for an amphogenic brood of forty animals is about 8% and for a brood of eighty animals about 5·6%. Similarly, the following broods do not differ significantly from being amphogenics ($P = 0{\cdot}05$ level), 8:2, 14:6, 20:10, 26:14, 31:19 and 59:41.

(1) *Descendants of thelygenic female A*

Female A was a thelygenic female obtained in a collection—she produced only one brood which consisted of 1 ♂ : 36 ♀♀. As is shown in Table 5, however, not one of her twelve daughters was a strong thely-

Table 5. *Descendants of female A*

Female A × male B produced brood 1 (1 ♂ : 36 ♀♀; animals BA to BV)

Female	No. of brood	Constitution of brood ♂♂ : ♀♀	% ♀♀	s %	Type of female
BC	27	36 : 17	32	±6·4	(*M*)
BD	28 + 90	38 : 67	64	±3·8	(*F*)
BF	94	23 : 3	12	±6·4	*M*
BG	31 + 32 + 122	16 : 20	56	±8·3	*A*
BH	96	63 : 3	5	±2·7	*M*
BK	33 + 118	50 : 0	0	± —	*M*
BM	60	39 : 44	53	±5·5	*A*
BN	34 + 127	60 : 35	37	±5·0	(*M*)
BO	39	22 : 14	39	±8·1	(*M*)
BP	109	13 : 18	58	±8·9	*A*
BQ	99	6 : 25	81	±7·0	(*F*)
BV	101	43 : 24	36	±6·0	(*M*)

I.e. female A produced 2 weak thelygenic, 3 amphogenic, 4 weak arrhenogenic and 3 strong arrhenogenic daughters.

genic; three of her daughters (BF, BH and BK) were strong arrhenogenics, four (BC, BN, BO and BV) were weak arrhenogenics, three (BG, BM and BP) were amphogenics and two (BD and BQ) were weak thelygenics. These results do not support any simple scheme of cytoplasmic inheritance of monogeny, and it was these results which suggested the genetic scheme given in Table XII of Howard (1940).

(2) *Descendants of thelygenic females CB and CC*

As is shown in Tables 6 and 7, the two strong thelygenic females CB and CC were both members of the same brood; while another female of this brood, female CD, was a strong arrhenogenic. The sons of female CD were mated with the daughters of females CB and CC—thus the granddaughters of females CB and CC (females EF, EG, GD to GJ and FL) are to a certain extent inbred.

Of the sixteen daughters of females CB and CC, nine were strong thelygenics, four weak thelygenics, one an amphogenic, one a weak arrhenogenic and one a strong arrhenogenic. Thelygeny does in this case, therefore, appear to be handed on by a female to a majority of her daughters. Two types of granddaughters of females CB and CC were examined—the daughters of strong thelygenic broods and the daughters of other types of broods. Of the seven daughters of strong thelygenic females, five were strong thelygenics, one an amphogenic and one an arrhenogenic (females EF, EG and GD to GH). Of the females from other than strong thelygenic broods (females HK to HM and FL), one was a weak thelygenic, one an amphogenic and two weak arrhenogenics. It is unfortunate that more broods were not obtained from similar females. Nevertheless, the results do confirm the suggestion that in the

descendants of females CB and CC thelygenic females do produce a majority of thelygenic daughters, and they do also suggest that the

Table 6. *Descendants of females CB and CC*

♀ E × ? ♂ produced brood 4 (1 ♂ : 4 ♀♀; animals CA to CD).
♀ CB × ♂ AL produced brood 29 (1 ♂ : 37 ♀♀; animals CBA to CBK).
♀ CC × ♂ AL produced brood 30 (0 ♂ : 25 ♀♀; animals CCA to CCJ).
♀ CD × ♂ AL produced brood 35 (64 ♂♂ : 0 ♀; animals CDA to CDG).

Female	No. of brood	Constitution of brood ♂♂ : ♀♀	% ♀♀	s %	Type of female
CBA	87	1 : 40	98	± 2·2	*F*
CBB	116 + 130	16 : 51	76	± 5·1	(*F*)
CBC	93	38 : 76	67	± 4·4	(*F*)
CBD	123	7 : 0	0	± —	*M*
CBE	110	2 : 10	83	± 10·9	(*F*)
CBG	107	0 : 7	100	± —	*F*
CBJ	88 + 167	3 : 39	92	± 4·2	*F*
CBK	106	2 : 22	92	± 5·5	*F*

I.e. 4 strong thelygenics, 3 weak thelygenics, and 1 strong arrhenogenic.

CCA	120	1 : 36	98	± 2·3	*F*
CCC	87	0 : 22	100	± —	*F*
CCD	102 + 132	1 : 89	99	± 1·0	*F*
CCE	104	0 : 12	100	± —	*F*
CCF	115	18 : 9	33	± 9·4	(*M*)
CCG	103	12 : 28	70	± 7·3	(*F*)
CCH	117 + 129	38 : 44	54	± 4·9	*A*
CCJ	89	3 : 23	88	± 6·4	*F*

I.e. 5 strong thelygenics, 1 weak thelygenic, 1 amphogenic and 1 weak arrhenogenic.

Total: 9 strong thelygenics, 4 weak thelygenics, 1 amphogenic, 1 weak arrhenogenic and 1 strong arrhenogenic.

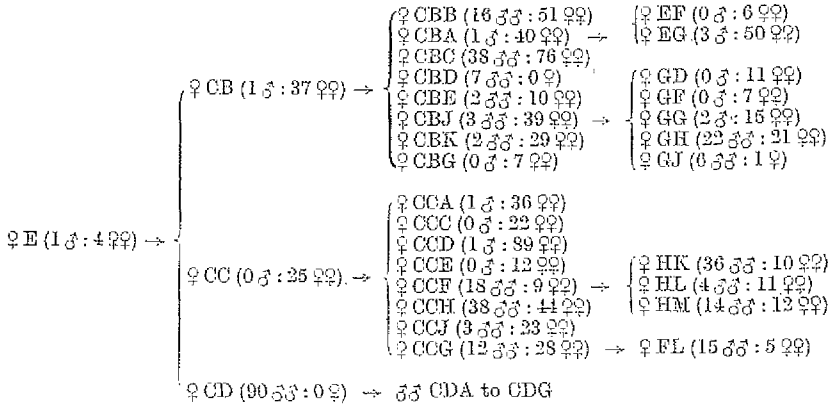
♀ CBA × ♂ CDE produced brood 87 (1 ♂ : 40 ♀♀; animals EC to EK).
♀ CBJ × ♂ CDG produced brood 88 (1 ♂ : 32 ♀♀; animals GC to GM).
♀ CCF × ♂ CDD produced brood 115 (18 ♂♂ : 9 ♀♀; animals HJ to HM).
♀ CCG × ♂ CDB produced brood 103 (12 ♂♂ : 28 ♀♀; animals FH to FL).

Female	No. of brood	Constitution of brood ♂♂ : ♀♀	% ♀♀	s %	Type of female
EF	148	0 : 6	100	± —	*F*
EG	155	3 : 50	94	± 3·3	*F*
GD	150	0 : 11	100	± —	*F*
GF	160	0 : 7	100	± —	*F*
GG	154	2 : 15	88	± 7·9	*F*
GH	100	22 : 21	49	± 7·5	*A*
GJ	168	6 : 1	14	± 13·2	*M*
HK	165	36 : 10	22	± 6·1	(*M*)
HL	164	4 : 11	73	± 11·4	(*F*)
HM	169	14 : 12	46	± 9·8	*A*
FL	149	15 : 5	25	± 9·7	(*M*)

I.e. thelygenic ♀ CBA produced 2 thelygenic daughters; thelygenic ♀ CBJ produced 3 thelygenic, 1 amphogenic and 1 arrhenogenic daughters; weak arrhenogenic ♀ CCF produced 1 weak arrhenogenic, 1 amphogenic and 1 weak thelygenic daughters; and weak thelygenic ♀ CCG produced 1 weak arrhenogenic daughter.

non-strong thelygenic daughters of thelygenic females differ genetically from the strong thelygenic daughters. Thus not one of the daughters of a non-strong thelygenic female is a strong thelygenic.

Table 7. *Descendants of females CB and CC (see also Table 6)*



(3) *Descendants of thelygenic female DA*

Of the eight daughters of the strong thelygenic female DA, seven are strong thelygenics and one a weak thelygenic (see Table 8). Also of the four daughters of the strong thelygenic female DAF (herself a daughter of female DA), three are strong thelygenics and one an amphogenic. These results certainly suggest that thelygeny is transmitted by a female to nearly all her daughters either in the cytoplasm or in the Y-chromosome.

Table 8. *Descendants of female DA*

♀ DA × ♂ SB produced brood 47 (0♂ : 30 ♀♀; animals DAA to DAH).
♀ DAF × ♂ DBB produced brood 74 (2♂♂ : 42 ♀♀; animals DF to DN).

Female parent	No. of brood	Constitution of brood ♂♂ : ♀♀	% ♀♀	s %	Type of female
DAA	81	0 : 13	100	± —	*F*
DAB	108	3 : 78	96	±2·2	*F*
DAC	91	0 : 31	100	± —	*F*
DAD	126	7 : 49	88	±4·4	*F*
DAE	92	0 : 21	100	± —	*F*
DAF	74	2 : 42	95	±3·2	*F*
DAG	98	11 : 23	68	±8·2	(*F*)
DAH	125	0 : 29	100	± —	*F*
DH	156	8 : 6	43	±13·2	*A*
DK	151	0 : 83	100	± —	*F*
DM	159	0 : 16	100	± —	*F*
DN	161	0 : 15	100	± —	*F*

(4) *Descendants of arrhenogenic female AB*

The strong arrhenogenic female AB was a daughter of female C (a weak thelygenic female; 7 ♂♂ : 14 ♀♀). Also daughters of female C (see Table 9) were female AF (a weak thelygenic), female AJ (a strong thelygenic in one year and a strong arrhenogenic in the next, see Table 4) and female CE (a strong thelygenic). Female AB also appears to become more arrhenogenic as she grows older, see Table 4.

Of the six daughters of female AB, three are strong arrhenogenics, one an amphogenic and two strong thelygenics (see Table 9). Thus a strong arrhenogenic female produces mainly strong monogenic daughters,

but these monogenic daughters include both strong thelygenics and strong arrhenogenics.

As has been previously mentioned, Vandel (1938) found that in *Trichoniscus* thelygenic females often produced mainly arrhenogenic

Table 9. *Descendants of female AB*

♀ C × ?♂ produced brood 2 (4 ♂♂ : 9 ♀♀; animals AB to AN).
♀ C × ♂ B produced brood 7 (3 ♂♂ : 5 ♀♀; animals CE to CH).
♀ AB × ♂ B produced brood 8 (22 ♂♂ : 9 ♀♀; animals KC to KO).
♀ AB × ♂ AM produced brood 25 (40 ♂♂ : 1 ♀; animals ZA and ZB).

Female parent	No. of brood	Constitution of brood ♂♂ : ♀♀	% ♀♀	s %	Type of female
AB	8 + 25	62 : 10	14	±4·1	*M*
AF	10 + 49	19 : 46	71	±5·6	(*F*)
AJ*	26 + 44 + 69	17 : 57	77	±4·9	(*F*)
CE	43	4 : 39	91	±4·9	*F*
KE	79	20 : 2	9	±6·1	*M*
KH	77	11 : 0	0	± —	*M*
KJ	133	14 : 0	0	± —	*M*
KM	71	0 : 15	100	± —	*F*
KO†	64	11 : 15	58	±9·7	*A*
ZB	124	1 : 8	89	±9·9	*F*

* ♀ AJ—see Table 4, particularly brood 69 (9 ♂♂ : 0 ♀).
† ♀ KO—brood 64, male parent was a French animal.
Of the 6 daughters of female AB, 3 were strong arrhenogenics, 1 an amphogenic and 2 strong thelygenics.

daughters. This change from one type of monogeny to the other is very hard to explain. It may, however, be of importance to note that it can also take place in the same female, e.g. female AJ above.

(5) *Descendants of amphogenic female EA*

Brood 24 (46 ♂♂ : 47 ♀♀) from female EA was chosen for inbreeding in an attempt to obtain lines breeding true for amphogeny. It was found, however (see Table 10), that brood 24 females were either arrheno-

Table 10. *Descendants of female EA*

♀ EA × ♂ SB produced brood 24 (46 ♂♂ : 47 ♀♀; animals EAA to EAP).
♀ EAF × ♂ EAE produced brood 73 (4 ♂♂ : 17 ♀♀; animals AP to AR).

Female parent	No. of brood	Constitution of brood ♂♂ : ♀♀	% ♀♀	s %	Type of female
EAB	85	5 : 0	0	± —	*M*
EAF	73	4 : 17	81	±8·6	(*F*)
EAG	70	0 : 16	100	± —	*F*
EAH	83 + 158	14 : 2	13	±8·4	*M*
AP*	134	0 : 28	100	—	*F*
AR	136	0 : 10	100	—	*F*

* ♀ AP was a white mutant female.

genics or thelygenics. It was also found that two daughters of one of the brood 24 thelygenic females were strong thelygenics. There is thus no doubt that the apparently amphogenic female EA produced daughters which were genetically monogenic. One possible explanation of this result is that female EA, although an amphogenic herself, was a daughter of a monogenic female (cf. the results of Rhoades (1933) on male sterility

in maize; these results are discussed later in this paper). Vandel (1938) also describes a type of female which he calls a mixt. Mixts produce amphogenic broods but are the descendants of monogenic females and themselves produce monogenic daughters.

(6) *Descendants of amphogenic female FB*

Descendants of the amphogenic female FB have been inbred in a second attempt to obtain lines breeding true for amphogeny. The results are shown in Table 11. It is unfortunate that the broods from the

Table 11. *Descendants of female FB*

♀ FB × ?♂ SB produced brood 51 (94 ♂♂ : 101 ♀♀).
♀ FB, no ♂ since brood 51, produced brood 61 (34 ♂♂ : 32 ♀♀).
♀ FB, no ♂ since brood 51, produced brood 63 (8 ♂♂ : 12 ♀♀).
Total: 136 ♂♂ : 145 ♀♀.

Female parent	Male parent	Constitution of brood ♂♂ : ♀♀	No. of brood
FBB	FBA	3 : 3	135
FBD	FBD	10 : 8	137
FBE	FBC	5 : 6	138
FBF	FBC	0 : 2	139*
FBG	FBA	6 : 5	140*
FBH	FBA	6 : 9	141*
FBK	FBJ	2 : 1	144
FBL	FBJ	10 : 15	142
FBM	FBJ	7 : 7	143
	Total	49 : 56	

Animals FBA to FBM were all members of brood 63.
* Broods 139, 140 and 141, which were all from black females × black males, showed segregations for black *v.* white body colour. It thus seems that either female FB or the male parent of brood 63 was heterozygous for recessive genes for white body colour.

brood 63 females are so small. There is, however, some indication that all the daughters of the amphogenic female FB might be amphogenics. If female FB and her daughters are true amphogenics, it is interesting to note that there may be a small excess of females, the supposed heterozygous sex, over males in amphogenic broods.

(7) *Summary and discussion*

The results given in §§ 1–6 of Part III of this paper may be more or less summarized as:

(*a*) ♀ A (strong thelygenic) → $2\,(F)+3\,A+4\,(M)+3\,M$;
(*b*) ♀ CB and ♀ CC (strong thelygenics) → $9\,F+4\,(F)+1\,A+1\,(M)+1\,M$;
♀ CBA and ♀ CBJ (strong thelygenics) → $5\,F+1\,A+1\,M$;
(*c*) ♀ DA and ♀ DAF (strong thelygenics) → $10\,F+1\,(F)+1\,A$;
(*d*) ♀ AB (strong arrhenogenic) → $3\,M+1\,A+2\,F$;
(*e*) ♀ EA (amphogenic) → $1\,F+1\,(F)+2\,M$;
(*f*) ♀ FB (amphogenic) → $7\,A$;

where F = strong thelygenic, A = amphogenic and M = strong arrhenogenic, etc. Thus in two cases, (*b*) and (*e*), the results do suggest that a thelygenic female produces mainly thelygenic daughters and in another

case, (*f*), that an amphogenic female produces mainly amphogenic daughters. Such results would be expected if the inheritance of thelygeny and amphogeny was cytoplasmic (or if due to factors in the *Y*-chromosome). The other cases, particularly (*a*), appear at first sight to disprove the hypothesis of cytoplasmic inheritance of monogeny and amphogeny. However, if we examine the data of Rhoades (1933) on the inheritance of male-sterility in maize—this is one of the most thoroughly investigated cases of cytoplasmic inheritance—we see that the irregularities in the *Armadillidium* results would not be unexpected if the inheritance of monogeny and amphogeny was cytoplasmic. Thus Rhoades found that, of eleven cultures from backcrosses of male-sterile individuals with unrelated normal lines, six cultures contained male steriles only and five cultures both male steriles and normals. Also when normal plants from these mixed cultures were bred from they produced some cultures containing male steriles only, other cultures containing both normals and male steriles and others containing normal plants only.

On the other hand, it must be recognized that the results given in this paper do not prove that amphogeny and monogeny are inherited cytoplasmically in *Armadillidium*. Considerable further work is obviously required on this rather difficult problem. One of the best lines of attack would appear to be to test whether the male parent has any effect on the type of daughters produced. Before this can be done, however, it is necessary to have lines which are breeding more or less true for amphogeny and monogeny.

IV. THE EFFECT OF MONOGENY ON THE COMPOSITION OF NATURAL POPULATIONS

(1) *Monogeny as an outbreeding mechanism*

One effect of monogeny is that it restricts inbreeding; thus, brother-sister mating cannot take place in a thelygenic brood since such broods contain no males. Also the daughters of a thelygenic female have no male cousins on the maternal side if thelygenic females always produce thelygenics and are themselves produced only by thelygenics. Monogeny is thus an outbreeding mechanism analogous to those found in the higher plants and fungi (Mather, 1940, 1942). It is of interest to note in this connexion that natural populations of *Armadillidium* do contain recognizably different genetical types in quite high percentages (see Table XIII of Howard, 1940). These include the dominant red form and two dominant sex-limited forms, types C and D. Recessive genes are also apparently present in the heterozygous condition—some evidence has been obtained for two recessives for white body colour (the ratios for black : white in families 139, 140 and 141 of Table 11 appear to be 9 : 7 and not 3 : 1) and also of another for yellow body colour.

An *Armadillidium* population containing only thelygenic and amphogenic females and males resembles to a certain extent the gynodioecious

species of flowering plants (see Lewis, 1941) in which the male-sterile plants must be pollinated by the hermaphrodites while the hermaphrodites may be either selfed or pollinated by other hermaphrodites.

Table 12

(1) Drosophila.
  (*a*) Normal males: $XY \rightarrow 50\,\%$ X sperms $+ 50\,\%$ Y sperms.
  (*b*) Sex-ratio males: $X^F Y \rightarrow 100\,\%$ X^F sperms.

(2) Armadillidium (*gene for thelygeny on Y-chromosome*).
  (*a*) Amphogenic females: $XY \rightarrow 50\,\%$ X eggs $+ 50\,\%$ Y eggs.
  (*b*) Thelygenic females: $XY^F \rightarrow 100\,\%$ Y^F eggs.

(3) Armadillidium (*cytoplasmic determination of thelygeny*).
  (*a*) Amphogenic females: $C^N(XY) \rightarrow \begin{cases} 50\,\% \; C^N(X) \text{ eggs} \rightarrow \text{males.} \\ 50\,\% \; C^N(Y) \text{ eggs} \rightarrow \text{females.} \end{cases}$
  (*b*) Thelygenic females: $C^F(XY) \rightarrow 100\,\%$ $C^F(Y)$ eggs $\rightarrow$ females.
  $50\,\%$ of the C^N cytoplasm will be lost since the sperms from the males carry no cytoplasm. No C^F cytoplasm will be lost in this way since the thelygenic females produce no males.

(4) *Gynodioecious species of flowering plant* (*cytoplasmic determination of male sterility*).
  (*a*) Hermaphrodites: $C^N(AA) \rightarrow 100\,\%$ ovules $C^N(A)$.
  (*b*) Male steriles: $C^F(AA) \rightarrow 100\,\%$ ovules $C^F(A)$.

For full description, see text.

Similarly, all the daughters of thelygenic females have to mate with males from amphogenic broods while the daughters of amphogenic females may mate with either their brothers or with males from other amphogenic broods.

(2) *The effect of monogeny on sex ratios in natural populations*

Monogeny, particularly thelygeny, may have a very large effect on the sex ratio in natural populations. Thus if we consider the simple case in which thelygenic females produce only thelygenic daughters and amphogenic females only amphogenic daughters, and if in addition it is assumed that the broods from thelygenic females are of the same size as broods from amphogenics and that the daughters of thelygenics have the same viability as the daughters of amphogenics, then given random mating in a large population it is obvious that thelygenic cytoplasm (or thelygenic Y-chromosomes) will increase twice as fast as amphogenic cytoplasm (or amphogenic Y-chromosomes). This process is shown in Table 12. This means that the female population would soon consist entirely of thelygenic females and also that there would soon be no males in the population. The sex-ratio case in *Drosophila* (see Dobzhansky, 1939, p. 365) has a similar effect on the constitution of a population. This case is also shown briefly in Table 12. In a gynodioecious species of flowering plant, however, given equal seed production by the male steriles and hermaphrodites, the rate of increase of male-sterile cytoplasm is equal to that of normal cytoplasm (see Table 12). Also as pointed out by Lewis (1941), the percentage of male steriles will cease to increase when their higher viability (due to outbreeding) is countered by their reduced reproduction rate due to a shortage of pollen (it is

assumed that the hermaphrodites will be more efficiently pollinated than the male steriles under such conditions). Similar conditions, i.e. a shortage of males, are not likely to produce the same effect in animals—there is no reason for believing that in woodlice a male would tend to mate more often with amphogenic females than with thelygenics.

In *Armadillidium* and in *Trichoniscus*, however, the situation is not so simple as we have so far suggested in this discussion. Thus in *Armadillidium* thelygenic females do not produce all thelygenic daughters, and in *Trichoniscus* thelygenic females produce about one-half thelygenic daughters and one-half arrhenogenic daughters. The effects of these complications on the constitution of populations are considered below.

(3) *Possible stable types of populations*

The first type of population considered is that in which amphogenic females produce only amphogenic daughters and in which thelygenic females produce one-half arrhenogenic and one-half thelygenic daughters. It is shown in Table 13 that such a population is stable. Such populations

Table 13

(*a*) *Amphogenics, thelygenics and arrhenogenics.*

Amphogenic females produce 50 % males + 50 % females.
Thelygenic females produce 50 % thelygenics + 50 % arrhenogenics.

Such a population is stable as is shown below:

30 amphogenic females ⟷ 30 amphogenic females, 30 males
50 males
10 arrhenogenic females ⟶ 20 males
10 thelygenic females ⟷ 10 arrhenogenic females, 10 thelygenic females

(*b*) *Thelygenics and arrhenogenics. No amphogenics.*

Thelygenic females produce 50 % thelygenics + 50 % arrhenogenics.

Such a population is also stable:

50 males
25 arrhenogenic females ⟶ 50 males
25 thelygenic females ⟷ 25 arrhenogenic females, 25 thelygenic females

do appear to occur in *Trichoniscus*. Thus Vandel (1938) found that of eighty-eight monogenic females obtained from collections forty-one were arrhenogenics and thirty-two thelygenics (the other fifteen animals consisted of thirteen allelogenics and two mixts). Also of fifty-two daughters of perfect thelygenic females twenty-seven were arrhenogenics and sixteen thelygenics (the other nine were allelogenics and mixts). As is shown in part (*b*) of Table 13 it is also possible to imagine a population in which there are no amphogenic females. Vandel did find populations with under 50 % of the females of the amphogenic type. Moreover, *Sciara coprophila* is an example of an animal which has no amphogenic females but only 50 % of thelygenics and 50 % of arrhenogenics. In this animal also (Metz, 1938) thelygenics do produce 50 % thelygenic and 50 % arrhenogenic daughters. In *Trichoniscus*, however, Vandel (1938) found that all the daughters of one thelygenic female might be thelygenics while all the

daughters of another might be arrhenogenics. Thelygenic females producing one-half thelygenics and one-half arrhenogenic daughters were not found.

The second type of population to be considered is that in which amphogenic females produce only amphogenic daughters and in which thelygenic females produce some thelygenic and some amphogenic daughters. This case is considered in Table 14. As can be seen from this

Table 14

Assumptions

(*a*) Amphogenics produce 50 % males + 50 % amphogenic females.
(*b*) Thelygenics produce p thelygenic females : $q = (1-p)$ amphogenic females.
(*c*) Amphogenic and thelygenic broods are of the same size, i.e. thelygenic broods contain twice as many females as amphogenic broods.
(*d*) The offspring of amphogenic and thelygenic females have equal viabilities.

Then, if a population contains F thelygenic and $1-F$ amphogenic females, for equilibrium conditions between amphogenic and thelygenic females

$$\frac{1-F+2(1-p)F}{1-F} = \frac{2pF}{F},$$

from which we find that $$p = \frac{1+F}{2}.$$

Also such a population will contain $1-F$ males and $1-F+2(1-p)F+2pF$ females.

Hence the ratio $\frac{\text{females}}{\text{total animals}} = \frac{1+F}{2}$.

Females		Values of		Population
% amphogenics	% thelygenics	$1-p$	p	% females/total animals
100	0	0·50	0·50	50
90	10	0·45	0·55	55
80	20	0·40	0·60	60
70	30	0·35	0·65	65
60	40	0·30	0·70	70
50	50	0·25	0·75	75
40	60	0·20	0·80	80
30	70	0·15	0·85	85
20	80	0·10	0·90	90
10	90	0·05	0·95	95
0	100	0·00	1·00	100

table a whole range of stable populations are possible depending upon the proportion of amphogenic daughters produced by thelygenic females. The application of these results to *Armadillidium* populations is considered in the next section.

(4) Armadillidium *populations*

It can be seen from Table 15 that about one-half of the females from collections are amphogenics and one-half thelygenics. These females, however, are not a random sample but were in many cases chosen because they showed different colour types. It can also be seen from Table 15 that no arrhenogenic females occurred. According to Table 14 a population containing 50 % of thelygenic females would be expected to have about 75 % of females, and the thelygenic females in such a population would be expected to produce 3 thelygenic : 1 amphogenic daughters (assuming that the population is a stable one). The percentages of females in a number of populations are given in Table 16. Most of the females

in Table 15 came from collections A–D. These four collections have a mean percentage of females of about 74%. Of the thelygenic females considered in Part III of this paper, females E and DA came from these

Table 15. *Females from collections*

Description of female	Name of female	No. of brood	Constitution of brood ♂♂ : ♀♀	Type of female
Black, type B	C	2	4 : 9	*A*
,, ,,	EA	24	46 : 47	*A*
,, ,,	FA	22+66	0 : 87	*F*
,, ,,	FB	51+61+63	136 : 154	*A*
,, ,,	FC	52+62	9 : 174	*F*
,, ,,	FD	(see Table 4)		?
,, ,,	H	20	23 : 29	*A*
,, ,,	KA	38+80	1 : 44	*F*
,, ,,	U	17+48	0 : 68	*F*
,, ,,	V	52	39 : 41	*A*
Red, type B	A	1	1 : 36	*F*
,, ,,	JB	46+128	125 : 173	*A*
,, ,,	JD	45+65	59 : 72	*A*
Black, type C	FE*	58	1 : 62	*F*
,, ,,	FF	59+67	8 : 97	*F*
,, ,,	GA	37	0 : 13	*F*
,, ,,	JC	42	22 : 14	*A*
Black, type D	DA	47	0 : 30	*F*
,, ,,	DB	(see Table 4)		?
,, ,,	DD	50	5 : 8	*A*
,, ,,	DE	54+68	40 : 62	*A*
Yellow	FG†	114+163	22 : 44	*A*

I.e. 11 amphogenics and 9 thelygenics (also ♀ FD and ♀ DB).
* ♀ FE was homozygous for type C.
† ♀ FG—the yellow in this case might be a modified type D.

Table 16. *Sex ratios in wild populations*

Collection no.	Place of collection	Constitution of collection ♂♂ : ♀♀	% ♀♀
A	First wood on Gogs	22 : 81	78
B	Trumpington	17 : 31	65
C	Far wood on Gogs	14 : 79	85
D	Madingley	11 : 25	69
E	Fen Ditton	24 : 34	59
F	University farm	19 : 23	55
10	Worsted lodge	11 : 21	66
11	First wood on Gogs	4 : 13	77
12	First wood on Gogs	10 : 19	66
14	Fleam Dyke	23 : 20	47
15	Fulbourn	28 : 53	65
16	University Farm	14 : 16	53
17	Botanic Gardens	8 : 9	53
18	Wendens Ambo	11 : 15	58
19	Wendens Ambo	69 : 43	38
20	Wendens Ambo	84 : 61	42
21	Wendens Ambo	14 : 20	59
22	Abington	31 : 48	61
23	University Farm	7 : 20	74

four populations while female B came from a population not given in Table 16. It is thus of some interest to note that of the twenty-four daughters of the thelygenic females CB, CC and DA, sixteen were strong thelygenics.

It will also be noted that only three of the populations in Table 16 show an excess of males and in only two of these is there a large excess.

These figures for *Armadillidium* populations are not very satisfactory and the assumptions made in the calculations in Table 14 are also known to be only partially true—thus no account has been taken of arrhenogenic females or of amphogenic females which produce thelygenic daughters. Nevertheless, they do give some idea of the equilibrium conditions in such populations. The calculations also show the significance of thelygenic females not breeding absolutely true for thelygeny.

The small percentages of males in some populations suggests the importance of knowing how many females a single male can impregnate in one year. Under laboratory conditions this has been found to be at least three or four. It also appears that a single impregnation gives a female enough sperms for producing broods in two years.

V. Summary

1. Three types of female are found in the woodlouse *Armadillidium vulgare*—amphogenics which produce broods consisting of 50% males +50% females, thelygenics which produce broods consisting nearly entirely of females, and arrhenogenics which produce broods consisting nearly entirely of males.

2. Monogeny (thelygeny and arrhenogeny) is explained on Vandel's hypothesis. Assuming that the females are the heterozygous sex (chromosomes XY), it is suggested that in monogenics segregation of the sex chromosomes into the eggs and polar bodies is not random—all the eggs of a thelygenic female receive a Y-chromosome and all the eggs of an arrhenogenic female an X-chromosome.

3. Genetical ratios show that normal segregation of the autosomes takes place in the eggs of monogenic females and that the eggs of such females do not develop parthenogenetically.

4. In most cases different broods from the same female have similar sex ratios.

5. The inheritance of monogeny and amphogeny was studied in the descendants of four thelygenic females (two of them were sisters), of one arrhenogenic female and of two amphogenic females. The results support to a certain extent the suggestion that monogeny and amphogeny are inherited cytoplasmically (or in the Y-chromosome). A thelygenic female may, however, produce amphogenic daughters and an amphogenic female thelygenic daughters.

6. The effect of monogeny on the composition of natural populations is considered. It is shown that thelygeny may have a large effect on the sex ratios in populations. Most *Armadillidium* populations contain more than 50% females and of these females about 50% are amphogenics and 50% thelygenics.

REFERENCES

DOBZHANSKY, T. (1939). Experimental studies on genetics of free-living populations of *Drosophila*. *Biol. Rev.* **14**, 333–68.

HOWARD, H. W. (1940). The genetics of *Armadillidium vulgare* Latr. I. A general survey of the problems. *J. Genet.* **40**, 83–108.

LEWIS, D. (1941). Male sterility in natural populations of hermaphrodite plants. The equilibrium between females and hermaphrodites to be expected with different types of inheritance. *New Phytol.* **40**, 56–63.

MATHER, K. (1940). Outbreeding and separation of the sexes. *Nature, Lond.*, **145**, 484–87.

MATHER, K. (1942). Heterothally as an outbreeding mechanism in fungi. *Nature, Lond.*, **149**, 54–6.

METZ, C. W. (1938). Chromosome behaviour, inheritance, and sex determination in *Sciara*. *Amer. Nat.* **72**, 485–520.

RHOADES, M. M. (1933). The cytoplasmic inheritance of male sterility in *Zea Mays*. *J. Genet.* **27**, 71–93.

VANDEL, A. (1938). Recherches sur la sexualité des isopodes. III. Le déterminisme du sexe et de la monogénie chez *Trichoniscus* (*Spiloniscus*) *provisorius* Racovitza. *Bull. biol.* **72**, 147–68.

VANDEL, A. (1939). Sur le mode de répartition des sexes chez l'isopode terrestre, *Armadillidium vulgare* (Latr.). *C.R. Acad. Sci., Paris*, **208**, 1050–52.

VANDEL, A. (1941). The genetics of sexuality in terrestrial isopods. *Proc. 7th Int. Gen. Congr. Edinb.* pp. 306–7, August 1939.