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“STICK” AND “MULTILUNAR,” A FOURTH LINKAGE GROUP IN THE SILKWORM¹

Yoshimaro TANAKA and Seichi MATSUNO

I. ORIGIN OF “STICK”

Among 121 larvae in a lot, No.193 p95-1, reared in the third season 1919, 10 caterpillars were found to be abnormal. They had rather small and slender body, exceedingly stiff in touch. The pedigree of this family had been exactly known for more than twelve generations, each generation being subjected to minute observation, and no similar occurrence in any previous generation was recorded. The pedigree is given in the Table 1.

Table 1

131x9 (Japanese bivoltine, 4m, marking pale quail, cocoon white, eggs purple)	131M14-1 (Chinese univoltine, 3m, marking plain, cocoon yellow, eggs blue)
141A11	141M37
142A22	
151A99	151A17
♀	♂

¹ Contributions from the Sericultural Laboratory, Kyushu Imperial University, No. 9. The experiments were made at the Fukushima Branch of the Imperial Sericultural Experiment Station up to 1922, since then at our university.

152A382	plain, yellow, 3m.	(1)
161A316	plain, yellow and white, 3m.	(1)
162p6	plain, yellow, 3m.	(3)
171p95-1	plain, yellow, 3m.	(4)
172p95-1	plain, yellow	(5)
181p95-1	" "	(12)
182p95-1	" "	(8)
191p95-1	plain and pale quail, yellow.	(7)
192p95-1	" " "	(12)
193p95-1	plain and pale quail, yellow.	(9)
<div style="display: flex; justify-content: center; align-items: center; gap: 20px;"> <div style="text-align: center;"> <div style="border-top: 1px solid black; width: 100px; margin: 0 auto;"></div> <div style="display: flex; justify-content: space-around; width: 100px;"> Normal Abnormal </div> <div style="display: flex; justify-content: space-around; width: 100px;"> III IO </div> </div> </div>		

Legends:

The figures enclosed in parentheses represent the numbers of egg-batches, the larvae from which were reared in the same lot.

"4m" or "3m" means passing through four or three molts respectively before spinning ("mounting").

The mutants were mated among themselves, and bred true for more than sixteen generations up to the present year. The new strain was named "stick," and has been kept homozygous for the plain marking and the yellow cocoon color. As to the molting character, it has not yet been fixed, but segregates a small percentage of "four-molters," while most of the larvae spin cocoons after three molts, i. e. "three-molters." In order to avoid unfavorable effects, if anything, due to intensive inbreeding, we are keeping the strain in "mixed culture" or rearing the offspring from more than two different mothers, phenotypically alike, in the same lot.

The normals of the lot 193p95-1 were also mated inter se, which segregated in mixed cultures a small numbers of "stick" in F_1 , F_2 and F_3 . After F_4 generation no "stick" has appeared in this strain up to F_{11} , when it was discarded.

II. DESCRIPTION OF "STICK" (Plate 2, Figs. 4-6)

The stick silkworm is small and thin in the body-form, and as hard to the touch as a piece of wood. It bends the body apparently with difficulty. Its body-weight, the silk-weight of the cocoon as well as the egg-size are much inferior to the normal as shown in the following tables.

Table 2

Average live weight on the sixth day of the last instar. (Unit gram.)

Lot No.	Larval characteristics	Average individual weight in gram			
		Normal female	Normal male	Stick female	Stick male
21ah8-2	pY,3m	2.054 (50) ²	1.552 (50)	1.352 (25)	1.112 (25)
21ah8-3	pY,py,3m	2.034 (50)	1.576 (50)	1.378 (18)	1.115 (20)
21ah8-5	pY,py,3m	1.950 (50)	1.588 (40)	1.250 (9)	0.984 (16)
21ah8-9	pY,3m	1.885(100)	1.445 (70)	1.350 (20)	1.096 (25)
Average		1.981	1.540	1.333	1.077

For the sake of comparison, the figures of the last row in the above table are shown below in percentages, the weight of the normal female being taken as 100.

Normal	Normal	Stick	Stick
♀	♂	♀	♂
100.00	77.73	67.13	54.36

The full-grown larval weight of stick male as represented in percentage of the normal male will be 69.94.

Table 3

Average pupal weight. (Unit gram.)

Weighing was performed in most cases on the tenth day after "mounting."

Lot No.	Larval characteristics	Normal	Normal	Stick	Stick
		♀	♂	♀	♂
20ah8-2	pY,3m	0.855	0.611	0.619	0.461
20bh8-2	pY,3m	0.868	0.643	0.633	0.467
20bh8-3	pY,3m	0.910	0.636	0.628	0.503
20bh8-4	pY,3m	0.811	0.627	0.559	0.463
20ch8-1	pY,4m	1.365(21)	1.027(37)	0.813(12)	0.406(18)
20ch8-3	pY,4m	1.132(23)	0.899(25)	0.780(2)	0.601(8)
20ch8-4	pY,3m	0.875(7)	0.710(45)	0.612(8)	0.516(35)
"	pY,4m	0.924(5)	0.962(33)	0.788(5)	0.708(50)
20ch8-5	pY,3m	0.751(50)	0.620(50)	0.556(46)	0.474(12)
Average		0.943	0.748	0.671	0.511

If we take the normal female as 100.

100.00	79.32	71.16	54.19
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The pupal weight of the stick male will, when represented in percentage of the normal male, be 68.31.

² The figures enclosed in parentheses are the numbers of caterpillars weighed.

Table 4

Lot No.	Molting characters	Silk weight. (Unit centigram)			
		Normal ♀	Normal ♂	Stick ♀	Stick ♂
20bh8-2	3m	8.73	8.47	6.01	5.42
20bh8-3	3m	10.51	10.90	7.10	6.45
20bh8-4	3m	9.16	8.51	5.66	5.72
2och8-1	4m	16.99	16.31	10.17	9.62
2och8-3	4m	13.00	12.70	9.90	8.50
2och8-4	3m	10.30(7)	10.11(45)	6.81(8)	5.96(35)
2och8-4	4m	10.00(5)	14.10(33)	9.20(5)	9.71(50)
2och8-5	3m	8.35(50)	8.63(50)	6.10(46)	5.94(12)
Average		10.88	11.22	7.62	7.17
Percentage		100.00	103.13	70.04	65.90

Male and female averaged, the ratio of normal and stick as to the silkweight is 100 : 66.92.

We learn from the preceding tables that "stick" is less heavy in live-weight than the normal larvae by 30 to 35%, and produces silken substance corresponding to 67% of the normal in average.

Stick grows slower and experiences some difficulty in shedding the old skin in molt. Usually a greater proportion of stick is lost during the larval life when stick and normal fed together on the same tray.

The characteristics are not striking in younger stages of the larva, and in the beginning period even in later instars, i. e. within two or three days after ecdysis. They are most easily appreciable just before a molt or before "mounting." The stick silkworm resembles "stony"³ and "constricted"³ so far as the body stiffness is concerned, but the former differs in being smooth on the body surface while the two latter have bodies segmentally constricted so that they remind us of a piece of bamboo.

III. MULTILUNAR (Plate 2, Figs. 7-9.)

This marking consists of a series of pairs of large, brown, rounded spots that develop after the first molt on the dorsal surface of the abdominal segments. As to the hereditary behavior of this marking, it has already been described by ISHIWATA and ARAKI (1902-1905), TOYAMA

³ These characters will be described elsewhere

(1908-1909), especially in detail by one of us (TANAKA 1916). But no linked gene with this marking has yet been known.

IV. NORMAL x STICK

1) F_1 generation.

This crossing was made reciprocally, ten batches of F_1 eggs hatched and were reared. All F_1 caterpillars, in a total of 2483, were normal indistinguishable from pure normals. Stick is a complete recessive to normal.

2) F_2 generation.

The F_2 larvae from different egg-batches were reared in separate lots, and counted when full-grown. The result follows:

Table 2

P	Lot No.	Normal	Stick	Totals
Normal ♀ x Stick ♂	203h813	178	60	238
"	203h814	134	34	168
"	203h815	155	44	199
"	203h816	124	51	175
"	203h817	222	60	282
"	203h818	90	27	117
"	211h824	166	53	219
"	222h826	73	34	107
"	222h261	57	33	90
Stick ♀ x Normal ♂	203h81	281	90	371
"	203h82	203	64	267
"	203h89	158	56	214
"	203h811	120	33	153
"	203h814	149	40	189
"	203h820	87	32	119
"	203h821	210	52	262
"	222h819	25	11	36
"	222h820	129	35	164
"	222h821	111	34	145
"	222h822	103	40	143
Totals		2775	883	3658
Expectation		2743.5	914.5	
Deviation		+31.5	-31.5	
Standard deviation		±26.19	±26.19	

Thus 3 : 1 ratio has evidently been realised.

3) Back-crossing.

Table 6

Mating	Lot No.	Normal	Stick	Total
F ₁ ♀ x stick ♂	202h84	102	85	187
"	203h84	191	197	388
"	203h85	201	170	371
Stick ♀ x F ₁ ♂	202h83	75	71	146
"	203h86	82	60	142
Totals		651	583	1234
Expectation		617	617	
Deviation		+ 34	- 34	
Standard deviation		± 17.57	± 17.57	

The deviation is not larger than twice the standard deviation, so that the experimental result is not inconsistent with a 1 : 1 ratio as expected.

V. LOWER PROPORTION OF SURVIVORS IN STICK

From the results mentioned above, we learn that stick is due to a simple recessive mutation which occurred in the pedigree in a stage some previous to the autumn 1919. The fact that the experimental numbers of stick always face below the theoretical expected numbers, though not far below, is not merely accidental, but is owing to the inferior viability or lesser powers of survival. This is partly due to general weakness of the mutant and partly to its retarded growth, thus making stick more likely to be lost in the course of rearing. How many sticks are lost depends on environmental conditions. If 5% of the numbers of survived sticks is added to the results given in tables 5 and 6, the ratios will come very close to the expected as follows:

Table 7

	Normal	Stick	Totals
F ₂	Actual numbers	2775	883
	Corrected numbers	2775	927
	Theoretical numbers	2776.5	925.5
	Deviation	- 1.5	+ 1.5
	Standard deviation	± 26.3	± 26.3
Back cross	Actual numbers	651	583
	Corrected numbers	651	612
	Theoretical numbers	631.5	631.5
	Deviation	+ 19.5	- 19.5
	Standard deviation	± 17.8	± 17.8

VI. SYMBOLS

The mutant stick will be represented by sk , and its normal allelomorph by Sk . That the symbols for Multilunar and its normal gene are L and l respectively is shown in a previous paper by one of us (TANAKA 1916).

VII. CROSSING-OVER VALUE

All hybrid individuals produced by crossing $L \times sk$, in a total of 1664, were Multilunar normal.

In F_2 , four possible classes, Multilunar normal ($L Sk$), Multilunar stick ($L sk$), not-Multilunar normal ($l Sk$) and not-Multilunar stick ($l sk$), have appeared in a ratio remarkably different from 9 : 3 : 3 : 1, showing evidently a linkage relation between L and sk .

Table 3

P	F_2 lot No.	$L Sk$	$L sk$	$l Sk$	$l sk$	Totals
$L \text{ } \varphi \times sk \text{ } \delta$	223s11	52	5	4	13	74
"	223s12	54	0	2	20	76
"	223s13	64	0	3	11	78
"	223s14	47	5	2	18	73
"	223s15	201	6	13	47	267
$sk \text{ } \varphi \times L \text{ } \delta$	224h831	235	23	22	61	341
"	224h832	253	21	38	52	364
"	224h833	220	18	19	38	295
"	224h834	188	19	20	46	273
"	224h835	151	14	16	36	217
"	232l441	163	12	10	32	217
"	232l442	187	15	14	35	251
"	232l443	170	14	16	33	233
"	232m44	113	14	13	28	168
Totals		2099	166	192	470	2927

The crossing-over value calculated from the preceding result is 24.47 %.

Mating double recessives and F_1 dihybrids.

$$a) \frac{l sk}{l sk} \varnothing \times \frac{L Sk}{l sk} \delta$$

Table 9

P	Lot No.	L Sk	L sk	l Sk	l sk	Total
L Sk ♀ x l sk ♂	232l411	37	24	16	37	114
"	232l412	47	23	22	35	127
"	234l413	68	26	26	60	180
"	234l414	59	31	21	58	169
"	234l415	46	20	27	39	132
"	232l416	67	19	26	53	165
"	232l417	64	16	19	43	142
"	232l418	45	15	13	47	120
"	232l419	59	16	17	48	140
"	232l420	47	13	8	34	102
"	232l421	63	32	23	73	191
"	232l422	52	23	30	55	160
"	232l423	59	14	15	46	134
"	232l424	59	12	14	55	140
"	232l425	48	23	17	33	121
sk ♀ x L ♂	233l45	68	21	34	77	200
"	233l451	23	10	18	39	90
"	233l452	69	13	20	72	174
"	233l453	55	26	32	79	192
Totals		1035	377	398	983	2793

$$b) \frac{1 \text{ sk}}{1 \text{ sk}} \text{ ♀ } \times \frac{L \text{ sk}}{1 \text{ Sk}} \text{ ♂}$$

1 Sk ♀ x L sk ♂	244l51	104	308	319	103	834
(mixed culture)						

Thus there were 982 cross-overs altogether among 3627 individuals, which correspond to 27.07% of the total. Averaging F_2 and back-cross results we get 25.77%. The differential survivorship mentioned does not affect the crossing over value at all.

$$c) \frac{L \text{ Sk}}{1 \text{ sk}} \text{ ♀ } \times \frac{1 \text{ sk}}{1 \text{ sk}} \text{ ♂}$$

The heterozygous females were tested by mating them to the double recessive males, and only two phenotypes were obtained as expected. There occurs no crossing-over in the female sex as in other cases of linkage in *Bombyx*.

Table 10

Lot No.	L Sk	L sk	l Sk	l sk	Total
242l431	131	0	0	130	261
242l432	142	0	0	129	271
242l433	184	0	0	203	387
Totals	457	0	0	462	919
Expected	459.5	0	0	459.5	

The actual numbers accord exactly with the expectation, without any correction, owing, perhaps, to favorable conditions.

VIII. SUMMARY AND CONCLUSION

a) *Stick* appeared as a simple recessive mutation in the third season culture of 1919. The family in which the mutants were discovered was F_{10} generation of a hybrid between a Japanese bivoltine white (four molts, pale-quail marking) and a Chinese univoltine yellow (three molts, plain-skinned).

b) The body of the *stick* caterpillar is thin and stiff and is easily distinguishable from normal by inspection. The growth of *stick* is always slower than that of normal.

c) A greater percentage of *stick* is lost during the larval development than of normal. This accounts for the deficient numbers of *sticks* observed in experiments. The survivorship of *stick* is inferior to normal roughly by 5%. The differential viability is however, scarcely noted in favorable conditions.

d) *Multilunar* and *stick* are linked in inheritance, and the crossing-over between them is proved to be about 25.8%. It has been shown that *Multilunar* is inherited independently from the genes of the first, second and third linkage groups (TANAKA 1916, 1922, OGURA 1922), thus it forms, with *stick*, a fourth linkage group in the silkworm.

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EXPLANATION OF PLATE 2

- Figs. 1-3. Normal. (1 Sk)
 Figs. 4-6. *Stick*. (1 sk)
 Figs. 7-9. *Multilunar*. (L Sk)
 Figs. 10-12. *Multilunar stick*. (L sk)

Note:—No. 7 is in a contracted state of the body in contrast to No. 10 which shows the body fully extended. This is why the former is seen to be smaller than the latter.

