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ON THE PIGMENTATION OF THE BODY LOUSE *PEDICULUS HUMANUS* L.

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Nymphs and adults of the human body louse show considerable variability in their degree of pigmentation. This variability is illustrated in fig. 1, which shows the range in pigmentation from colourless specimens to those with very dark brown or black sclerites and a greyish darkening of the softer parts of the cuticle. The amount of body colour has sometimes been used as a secondary diagnostic character to distinguish subspecies (e.g. a dark variety on negroes) or quoted as a difference between the head and body races. It seems, however, that no reliance can be placed on this as a taxonomic character.

In 1917, Hindle made some preliminary breeding experiments from which he concluded that the degree of pigmentation was inherited; and he claimed to have isolated a colourless strain. At this point his work was interrupted by military service in the first World War, and was apparently never described in detail.

Two years later Nuttall (1919) published a paper which appeared to discredit Hindle's observations, for he found that the colour of the background during nymphal development had a profound effect on the colour of adult lice. Individuals which had been reared on a white background were pale, while those from a black background were pigmented. The colour could be modified during the forty-eight hours preceding the final moult but, when the adult stage was reached, it was invariable. Nuttall came to the conclusion that Hindle must have been misled and quotes the case as a warning to investigators engaged in the study of heredity.

It seemed surprising that two careful workers should have reached opposing conclusions and therefore corroborative experiments were undertaken. The investigation was conducted in four stages to answer the following questions:—

1. Is the pigmentation of lice dependent on the background during development?
2. If so, is this acquired character inherited?
3. Is it possible to isolate dark and light strains reared on the same background?
4. If so, what is the result of crossing such strains?

Technique.—The lice used were taken from a stock of body lice reared in the laboratory for at least five years by the methods described by Buxton (1939). They were kept in gauze-bottomed pill-boxes worn against the skin of the leg allowing them to feed at will during 12–15 hours a day. Under such conditions they flourish and, after the first feed, there is usually only a negligible mortality.

The degree of coloration was estimated visually in the living specimens, which were classified according to their resemblance to the four arbitrary types shown in fig. 1, namely: DD (very dark); D (dark); L (light); LL (unpigmented).

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The results can be conveniently summarised in diagrams (figs. 2, 3 and 4) showing the proportions of the four gradations of pigmentation in various families.

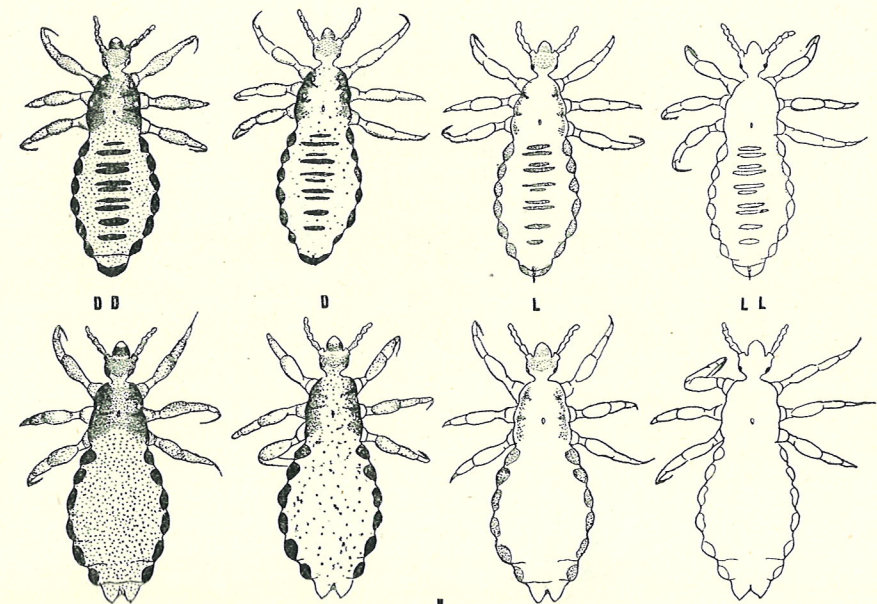


FIG. 1.—The four degrees of pigmentation referred to in the text. Above male lice, below female lice. (Drawn from life.)

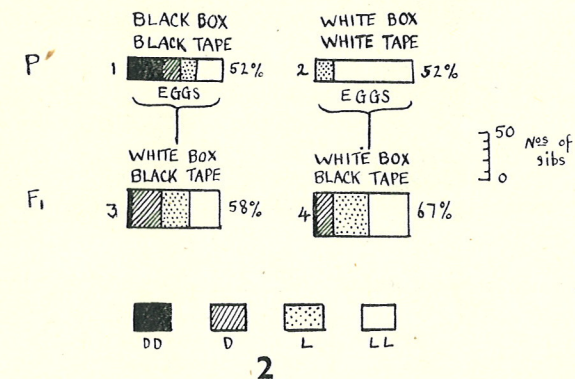


FIG. 2.—Diagram illustrating Experiments 1 and 2. Each block represents a family. The depth is proportionate to the number of sibs and the proportions of different grades of pigmentation are indicated horizontally by shading. Figures on the left of each block give the number of the family. The percentage on the right of the block gives the proportion of females.

Experiment 1.—The nymphs hatched from a batch of eggs were divided into two groups and one group reared in a black-lined pill box on black tape while the other group was kept in a white box on white tape. From the black diagrams in fig. 2 it will be seen that there were considerably more pigmented

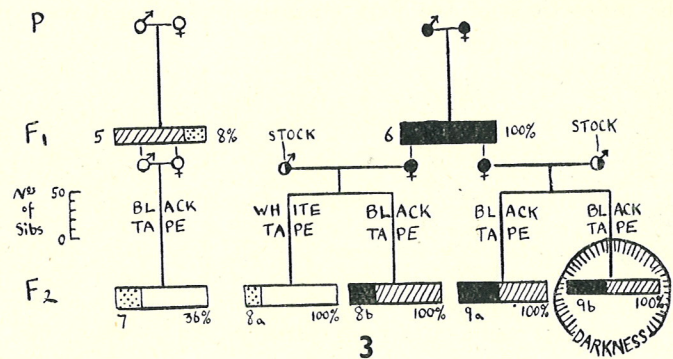


FIG. 3.—Diagram illustrating Experiment 3. (Symbols as in fig. 2.)

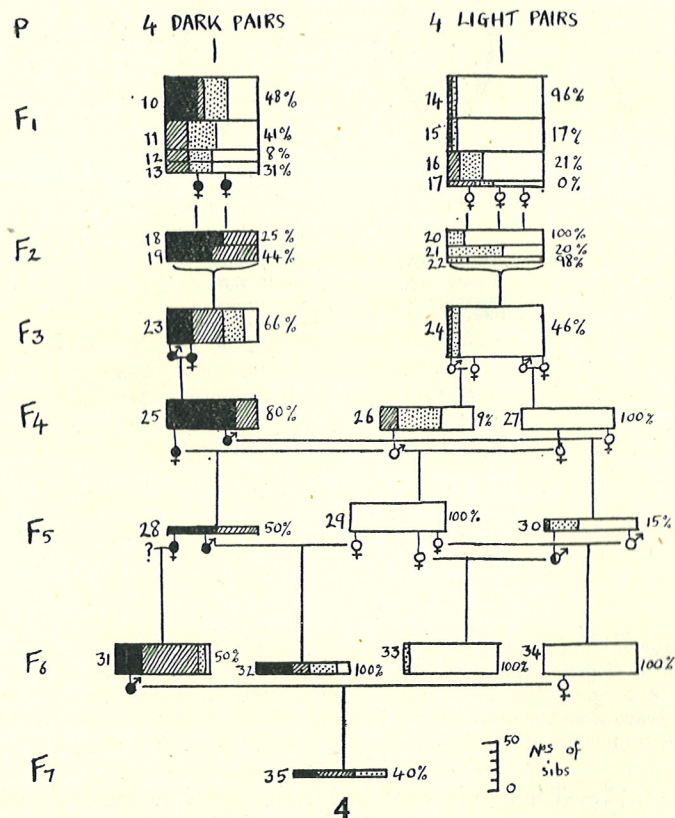


FIG. 4.—Diagram illustrating Experiment 4. (Symbols as in fig. 2.)

adults in the black box than in the white box as would be expected from Nuttall's experiments. Nevertheless, it is noteworthy that there is a substantial proportion of pale lice in the dark box and a small number of dark lice in the white box.

Experiment 2.—Eggs laid by the two groups of lice described above were incubated and the progenies reared separately, but under identical conditions, namely on black tape in white boxes. On their becoming adult they were examined and categorised, the proportions of dark and light individuals being shown in fig. 2 (families 3 and 4). Both groups showed about the same proportions of dark lice; there was no indication of an inherited tendency to darken.

Experiment 3.—A dark and a light virgin female isolated from the breeding stock were mated respectively with a dark and a light male. Their offspring were reared separately but under identical conditions on black tape in white boxes. When they had become adult it was found that the proportions of dark lice was much higher among the progeny of the dark pair. (See fig. 3, F1.) From the pale family (5) a light pair was mated and their offspring reared normally on black tape. The dark family (6) was unfortunately entirely composed of females. Two of them were mated with moderate coloured males from the general stock and the egg batches from both matings were each divided into two and treated as follows:—

- { Group 8a : Reared normally on white tape.
- { „ 8b : Reared normally on black tape.
- { „ 9a : Reared normally on black tape.
- { „ 9b : Reared in complete darkness. (Under a black bandage while feeding and in a light-tight tin when off the leg. Checked by inclusion of photographic paper which was subsequently developed.)

The resulting adult colorations of these groups are illustrated in fig. 3 (F2 generation). Two conclusions can be drawn from them:—

- (i) Since the “dark” group (8a) which was reared on white tape was as pale as the pale-selected family (9) on black tape, it appears that it is the ability to darken which is inherited and not a residual dark colour.
- (ii) Dark coloration can be developed in complete darkness. Since this is contrary to Nuttall's results, the experiment was repeated; 1st stage nymphs taken from the breeding stock were reared in tins under different conditions with the following results:—

Rearing conditions	Coloration of adults
White tape : exposure to light	0% D and DD
Black tape : exposure to light	42% „
White tape : complete darkness	53% „

Experiment 4.—Throughout this experiment all families were reared under similar conditions : namely black tape in white boxes.

The attempt was made to isolate two strains; one incapable of reacting to background and one reacting strongly, and then to try cross matings.

Isolation of strains.—Four light and four dark pairs from the general stock were mated and their progenies, reared separately, are shown as the F1 generation in fig. 4. They show some evidence of inheritance of pigmentation already.

Unfortunately it was not possible to obtain known matings in this generation, but two very dark and three very light females were selected and their

progenies reared separately to become the F2 generation. The effect of selection was now more marked. The eggs laid by the dark families were united and the general egg stock of the light families was similarly combined. These two groups became the families shown as F3 in the diagram. From them a very dark pair and two very pale pairs were isolated as virgins and mated to produce the F4 families.

At this point the selection for light and dark strains ceased. Marked differences in the proportions of the four colour groups had been obtained by selective breeding of lice reared under the same conditions.

Cross matings.—Cross matings were now carried out with individuals in various families in generations F4, F5 and F6.

The experiment was complicated and handicapped by the frequent occurrence of unisexual families, especially all-female families,¹ which were also frequently encountered in experiment 3. On account of this difficulty, only a limited number of the desired matings were possible: their results did not yield very definite conclusions, but can be summarised as follows:—

Families (30), (32) and (35) are all the progenies of very dark males and very pale females; they are all intermediate in grading. Family (28) was the only one from a dark female mating with a light male, and a rather high nymphal mortality renders the results unreliable.

In general, one might conclude that there is no evidence of a simple or sex-linked inheritance. Probably more than one gene is involved and the selection was not continued long enough to isolate pure strains.

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¹ It is, perhaps, worth noting that two females of the all-female family 6, and three females of the all-female family 29, gave all-female progeny, though mated with different males. In Hindle's (1917) data, there is a record of one family (No. 4 of "second generation") of 13 males and 15 females. Five of the latter were mated with males from other families and gave two all-female and three all-male families.

There seems to be a tendency for the females of certain families to produce unisexual progenies.

APPENDIX: CONSTITUTION OF THE VARIOUS FAMILIES.

M = Males; F = Females.

DD, D, L and LL indicate coloration as shown in fig. 1.

Family No.	DD		D		L		LL	
	M	F	M	F	M	F	M	F
1	3	3	3	3	1	3	5	4
2	0	0	0	0	2	2	10	11
3	0	1	3	4	5	10	8	7
4	1	1	5	10	7	7	3	13
5	0	0	10	0	2	1	0	0
6	0	19	0	0	0	0	0	0
7	0	0	0	0	4	2	10	6
8a	0	0	0	0	0	4	0	19
8b	0	5	0	13	0	0	0	0
9a	0	5	0	6	0	0	0	0
9b	0	7	0	12	0	0	0	0
10	3	11	2	2	9	3	7	9
11	0	0	6	1	7	2	6	10
12	0	0	3	0	3	0	6	1
13	0	0	3	0	0	3	6	1
14	0	0	0	3	0	2	2	38
15	0	0	2	0	2	0	25	6
16	0	1	4	0	6	0	14	8
17	0	0	2	0	1	0	3	0
18	7	2	2	1	0	0	0	0
19	4	5	5	2	0	0	0	0
20	0	0	0	0	0	3	0	16
21	0	0	0	0	5	1	3	1
22	0	0	0	0	2	0	3	2
23	1	11	6	6	3	5	3	4
24	0	0	2	1	1	4	19	23
25	4	21	2	3	0	0	0	0
26	0	0	6	0	10	0	5	2
27	0	0	0	0	0	0	0	19
28	1	2	2	1	0	0	0	0
29	0	0	0	0	0	0	0	29
30	0	0	2	0	3	0	6	2
31	4	5	8	10	2	0	1	0
32	0	4	0	2	0	3	0	1
33	0	0	0	0	0	3	0	33
34	0	0	0	0	0	0	0	28
35	0	1	1	1	2	0	0	0

