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THE 'HEAD' AND 'BODY' RACES OF *PEDICULUS HUMANUS* L.

By J. R. BUSVINE, *Entomology Department, London School of Hygiene and Tropical Medicine*

(With Plate I and 7 Figures in the Text)

CONTENTS

I. THEORETICAL SECTION

A. Introduction

In his 'Monograph of the Sucking Lice', Ferris (1935) reviews the evidence relating to the status of *Pediculus* '*capitis*' and *P.* '*corporis*'. He points out that some of this evidence is conflicting, so that it is difficult to reach a final decision. He says: 'we have gone as far as we can on the basis of the conventional methods of the systematist. It remains for extensive experimental work to carry further the investigation of the problem which has been set.' In recent years, other aspects of louse biology have received considerable attention; but with this particular problem, little progress has been made since the fundamental studies of Bacot, Nuttall, Keilin, Hase and Sikora at the time of the first World War. This paper is a contribution towards the deficit.

B. Summary of the evidence

(1) *Morphological*

There are some obvious differences between typical specimens of lice taken from the head and from the body; and, given a few such thoroughly typical specimens, almost any systematist would be inclined to recognize them as separate species. If larger, more representative, samples are examined, however, the following conclusions will be drawn:

(a) Size and proportion

The average size of head lice is less than the average size of body lice, whether gross body length or the size of any particular part is measured. However, there is considerable variation and overlap, so that it is possible to find small body lice which are exceeded by the largest head lice, and the same is true of measurements of parts of the body.

A prominent example is provided by the antennae of the two forms which show considerable differences in proportions, the ratio of their lengths being about 5 to 4. On the other hand, there is little or no difference in thickness so that those of the body louse appear noticeably more slender.

This difference has long been recognized and is noted by Nuttall. However, Ferris observes that 'gradations between the two extremes appear in material which may reasonably be used in this comparison'.

(b) Shape

The lateral indentations between segments of the abdomen are more pronounced in typical head lice than in body lice. This is, however, too vague and unreliable a character for the identification of individual lice.

According to Freund (1925) there are differences in the form and chaetotaxy of the genitalia of the two races; but Ferris discusses these in detail and dismisses them as trivial and inconstant.

(c) *Colour*

Head lice are generally darker than body lice; but this is a very variable character, largely depending on the environment (background coloration).

(d) *Musculature*

An interesting difference between the two forms was pointed out by Landois (1865), but seems to have been overlooked by most authors except Sikora. According to Landois, the body race has two sets of longitudinal muscles on the ventral body wall of the abdominal segments 4 and 5. (See Plate I.) In the head louse only the muscles on the 5th segment are present. This would prove an important categorical distinction, but unfortunately Sikora observes (1919) that it is not absolutely consistent. She attributes this to interbreeding between the two races, remarking that the pure body strain is comparatively rare.

(e) *Dimensions of the egg*

In a recent study, Alpatov, Nastukova & Chartulari (1945) measured six dimensions of the louse egg and took the position of the egg cement as a seventh character. From these measurements, averages with standard errors were calculated and are given in tabular form. On the basis of these figures, it seems clear that the eggs of the head and body forms of lice are recognizably distinct (judged by means) in natural populations.

(2) *Influence of environment on morphological differences*

Nuttall believed that many of the characters of the louse, and in particular those distinguishing the head and body forms, were dependent on the environment. If, however, a critical examination is made of the data on which he bases his conclusions, some of it will be found imprecise or otherwise unsatisfactory. Thus:

(a) *Concerning pigmentation of lice*

Contrary to Hindle's (1917) conclusions, Nuttall (1919*a*) states that 'pigmentation in *Pediculus* is not an hereditary character; its presence depends entirely upon the nature of the background upon which the insect lives and is a character that may be acquired in a couple of days'. This statement is too categorical. I have shown recently (1946) that although the pigmentation itself is not inherited, the ability to react to a background is hereditable, so that there is some genetic mechanism involved.

(b) *Transformation of 'capitis' to 'corporis'*

Nuttall states (1919*b*) that 'typical *capitis* lose all their distinctive morphological characters when raised experimentally on man under conditions which are favourable for the propagation of *corporis*, and they acquire all the morphological characters of *corporis* after four or more generations'. This is based on the following evidence:

(i) Sikora (1917) bred head lice for several generations on her arm. She stated that the head louse appeared to increase in size and become more like the body louse up to the 5th generation. Later, however, she recanted and affirms (1919) that head lice up to the 11th generation were quite recognizably distinct. This second paper is not mentioned by Nuttall or by Ferris.

(ii) Howlett (1918), in a brief paper, describes an experiment in which head lice (from an unstated source) were liberated on the body of his assistant. They tended to return to the head, but this reaction became less marked in F_1 and F_2 generations, while characters typical of the *corporis* form appeared.

(iii) Keilin & Nuttall (1919) record that they received from Bacot specimens of a *corporis* strain that had been reared by him for 2 years in the laboratory. These were found to be intermediate in character between typical *capitis* and typical *corporis*. A year later a further batch of the same strain was received, and the specimens were now found to be entirely of the *corporis* type.

The main criticism of this data is that it is mainly qualitative; the only figures given are a few measurements made by Sikora. Howlett and Keilin and Nuttall confine themselves to the bald statement that the typical *corporis* characters were observed.

Recently, however, a Russian paper has given support to this apparent mutability of the *capitis* strain. Alpatov *et al.* (1945) found that the eggs of a strain of head lice became similar in dimensions to those of body lice when reared in the laboratory. The change was apparently accomplished in the first generation and continued for several more.

(3) *Results of crossing 'capitis' and 'corporis' strains*

Bacot (1917) crossed strains of *capitis* and *corporis* and maintained the progeny for three generations. The cross-matings were easily accomplished and the 'hybrids' were vigorous. Keilin & Nuttall (1919), however, in examining Bacot's material, found an unusually high preponderance of hermaphrodites as compared with natural populations of either strain.

(4) *Biology of the two strains*

Bacot (1917) made numerous observations on the length of life, egg production and fertility of the head and body forms and gives his results in detail. His data are rather difficult to summarize quantitatively, but they clearly show a considerable difference between the two strains. The body louse, he says, 'is a larger, more robust and less active insect than *P. capitis*—the females having a relatively greater egg-carrying capacity than those of the head louse. The eggs are larger and the number laid (under the conditions of the experiments) is greater, while the habits associated with egg-laying differ, although placing the females of *humanus* under conditions applicable to *capitis* or vice versa may induce a considerable degree of uniformity.'

C. Conclusions

As Ferris suggests, there are certain inconsistencies in the available evidence regarding the status of the two forms of *P. humanus*. To illustrate this concisely, two columns can be drawn contrasting (1) the facts suggesting that the two forms are merely extremes of a single variable species, with (2) facts supporting the existence of two distinct varieties.

Supporting uniformity	Supporting heterogeneity
Morphological	
(a) Both types are variable and all degrees of every character can be found.	(a) Typical specimens differ obviously in several particulars, mainly of size and proportion.
(b) Nuttall, and certain other authors, believed that such morphological differences as exist are dependent on environment, and that the *capitis* form reared on the body becomes transformed into the *corporis* type.	(b) There is very little *quantitative* evidence for this. Also there is disagreement on the time required for the change (2–3 years with Bacot's material; four generations according to Howlett; one generation according to Alpatov and colleagues).
Hybridization	
The two forms can readily be crossed and the progeny are vigorous and fertile.	There was an unusually high incidence of hermaphrodites in the progeny of Bacot's cross-matings, which is evidence of genetic incompatability.
Biology	
The general outlines of the biology are similar.	There are obvious differences in length of life, oviposition rate, etc.

II. EXPERIMENTAL SECTION

A. Methods

(1) *Sources of lice*

Specimens of lice were taken from naturally infested individuals in London at different times. The head lice were usually taken from women and the body lice from men. Whenever possible, it was ascertained that the subject had only one type of infestation; that is, not head *and* body lice together. Such specimens will be referred to, for convenience, as 'wild' lice.

In addition, cultures of lice were maintained in breeding capsules with regular or continuous opportunities for feeding on human blood; these will be referred to as 'captive' strains. In particular, four strains were cultured for comparatively long periods as indicated in the diagram of Fig. 1. B 12 is a strain of body lice which has been maintained in the Department of Entomology of the London School of Hygiene and Tropical Medicine for about 10 years. In 1940 and 1941 it was reinforced by additional wild body lice. The lice in this culture are given opportunity to feed for about 12 hr. daily. B 24 was a strain taken from B 12 and worn day and night to allow opportunity to feed 24 hr. per day.

H 24 was a strain of head lice started from an infested person in February 1943 and maintained for over 2 years in captivity with opportunity to feed 24 hr. per day. H 12 was split off from H 24 and worn for 12 hr. daily. In July 1945, H 24 and H 12 were unfortunately lost and B 24 was discontinued 2 months later.

(2) *Methods of rearing in the laboratory*

The lice were reared in captivity in small feeding boxes or tins as described by Buxton (1940), with, however, one small difference. Head lice, as pointed out by Rocha-Lima & Sikora (1925) do not readily feed through gauze and they are also much more sensitive to starvation than body lice. Breeding boxes kept under the sock sometimes tend to slip about when walking so that opportunities to feed may be lost and head lice sometimes become weakened in such circumstances. Accordingly the head lice were kept in small flat tins bound to the ankles with elastic bandage. For the purpose of comparison the body lice were reared in exactly the same way.

(3) *Methods of fixing and preserving specimens*

It has often been remarked that lice are unsatisfactory subjects for measurement owing to their lack of a rigid cuticle and to their habit of taking large meals of blood at intervals, thereby distending the body. Preliminary tests showed that the method of preservation affects the final size; for example, half a batch of lice preserved in 50 % alcohol were from 2 to 10 % larger in several dimensions than the other half of the batch which was preserved in 100 % alcohol. To maintain uniformity, all lice were killed and preserved by plunging them into 70 % alcohol. All the various batches of specimens were kept in little plugged vials in a large bottle of this fluid.

The variation due to feeding was counteracted as far as possible by allowing the insects (whether wild or from laboratory strains) opportunity to feed on the skin for about an hour before they were killed and preserved. The majority of the specimens were, therefore, fully fed.

(4) *Methods of measurement*

For measurements of different parts of the body, lice were laid on their backs on a glass slide, covered with a portion of another slide and surrounded with 70 % alcohol run in from a pipette. Measurements were made by a micrometer eyepiece in an ordinary compound microscope. The total body length was observed through a 50 mm. objective (when the divisions of the scale recorded $\frac{1}{10}$ mm.) and the other dimensions were measured with a 16 mm. objective (when the divisions recorded $\frac{1}{60}$ mm.). As a rule, ten to twelve males and the same number of females were measured from each batch of lice and the means and standard deviations calculated from them.

B. Results of measurements

(1) *Samples of 'wild' populations*

(*a*) *Linear measurements of adult lice*

The principal dimensions which have been used to discriminate between *capitis* and *corporis* are the following: total body length, length of antennae, length of the 3rd segment of the antenna, width of the thumb-like process of the anterior leg of the male and the total length of the 3rd tibia. In actual practice, there is difficulty in measuring legs in whole specimens because they are usually curved under the body; even if they are partially straightened, there is likely to be a big error of parallax. Similar considerations apply to a smaller extent with regard to the antennae. I therefore chose to measure the

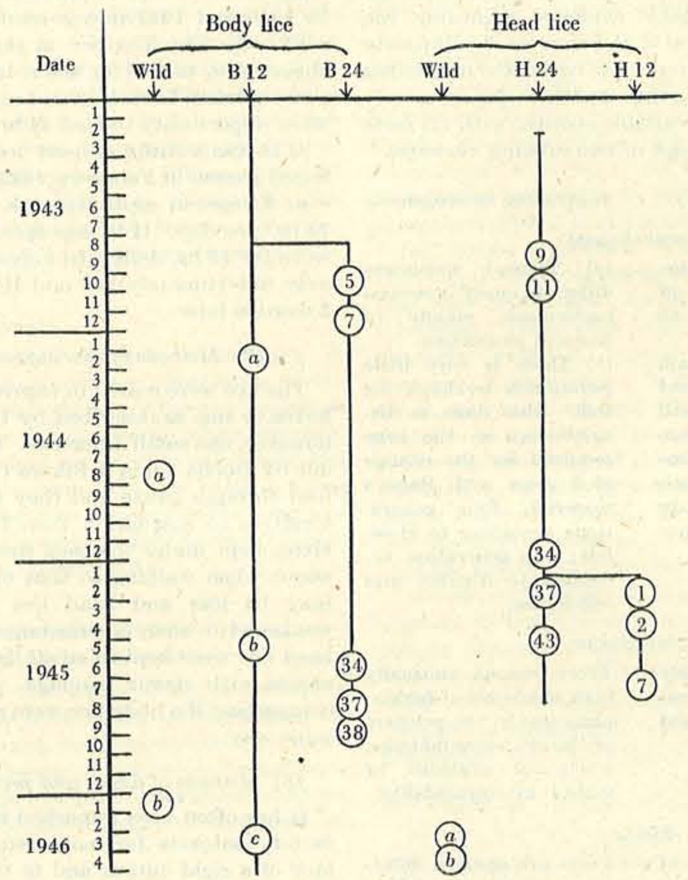


Fig. 1. Diagram to illustrate the origin of samples of lice from strains reared in captivity. H = head strain; B = body strain; 12 and 24 = number of hours per day they were allowed access to food. The figures in the circles give the number of generations under the stated conditions; the letters refer to other samples of lice, of unknown generations.

following dimensions: (*a*) total body length, (*b*) length of head, (*c*) width of head, (*d*) length of distal four segments of antenna, (*e*) length of 3rd antennal segment, (*f*) width of 3rd antennal segment. The exact location of these measurements are shown in Fig. 2. Tables 1 and 2 give the means of these dimensions for two 'wild' samples of body lice and two 'wild' samples of head lice. In all cases the means for body lice are significantly larger than those for head lice except for the *width* of the 3rd antennal segment, which is about the same in both forms. These facts are illustrated graphically in Fig. 3 in which it will be seen that for the first five dimensions, the means are distinct though there is a considerable overlap. (Some measurements of captive lice with the same means were included in these graphs.)

the 3rd antennal segment is least satisfactory; this may result from a greater error due to its smaller size relative to the scale divisions. From the practical point of view the first three dimensions are considerably more convenient to measure than the last three. When a whole louse is laid on a slide, the antennae may lie at an angle to the horizontal and cannot readily be levelled with the cover glass owing to the thickness of the body. Measurements of antennae at an angle have to be avoided owing to the error of parallax. In addition to this, the small dimensions of the antennal joints require a high power objective for accuracy.

Under the circumstances, it was considered satisfactory to use the first three dimensions in subsequent measurements.

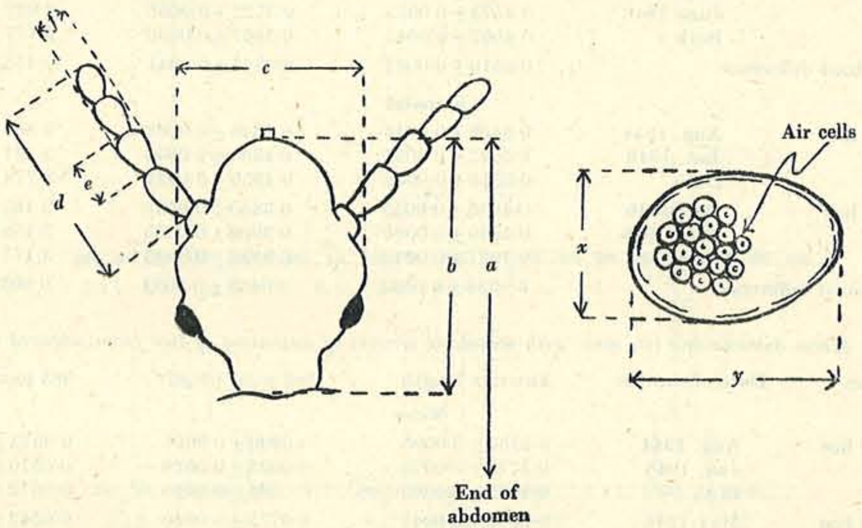


Fig. 2. Positions of measurements made to discriminate between different strains of lice. *a*, total length; *b*, head length; *c*, head width; *d*, antenna length (distal 4 segments); *e*, length of 3rd antennal segment; *f*, width of 3rd antennal segment. On right, the egg cap; *y*, length and *x*, width.

To form an impression as to the value of the various measurements in distinguishing between samples of head and body lice, the ratios of the differences between the means to their standard errors were calculated as follows:

Measurements on 'wild' lice	Difference / Standard error of difference		
	Males	Females	Average
(*a*) Head length	10·0	14·8	12·4
(*b*) Head width	8·5	15·1	11·8
(*c*) Body length	9·3	15·1	12·2
(*d*) Antenna length	11·7	15·6	13·1
(*e*) 3rd antennal segment	6·6	11·1	8·8

There seems to be no outstanding difference in the relative merits of the various measurements for discriminating between the two forms. The length of

(*b*) *Observations of abdominal musculature in females*

It is unfortunately somewhat difficult to determine the status of the abdominal muscles in the female lice preserved in 70 % alcohol. The muscles can be seen in a proportion of lice from the outside (as described by Sikora). But in other specimens, less well preserved, they are difficult to examine without very careful dissection. However, the following results were obtained by direct observation: of sixty-six wild body lice, the musculature could be distinguished in forty-four specimens. Of these, ten had muscles in segment 5 only, forty-five had muscle rows in segments 4 and 5 (and one specimen had in addition a pair of muscles in segment 3!—see Plate I). Of forty-one wild head lice, the muscles could be observed in thirty-three specimens, all of which had muscles in segment 5 only.

In the samples examined, then, the muscles were confined to segment 5 in the head lice but were *usually* present in segment 4 as well in body lice.

(2) *Measurements of strains bred in captivity*

(*a*) *Linear measurements*

Samples of the four captive strains were preserved at various times, when there were sufficient adults

Table 3 gives mean figures for the head length and width and the total body length of samples preserved from the various strains at different times. A careful examination of this table reveals no consistent trend in any dimension of either of the head or body strains. The various samples do not show differences greater than would be expected in normal sampling of a population.

Table 1. *Mean dimensions (in mm. with standard errors) of lice from natural infestations*

Strain	Date of sample	Head length	Head width	Total length
		Males		
Body lice	Aug. 1944	0·5037 ± 0·0046	0·4016 ± 0·0043	3·322 ± 0·047
	Jan. 1946	0·5222 ± 0·0119	0·4000 ± 0·0043	3·150 ± 0·084
	Both	0·5112 ± 0·0057	0·4012 ± 0·0030	3·253 ± 0·047
Head lice	May 1946	0·4667 ± 0·0033	0·3542 ± 0·0033	2·675 ± 0·052
	June 1946	0·4573 ± 0·0055	0·3722 ± 0·0055	2·822 ± 0·070
	Both	0·4602 ± 0·0045	0·3667 ± 0·0050	2·777 ± 0·054
Combined difference		0·0510 ± 0·0051	0·0345 ± 0·0041	0·476 ± 0·051
		Females		
Body lice	Aug. 1944	0·5406 ± 0·0016	0·4346 ± 0·0062	3·808 ± 0·082
	Jan. 1946	0·5622 ± 0·0095	0·4350 ± 0·0040	3·737 ± 0·042
	Both	0·5515 ± 0·0022	0·4350 ± 0·0037	3·774 ± 0·046
Head lice	May 1946	0·4955 ± 0·0035	0·3850 ± 0·0030	3·183 ± 0·033
	June 1946	0·4959 ± 0·0080	0·3909 ± 0·0035	3·158 ± 0·104
	Both	0·4957 ± 0·0040	0·3882 ± 0·0023	3·171 ± 0·034
Combined difference		0·0558 ± 0·0032	0·0468 ± 0·0031	0·603 ± 0·040

Table 2. *Mean dimensions (in mm. with standard errors) of antennae of lice from natural infestations*

Strain	Date of sample	Antenna length	3rd joint length	3rd joint width
		Males		
Body lice	Aug. 1944	0·3750 ± 0·0095	0·0990 ± 0·0025	0·0573 ± 0·0019
	Jan. 1946	0·3778 ± 0·0075	0·0932 ± 0·0026	0·0570 ± 0·0013
	Both	0·3762 ± 0·0060	0·0965 ± 0·0019	0·0572 ± 0·0012
Head lice	May 1946	0·3083 ± 0·0047	0·0772 ± 0·0040	0·0542 ± 0·0023
	June 1946	0·3188 ± 0·0059	0·0855 ± 0·0027	0·0625 ± 0·0015
	Both	0·3153 ± 0·0043	0·0827 ± 0·0023	0·0597 ± 0·0017
Combined difference		0·0609 ± 0·0052	0·0138 ± 0·0021	−0·0025 ± 0·0015
		Females		
Body lice	Aug. 1944	0·3903 ± 0·0060	0·1013 ± 0·0025	0·0612 ± 0·0012
	Jan. 1946	0·3820 ± 0·0067	0·0980 ± 0·0027	0·0597 ± 0·0010
	Both	0·3862 ± 0·0057	0·0997 ± 0·0019	0·0605 ± 0·0010
Head lice	May 1946	0·3092 ± 0·0035	0·0795 ± 0·0020	0·0613 ± 0·0023
	June 1946	0·3222 ± 0·0043	0·0840 ± 0·0012	0·0653 ± 0·0008
	Both	0·3160 ± 0·0030	0·0819 ± 0·0012	0·0633 ± 0·0012
Combined difference		0·0702 ± 0·0045	0·0178 ± 0·0016	−0·0028 ± 0·0011

available, as indicated in Fig. 1. Normally a population of two or three dozen adults was achieved in each generation, but sometimes there were less or the population was nearly unisexual. (Unbalanced sex ratios are common in small louse cultures.) It will be admitted that the disposition of these samples leaves much to be desired for making exact comparisons; but the work was done in the intervals of more urgent war-time tasks connected with insecticides.

Accordingly the figures for the various strains have been lumped together and the overall means are given in Table 4. This table also shows the standard errors for differences in class means. It will be seen that the difference between the head and body forms are in all cases highly significant.

The difference between lice fed 12 hr. and lice fed 24 hr. per day is also significant for most dimensions. The lice worn 24 hr. per day had a tendency to be smaller than those worn only 12 hr. per day and left

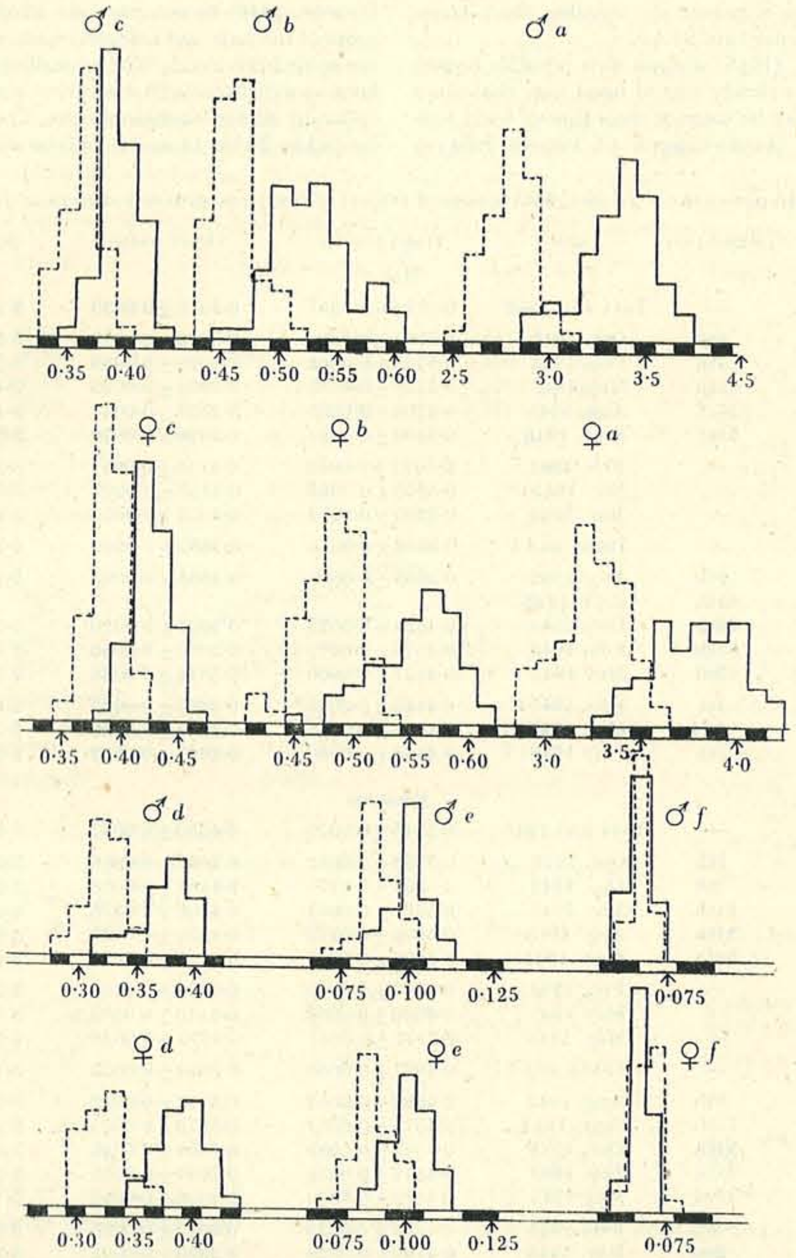


Fig. 3. Histograms showing distribution of sizes of various dimensions of head and body strains of lice. *a* = total body length; *b* = length of head; *c* = width of head; *d* = length of distal 4 segments of antenna; *e* = length of 3rd antennal joint; *f* = width of 3rd antennal joint. Solid line, body lice; dotted line, head lice.

at room temperature for the remaining period. It seemed likely that this might have been a temperature effect, and accordingly an experiment was designed to check this.

A batch of 1st-stage lice, fed once, was divided into two halves and one-half was fed 12 hr. per day and kept at room temperature for the other period, as usual. The other half was fed 12 hr. per day and kept on the body for the remaining 12 hr., but without opportunity to feed. Thus, both were fed 12 hr. a day, but one lot was, on the average, kept warmer than the other. The dimensions of the adults of these two half batches are given in Table 5. It will be seen that, in most dimensions, the lice reared under warm conditions were significantly smaller than those reared under cooler conditions.

Alpatov *et al.* (1945) suggest as a possible reason for the smaller average size of head lice, that their environment may be warmer than that of body lice. They give no measurements of human hair or Bourne, 1946) to compare air temperatures at the roots of the hair and between underwear and skin of the same individuals. The recording instrument was kept at a distance of 3 mm. from the skin by a glass collar in all the measurements. The results are recorded in Table 14 and it will be observed that the

Table 3. *Mean dimensions (in mm. with standard errors) of lice from strains maintained in breeding tins*

Strain	Generation	Date	Head length	Head width	Total length
			Males		
B wild	—	1944 and 1946	0·5112±0·0057	0·4012±0·0030	3·253±0·059
B 24	5th	Oct. 1943	0·5097±0·0098	0·3983±0·0077	3·383±0·093
	7th	Dec. 1943	0·5763±0·0063	0·4028±0·0035	3·367±0·025
	34th	May 1945	0·5138±0·0055	0·3900±0·0025	3·475±0·023
	37th	Aug. 1945	0·5208±0·0058	0·3833±0·0023	3·425±0·027
	38th	Sept. 1945	0·5308±0·0087	0·3820±0·0040	3·250±0·040
B 12	—	Feb. 1944	0·5072±0·0063	0·4116±0·0057	3·214±0·075
	—	May 1945	0·5305±0·0082	0·4152±0·0027	3·582±0·044
	—	Mar. 1946	0·5263±0·0082	0·4075±0·0053	3·225±0·030
H wild	—	1946*a* and *b*	0·4602±0·0045	0·3667±0·0050	2·777±0·054
H 24	9th	Aug. 1943	0·4555±0·0068	0·3555±0·0095	2·767±0·080
	11th	Sept. 1943	—	—	—
	34th	Dec. 1944	0·4528±0·0035	0·3667±0·0020	2·725±0·023
	37th	Feb. 1945	0·4575±0·0070	0·3607±0·0050	2·817±0·037
	43rd	May 1945	0·4627±0·0060	0·3612±0·0032	2·825±0·025
H 12	1st	Feb. 1945	0·4440±0·0060	0·3667±0·0032	2·867±0·034
	2nd	Mar. 1945	0·4458±0·0057	0·3653±0·0025	2·705±0·026
	7th	July 1945	0·4458±0·0050	0·3667±0·0032	2·933±0·032
			Females		
B wild	—	1944 and 1946	0·5515±0·0022	0·4350±0·0037	3·774±0·046
B 24	5th	Oct. 1943	0·5167±0·0012	0·4195±0·0068	3·575±0·096
	7th	Dec. 1943	0·5667±0·0107	0·4167±0·0068	3·575±0·086
	34th	May 1945	0·5667±0·0053	0·4208±0·0028	3·950±0·036
	37th	Aug. 1945	0·5800±0·0105	0·4250±0·0037	3·933±0·048
	38th	Sept. 1945	0·5695±0·0045	0·4195±0·0028	3·675±0·047
B 12	—	Feb. 1944	0·5167±0·0060	0·4398±0·0100	3·788±0·103
	—	May 1945	0·5680±0·0093	0·4445±0·0083	3·983±0·063
	—	Mar. 1946	0·5737±0·0042	0·4375±0·0028	3·783±0·038
H wild	—	1946*a* and *b*	0·4957±0·0040	0·3882±0·0023	3·171±0·034
H 24	9th	Aug. 1943	0·4682±0·0053	0·3792±0·0042	3·217±0·040
	11th	Sept. 1943	0·4575±0·0082	0·3875±0·0045	3·283±0·045
	34th	Dec. 1944	0·4682±0·0082	0·3908±0·0040	3·358±0·043
	37th	Feb. 1945	0·4847±0·0038	0·3987±0·0038	3·367±0·046
	43rd	May 1945	0·4875±0·0050	0·3820±0·0043	3·125±0·041
H 12	1st	Feb. 1945	0·4847±0·0032	0·3985±0·0005	3·464±0·021
	2nd	Mar. 1945	0·4750±0·0028	0·3930±0·0025	3·292±0·034
	7th	July 1945	0·4958±0·0080	0·4030±0·0027	3·608±0·017

B = body strain; H = head strain; 12 and 24 = number of hours allowed to feed per day.

clothing temperatures, nor do I know of any body of data in which this comparison can be made. (Though Marsh & Buxton (1937) and Mellanby (1932) record measurements of the body louse environment for sedentary people indoors at various temperatures.) Accordingly, some tentative experiments were made with a sensitive electrical thermometer (described by hair was usually *cooler* than the body environment. These data, admittedly limited, certainly give no support to the opposite suggestion.

(*b*) *Weights of adult lice*

A number of comparisons of weights of certain strains were made. For each sample, about ten live

lice of each sex from each strain were weighed individually on a torsion balance to the nearest 0·05 mg. The means and standard errors calculated from these weighings are given in Table 6. In general they confirm the results of the dimensional measurements, in that the head louse strain is consistently lower than the body strain and there are no obvious clusters of hatched eggs, the opercula were easily detached and could be placed on a glass slide for measurements with the micrometer eyepiece. In addition to measurements of the long and short diameters of the oval egg cap, a note was made of the number of air cells in it. This number was found to vary considerably in different eggs laid

Table 4. *Mean dimensions (in mm. with standard errors) of all lice in each strain reared in breeding tins*

Strain	Head length	Head width	Total length
	Males		
B12	0·5237±0·0043	0·4117±0·0025	3·353±0·041
B24	0·5303±0·0140	0·3907±0·0020	3·380±0·070
H12	0·4452±0·0029	0·3662±0·0027	2·836±0·070
H24	0·4573±0·0029	0·3618±0·0022	2·786±0·054
Differences B–H	0·1515	0·0744	1·111
12–24	−0·0187	0·0254	0·023
Interaction	0·0055	0·0166	0·071
Standard error	0·0152	0·0047	0·120
	Females		
B12	0·5600±0·0058	0·4402±0·0030	3·859±0·041
B24	0·5555±0·0052	0·4203±0·0022	3·811±0·036
H12	0·4852±0·0032	0·3990±0·0002	3·454±0·027
H24	0·4737±0·0030	0·3875±0·0020	3·270±0·022
Differences B–H	0·1566	0·0740	0·946
12–24	0·0160	0·0314	0·232
Interaction	0·0070	0·0084	0·136
Standard error	0·0090	0·0046	0·064

Table 5. *Mean dimensions (in mm. with standard errors) of a single brood of lice, halved and reared under slightly different conditions*

Strain	Conditions when not feeding	Head length	Head width	Total length
		Males		
B12	Cool	0·5595±0·0057	0·4167±0·0025	3·400±0·051
	Warm	0·5320±0·0045	0·4000±0·0045	3·475±0·029
Difference ± s.e.		0·0275±0·0051	0·0167±0·0036	−0·075±0·041
		Females		
B12	Cool	0·5917±0·0038	0·4528±0·0020	3·875±0·038
	Warm	0·5695±0·0055	0·4308±0·0028	3·892±0·051
Difference ± s.e.		0·0222±0·0047	0·0220±0·0024	−0·017±0·045

Cool = room temperature when not feeding; warm = skin temperature when not feeding.

trends tending towards fusion. The difference between the two strains is proportionally greater, as would be expected, since the weight will be roughly proportional to the volume and hence to the cube of any linear dimension.

(*c*) *Observations on the eggs*

An examination of eggs of the two strains was made and it was concluded that the most rigid portion, and one which allowed of precise measurement, was the egg cap or operculum. By brushing by the same female, but the average numbers were greater with body louse eggs than those of head lice.

Figs. 4 and 5 show graphically the distribution of the dimensions of the opercula and the numbers of air cells in them for a large sample of eggs from 'captive' head and body lice. In Fig. 5 the distribution of air cell numbers of fifty eggs from a natural infestation is also shown. These graphs, like those of Fig. 3, show distinct means with considerable overlaps.

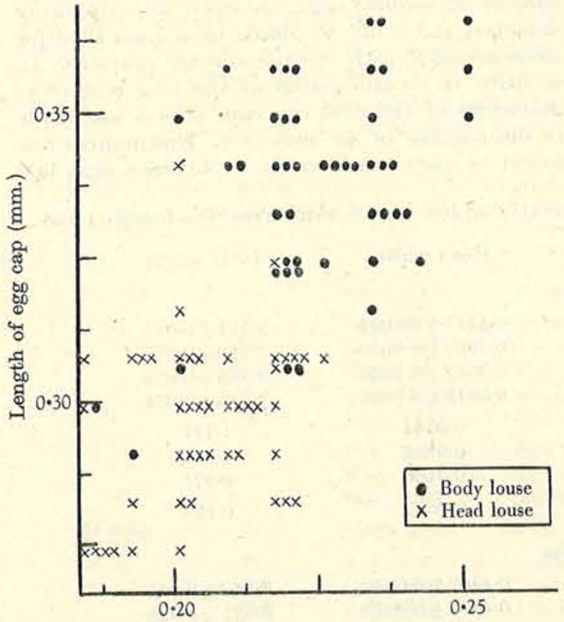


Fig. 4. Distribution of opercula measurements of eggs of head lice and body lice.

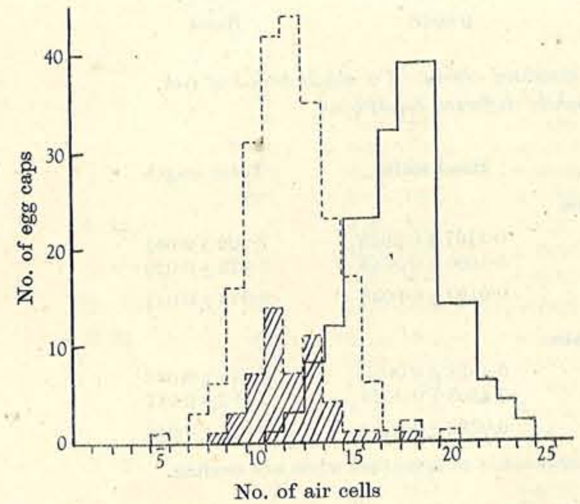


Fig. 5. Distribution of numbers of air cells in opercula of eggs of body lice (solid line) and head lice (broken line). The shaded portion gives the distribution of numbers of cells in fifty eggs from naturally infested hair.

(3) *Measurements of 'hybrids'*

(*a*) *Linear measurements*

A virgin female body louse of the strain B 24 (33rd generation) was mated with a male head louse of strain H 24 (33rd generation). The progeny were reared for several generations and samples were preserved of the F_1, F_2 and F_3 sibs. Some mean linear dimensions of the F_1 and F_3 adults are given in Table 7 and contrasted with similar measurements for all the B 24 and H 24 samples. It will be observed that the F_1 generation is intermediate in size between the body form and the head form, but the F_3 generation is indistinguishable from the body louse in size. The culture was worn for 24 hr. per day.

(*b*) *Weights of adults*

The mean live weights of samples of head lice, body lice and the F_1 and F_2 generations of hybrids are given in the two bottom columns of Table 6. These figures support the evidence of the linear measurements; the F_1 generation is intermediate in size, while the F_2 generation is indistinguishable from the B 24 strain in weight.

(4) *Biological observations on 'captive' strains*

The experiments to be described were all made during the summer of 1943 with head lice taken from the H 24 strain (being the 5th–8th generations in captivity) and body lice taken from the B 12 strain during the same period. The observations can conveniently be divided into bionomic data and miscellaneous experiments, the latter including resistance to starvation, mating choice and egg-laying preferences.

(*a*) *Bionomic data*

(i) *Egg stage.* Six batches of eggs from the body louse strain and six lots from the head louse strain were incubated at 30° C. and 75 % relative humidity. The percentages hatching on the subsequent days are shown in Table 8.

It will be noted that the incubation period of the two forms is very similar, but that the body louse eggs reach a higher final percentage hatch.

(ii) *Nymphal stages.* The following experiments were undertaken to compare the speed of development of the two strains in captivity. Larvae from louse eggs hatched in the incubator could be of different ages up to 24 hr. old and it was thought that this might affect the mortality during the first feed through gauze. (Partly starved lice, especially of the head strain, are unable to feed in this way.) Accordingly the experiments were all started with such lice as were able to take a meal in the breeding tin but were not more than 1 day old. From twenty-five to one hundred lice were used for each test and several tests were repeated twice.

The breeding tins were worn for different periods of the 24 hr. in different experiments, always keeping the appropriate head and body pair together. When not being worn, the tins were kept at room temperature. The results can best be shown diagrammatically and are set out in Figs. 6 and 7 which show the percentages moulting on different days and the pre-imaginal mortality of the two strains under different feeding conditions. Some of the salient points of the results are also recorded in Table 9.

The conclusions to be drawn from these results are rather similar to those arising from the egg data. The speed of development of the two forms is very similar; that is to say the various moults occur at similar intervals which vary according to the daily feeding period. The pre-imaginal mortality, however, is markedly higher in the head strain.

(iii) *Adult stage.* Adult lice were maintained under the same conditions of feeding as those described for the nymphal stages. Not more than two dozen adults were kept in a single tin and the females were kept slightly in excess of the number of males, since Buxton (1940) has shown that when females are in the presence of numerous males their length of life is shortened and the number of eggs per day decreases. Tapes carrying eggs were removed daily and incubated. By these means, it was possible to determine the individual lengths of life, the average numbers of eggs laid per female and the percentage hatch of the eggs under different conditions.

The overall means calculated from these data are given in Table 10. In this table it can be seen that, as Bacot showed, body lice live longer and lay more eggs per day than head lice. As regards the effect of different feeding periods per day, the length of life responds differently to egg production. Presumably owing to warmer average conditions, the metabolism of lice worn continually on the body is more rapid than lice fed 12 hr. per day; consequently the life span is exhausted earlier. Lice fed only 3 hr. per

Table 6. *Mean weights (in mg. with standard errors) of lice from 'captive' strains*

Date of sample	Strain	Generation	Males	Females
Nov. 1943	B24	6th	1·49 ± 0·051	2·40 ± 0·063
	H24	14th	0·90 ± 0·053	1·80 ± 0·017
Feb. 1944	B24	9th	1·39 ± 0·036	2·36 ± 0·101
	H24	18th	0·88 ± 0·030	1·64 ± 0·119
Aug. 1944	B24	19th	1·38 ± 0·040	2·41 ± 0·136
	H24	28th	0·84 ± 0·018	1·33 ± 0·033
Nov. 1944	B24	23rd	1·38 ± 0·059	2·36 ± 0·066
	H24	32nd	0·88 ± 0·025	1·29 ± 0·064
	(B × H) 24	1st	1·12 ± 0·020	1·73 ± 0·089
Dec. 1944	B24	24th	1·43 ± 0·033	2·49 ± 0·033
	H24	33rd	0·96 ± 0·018	1·36 ± 0·031
	(B × H) 24	2nd	1·47 ± 0·032	2·49 ± 0·156

Table 7. *Mean dimensions (in mm. with standard errors) of body strain, head strain and the 1st and 3rd generations of a cross between them. All fed 24 hr. per day*

Strain	Head length	Head width	Total length
		Males	
Body	0·5303 ± 0·0140	0·3907 ± 0·0020	3·380 ± 0·070
B × H Cross F_1	0·4909 ± 0·0073	0·3867 ± 0·0025	3·127 ± 0·030
B × H Cross F_3	0·5250 ± 0·0093	0·3905 ± 0·0032	3·350 ± 0·038
Head	0·4573 ± 0·0029	0·3618 ± 0·0022	2·786 ± 0·054
		Females	
Body	0·5555 ± 0·0052	0·4203 ± 0·0022	3·811 ± 0·036
B × H Cross F_1	0·5347 ± 0·0089	0·4209 ± 0·0035	3·708 ± 0·034
B × H Cross F_3	0·5575 ± 0·0063	0·4263 ± 0·0032	3·867 ± 0·038
Head	0·4737 ± 0·0030	0·3875 ± 0·0020	3·270 ± 0·022

Table 8. *Percentage hatch of batches of head lice and body lice incubated at* 30° C. *and* 75 % R.H.

Strain	Day of incubation: 7th	8th	9th	10th	11th	12th
Body lice	0	45	95	97	97	97
	0	10	81	99	99	99
	0	24	79	99	99	99
	0	12	63	97	97	97
	0	1	58	94	95	95
	0	31	91	96	96	96
Average	0	21	78	97	97	97
Head lice	0	50	83	85	85	85
	0	9	57	73	73	73
	0	19	64	80	83	83
	0	14	56	77	85	87
	0	5	60	87	91	91
	0	31	76	86	86	86
Average	0	24	66	81	84	84

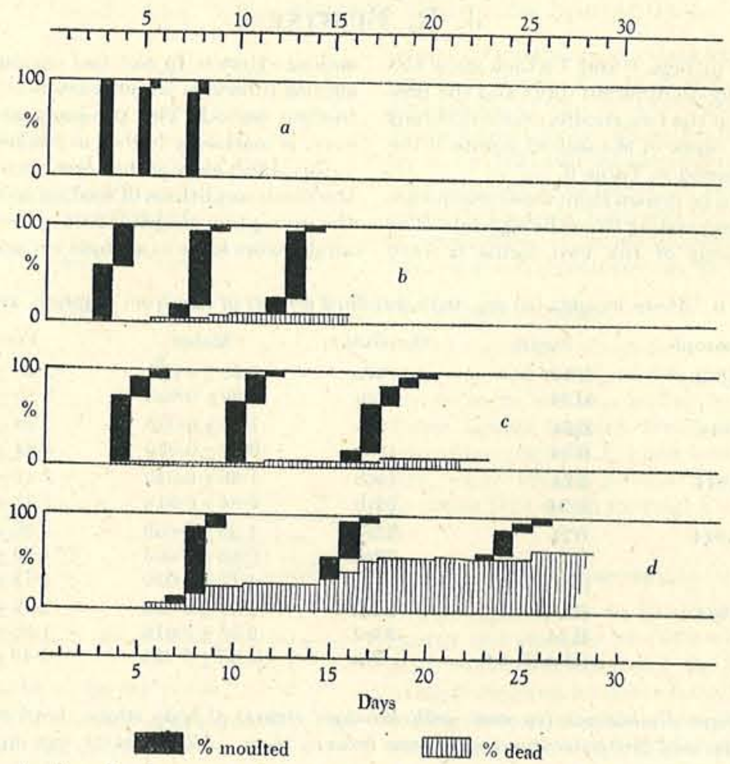


Fig. 6. Diagram illustrating development of body lice, showing the proportions moulting and dead. a = fed 24 hr./day; b = fed 12 hr./day; c = fed two periods of 3 hr./day; and d = fed 3 hr./day.

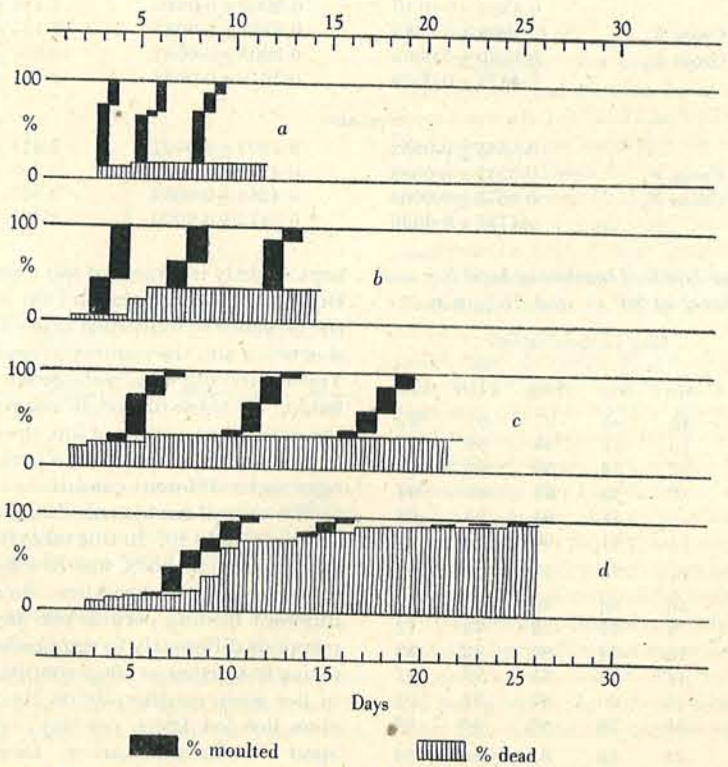


Fig. 7. Diagram illustrating development of head lice, showing proportions moulting and dead (a, b, c and d as in Fig. 6).

day, however, suffer from reduced nutrition which also curtails the life span. The optimum seems to be between 12 and 6 hr. feeding per day.

Daily egg production is directly dependent on the length of the daily feeding period; and this effect is so marked that the 24 hr. fed lice lay a greater total number of eggs per female despite the shorter average life.

(iv) *Additional experiments with a fresh body louse strain.* When these measurements of nymphal and adult life had been completed, it was perceived that the comparisons between the head strain and the body strain suffered from the anomaly that the latter had been maintained in culture for much longer than the former. Accordingly, a fresh culture of body lice was obtained from an infested man and, after four generations in captivity, experiments were done to determine the bionomic factors of the new strain. The results were as follows: (*a*) A batch of seventy-five 1st-stage larvae fed for 6 hr. per day moulted after averages of 5·0, 11·3 and 19·0 days. The total pre-imaginal mortality was 8 %. (*b*) A batch of twenty-five adults (twenty-one females and four males) were fed throughout life for 12 hr. per day. The average adult life of the females was 23·6 days; they laid 5·7 eggs per female per day over the optimum period and 108 eggs per female altogether of which 82 % hatched.

It will be found that in both these experiments, the development, adult life and egg production of the new strain was extremely similar to the ordinary body louse stock (B 12).

(*b*) *Miscellaneous experiments*

(i) *Resistance to starvation.* Adult lice of various strains were starved in incubators at 23 and 30° C. at 75 % relative humidity and in darkness. The insects were placed on pieces of tape in small vials and each was only examined for mortality once at the stated time. The percentages dead after the different intervals are shown in Table 11. These figures were calculated from rather small numbers (about ten lice of each sex), but the differences between the head and body forms are obviously very great. Rough curves drawn through these points give the following approximate periods for 50 % starvation:

Strain	23° C. Males (hr.)	23° C. Females (hr.)	30° C. Males (hr.)	30° C. Females (hr.)
Head lice	55	40	34	24
Body lice	86	80	45	36

Table 9. *Average times from hatching to various moults of head and body strains of lice worn for different periods of the day*

Strain	Worn on body (hr. per day)	Average time (days) from hatching to: 1st moult	2nd moult	3rd moult	Pre-imaginal mortality %
Body lice	24	3·1	5·3	8·3	0
	12	3·4	7·9	12·8	9
	2 × 3*	4·4	10·3	17·5	9
	3	8·0	15·8	24·3	64
Head lice	24	3·3	5·6	8·5	15
	12	3·5	7·6	12·2	35
	2 × 3*	5·3	11·5	17·6	32
	3	8·3	15·4	23·0	97

* I.e. 3 hr. in morning and 3 hr. in evening.

Table 10. *Statistics of adult life of head and body strains of lice. The figures in parentheses in the 'length of life' columns give the numbers of individuals from which the averages were calculated. Standard errors are also given in these columns*

Strain	Fed (hr. per day)	Average length of life (days ± S.E.): Males	Females	Eggs* per female/day	Total eggs/female	Average percentage hatch of eggs
Body lice	24	19·6 ± 1·41 (16)	19·8 ± 2·74 (9)	11·1	110	94
	12	30·4 ± 2·43 (14)	20·6 ± 3·04 (11)	5·7	98	91
	2 × 3	30·1 ± 1·38 (22)	24·8 ± 1·31 (46)	3·4	73	78
	3	13·2 ± 2·60 (10)	15·4 ± 2·81 (9)	1·7	15	0
Head lice	24	10·5 ± 0·65 (4)	9·1 ± 0·81 (9)	7·5	57	88
	12	—	22·1 ± 3·17 (9)	4·3	56	76
	2 × 3	—	17·3 ± 2·19 (9)	2·6	22	64

* Over main oviposition period.

(ii) *Mating choice.* In order to determine whether the head and body strains exhibit any preference for mating with their own strain, experiments were conducted in which the two forms were confined together in the same breeding tin and examined for mating at intervals. In order to determine the origins of pairs in copulation, some simple marking method was necessary. In spite of several attempts, no paint or lacquer was found which would persistently adhere to the cuticle of the louse. Therefore they were marked by amputation of one antenna. (Sometimes the left antennae of body lice and the right of head lice, and sometimes vice versa.) After a day to recover from the operation, the experiment was started with equal numbers of both forms. The matings observed in the course of seven experiments are recorded in Table 12. This table is of considerable interest. The totals of like and unlike matings are not very different (twenty-two and twenty-five respectively); but among the unlike matings there is a great preponderance of matings between body males and head females. A possible explanation of this fact (and the corresponding low number of reverse matings) is the position at copulation in which the male has to arch his abdomen upwards to effect the union. Such a position is probably easier for males with a *relatively* larger abdomen, which might explain the larger number of successful matings between the larger (*corporis*) males with smaller (*capitis*) females.

Table 11. *Results of starvation tests with body lice and head lice. The body lice used were from* B 24 *(8th generation) and stock (duplicate tests pooled) and the head lice were* H 24 *(17th generation)*

Temperature	Sex	Strain	Percentage dead after different periods (hr.) 24	41	48	72	96	120
30° C.	Males	Body lice	0	0	70	—	—	—
		Head lice	0	100	100	—	—	—
	Females	Body lice	0	90	100	—	—	—
		Head lice	100	100	100	—	—	—
23° C.	Males	Body lice	—	—	0	29	77	71
		Head lice	—	—	43	91	100	100
	Females	Body lice	—	—	0	12	95	100
		Head lice	—	—	71	100	100	100

Table 12. *Matings observed between head and body lice marked by amputation of one antenna*

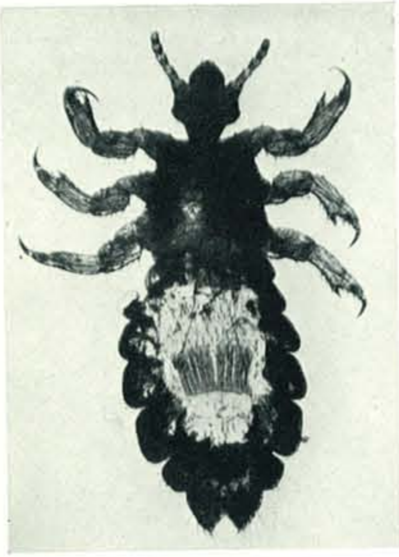
Test no.	No. of pairs	Matings observed H♂ H♀	H♂ B♀	B♂ H♀	B♂ B♀
1	8	1	0	4	3
2	2	1	0	0	1
3	16	4	1	3	3
4	?	0	1	2	1
5	10	1	1	7	2
6	3	0	0	1	1
7	10	1	0	5	3
Total	—	8	3	22	14

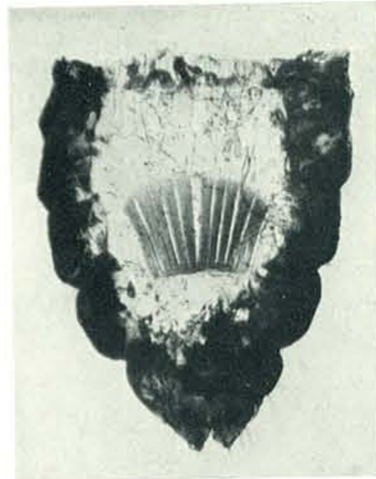
(iii) *Egg-laying preferences.* The following simple experiments were conducted to compare the egg-laying instincts of the two forms of lice. Large breeding tins were furnished with tufts of human hair, pieces of black voile and pieces of black tape. About a dozen adult lice (either of *capitis* or *corporis* strain) were put in each tin and the tins were worn on the leg for 24 or 48 hr. The eggs laid on the various materials were then counted, with the results shown in Table 13. It will be seen that there was considerable variation from one tin to another, but that the head lice showed a clearly marked aversion to laying eggs on the fibres of tape when other materials were available. (If they have no other choice, they will lay eggs on tape provided in an otherwise bare tin.) With both strains, the averages suggest a slight preference for human hair over voile, but this is of doubtful significance in view of the small number of tests.

(5) *Discussion of experimental section*

A variety of measurements of 'wild' head and body strains of lice have been given, including measurements of parts of the body, of the opercula of the eggs and of body weights. These measurements show that it is possible to find a variety of characters in which populations of the two forms of lice differ; but in all cases there are overlaps in the curves of distribution among individuals. From the systematic point of view, therefore, it is not possible to assign an individual to either race. However, Nuttall's statement (1919*b*) that 'typical *capitis* and *corporis* represent the extremes in the variation of one species *Pediculus humanus*...' is somewhat misleading, inasmuch as the two types are massed round quite distinct means.

The results of rearing head lice in captivity for 2 years proves that it is possible to breed this strain for about forty generations without any signs of


(*a*)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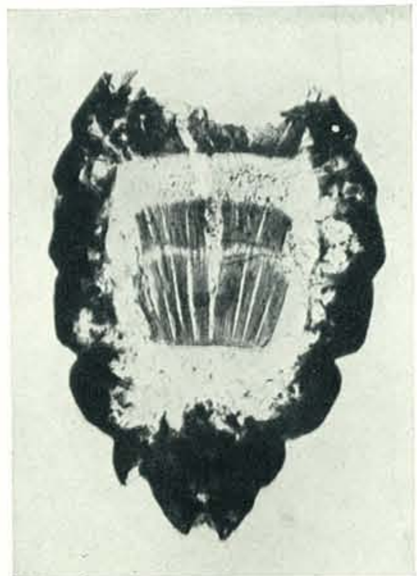
(*c*)


(*d*)

Dissections of lice to show ventral longitudinal abdominal muscles in the female. *a*, head louse; *b*, body louse with single set of muscles on segment 5; *c*, body louse with muscles on segments 4 and 5; *d*, abnormal body louse with muscles on segments 3, 4 and 5.

acquiring *corporis* characters. It must be admitted that the conditions (worn 24 hr. per day) were more favourable than those experienced by Bacot's strain (worn at night only). It seems not impossible that a *corporis* type could have been bred from Bacot's stock by natural selection (in the 2 or 3 years mentioned) since the *capitis* form is clearly a less efficient type. That such a change should have happened in 'four or more generations' seems unlikely, except with a strain which had been recently crossed with *corporis*. The measurements made on hybrids suggest either that *capitis* forms are rapidly weeded out, or that the *corporis* characters are dominant.

Table 13. *Results of tests showing egg-laying preferences of head and body strains*

Strain	Test	Eggs laid on different materials: Human hair	Voile	Tape
Body lice (B24)	I	70 (52%)	44 (32%)	22 (16%)
	II	66 (93%)	8 (7%)	0 (0%)
	III	36 (29%)	70 (56%)	18 (15%)
	IV	51 (40%)	18 (15%)	57 (45%)
	Average	— 53%	— 28%	— 19%
Head lice (H24)	I	62 (43%)	81 (57%)	0 (0%)
	II	145 (78%)	38 (22%)	0 (0%)
	III	60 (39%)	93 (61%)	0 (0%)
	IV	143 (80%)	36 (20%)	0 (0%)
	Average	— 60%	— 40%	— 0%

Table 14. *Measurements of temperature of the environment of head and body lice. 'Head temperature' taken among hair on the crown of the head. 'Body temperature' taken half way down side of the thorax. Both at 3 mm. from skin*

Subject	Indoors, air temperature 18·5° C.: Head temp.	Body temp.	Outdoors, air temperature 13·0° C.: Head temp.	Body temp.	Outdoor clothes worn
Man A	31·1	33·6	31·2	30·5	Beret, no overcoat
B	30·1	31·5	29·6	32·5	Light raincoat, no hat
C	33·0	33·9	30·0	31·3	Raincoat and peaked cap
D	31·3	33·3	29·7	31·0	Felt hat, no overcoat
Woman E	31·1	33·8	30·0	32·0	No hat or coat
F	32·6	33·4	31·7	29·6	No hat, light overcoat
G	33·0	33·0	30·8	29·6	No hat, light overcoat

It has long been known that head louse-body louse hybrids are fertile for at least three generations and I have found no trace of a preference for homogeneous matings. The question then arises of the frequency of cross-mating in nature. Nuttall, Hase and Sikora all speak of this possibility and record many cases of people infested with both head and body lice. Such opportunities for cross-mating would inhibit the development of separate varieties, which can only evolve in comparative genetic isolation.

It seems possible to me that, in recent years, the two types of infestation are becoming separated by affecting different types of host. The head louse has been shown to be most prevalent among young people, especially girls. A very high proportion of these are free from body lice, which seem to be largely restricted to those living a vagrant life among casual wards and common lodging houses. Accordingly the body louse hosts are frequently men and usually older; the very bad cases are often elderly, somewhat incapable men, living a solitary life.

Whatever may be the ultimate fate of the two types of louse, whether they survive long enough to develop into distinct species, it is clear that at present they are not sufficiently different to claim that rank. Since they are fairly similar in biology (speed of development) and since the hybrids are fertile and vigorous, they are more similar than the two races of *Calandra oryzae* described by Richards (1944). Moreover, it does not seem possible to distinguish them on morphological grounds as well as *Cimex lectularius* and *C. columbarius* (Johnson, 1939).

However, on the evidence that I have presented, there seem grounds for believing that there are some genetic differences between the two forms and they may perhaps be described as varieties. Since the typical form of head and body lice has remained recognizable since the days of Lineaus, there seem good practical grounds for retaining separate names, as follows:

Pediculus humanus humanus L.,
Pediculus humanus capitis De G.

SUMMARY

1. Measurements were made of the head length, head width, total body length, antenna length, length and breadth of 3rd antennal segment of head and body lice from natural infestations. In all measurements (except the last) the means were significantly different for the two forms, but in all cases there was considerable overlap.

2. Head lice reared continuously on the body for forty-three generations (over 2 years) did not change systematically in size. Body lice reared under similar conditions were likewise constant.

3. There was a highly significant difference between mean measurements of all the samples of head lice reared for up to 2 years on the body when compared with body lice reared for a similar period in the same way. The means for lice worn 24 hr. per day were less than those worn 12 hr. per day in both strains. An experiment showed that this is probably due to a difference in average temperature.

4. The mean live weights of head and body strains were even more distinct than linear dimensions on the several occasions when these were recorded.

5. Measurements of the dimensions of the opercula of the eggs of the two races and the numbers of air cells in them were distributed in the same way as the body measurements: that is, distinct means but overlapping individuals.

6. Ventral abdominal muscles in wild head lice are typically confined to segment 5. (The forty specimens examined adhered to this rule.) In wild body lice, muscles are usually also present in segment 4 as well.

7. Hybrids (female body × male head louse) were fertile for several generations. In size, the F_1 generation was intermediate, but the F_2 and F_3 generations became identical with the body louse strain.

8. Eggs of the body louse strain hatched at the same time as those of the head strain, but the body strain reached a significantly higher percentage hatch.

9. The times of moulting during development were studied in both races in relation to differing opportunities to feed (24, 12, 6 and 3 hr. per day). The two strains showed very similar reactions in regard to speed of development, but throughout there was a higher pre-imaginal mortality in the head strain.

10. Head lice were shown to be considerably more susceptible to starvation than body lice.

11. If adults of the two strains are mixed, there is no tendency towards homogeneous mating. Of the mixed matings, those between body louse males and head louse females are much more common than the reverse.

12. Female head lice show a slight difference in their egg-laying preferences when offered a choice of hair, voile and tape.

My thanks are due to Prof. P. A. Buxton, F.R.S., for a number of helpful suggestions based on his extensive knowledge of louse biology and to Dr J. O. Irwin for critical comments on the statistical issues.

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