THE BIOLOGY OF *PEDICULUS HUMANUS*.

By GEORGE H. F. NUTTALL, F.R.S.

(*From the Quick Laboratory, University of Cambridge.*)

(With Plates II and III and 12 Text-figures.)

CONTENTS.

	PAGE
Introduction	82

Part I.

PREVALENCE AND MODES OF DISSEMINATION.

Prevalence of lice among the poorer classes	83
Relative frequency of infestation with different lice	84
Greater prevalence of *capitis* in children and old people	84
Number of pediculi that may infest a person	86
Seasonal variation in the number of lice on man	87
Influence of climate on lice	90
Distribution of *corporis* on man's clothing and person	91
Distribution of *capitis* upon man's body	94
Modes of infestation and dissemination of *Pediculus*	94
Locomotory powers of lice on cloth and hair	99
Dissemination of lice by the wind	103
Dissemination of lice by house-flies	104

Part II.

METHODS.

Methods of raising lice experimentally	104
Attempts to raise lice by feeding them on animals, with notes on their occasional occurrence on different animals	112
Collecting, forwarding and preserving lice	113

Part III.

SPECIAL BIOLOGY.

The relative proportion of the sexes on the host	114
Disparity in the proportion of the sexes in different broods	115

	PAGE
Oviposition	117
The process of oviposition	118
Orientation and mode of attachment of the egg	121
Influence of temperature on oviposition	126
On the number of eggs laid by *P. humanus* under different conditions. Observations by previous authors	127
The number of eggs laid by *P. humanus* (*corporis*) under natural conditions. Daily average and total	129
The number of eggs laid by *capitis* in a wristlet	130
The preference shown by *corporis* for laying on certain fabrics	132
The number of eggs laid on hair as compared to cloth by *corporis* and *capitis*:	
Bacot's observations	134
The Author's observations	136
The "homing instinct" in respect to oviposition	138
The laying of unfertilized eggs	141
Summary regarding oviposition	141
Hatching: The time required for hatching	143
Delayed hatching	146
Development of the larva in the egg	147
Manner in which the larva issues from the egg	148
The empty shell	150
Fertility: Proportion of the eggs that hatch and that are fertile	152
Length of time a female remains fertile after fecundation	154
Fertilizing power of the male	155
Development from larva to adult—the moults	155
The act of moulting	156
Loss of life during development	160
Duration of the life-cycle of pediculi on man	161
Hypothetical number of descendants of one female within a limited period	162
Longevity of lice (different stages) when starved	164
Longevity of lice (adults) when fed	169
Feeding habits—the frequency with which lice feed—the gorging of lice—time occupied in feeding	171
Digestive processes	175
Some reactions of pediculi:	
Reactions to light—heliotropism—effect of light on development	176
Reactions to warmth—thermotactic reactions—effects of warmth on activities and metabolism	178
Do lice possess an olfactory sense?	180
Gregariousness	180
Vital resistance to immersion in water, cold, exposure to a vacuum and to mechanical pressure	180
Sham death, and the signs of death in lice	183
Natural enemies and parasites of lice	184

INTRODUCTION[1].

In the following account of the biology of *Pediculus humanus*, I have sought to bring together all that could be gathered from the publications of the many authors who have occupied themselves more or less with these insects, adding here and there my own observations[2]. I have sought throughout to give credit where it is due and have not withheld criticism where it appeared necessary.

Lice are insects which undergo an incomplete process of metamorphosis, *i.e.* they issue from the egg in an active form very similar, in essential particulars, to that of the adult. They are purely parasitic and live only on blood, *P. humanus* being a parasite of man and man only, its nearest related form occurring on monkeys. There are five stages in the life of the louse: (1) the nit or egg-stage, (2–4) the 1st, 2nd and 3rd larval stages, (5) the adult stage. In passing from the 1st larval stage to that of the adult, it undergoes three successive moults, increasing in size at each successive stage. The six legs, in all stages, are provided with a single large, curved, sharply pointed terminal claw specially adapted to progression on hair; it possesses simple eyes and 5-articled antennae; the mouthparts are adapted solely to the purpose of blood sucking.

GEOGRAPHICAL DISTRIBUTION. Human pediculi appear to occur in all parts of the world and on all races, but precise information is lacking, perhaps because lice are so universal. They are recorded from most parts of Europe, and by Murray (1861, p. 567) and a few other authors, from India, China, Africa, America and Australia.

I possess, or have examined up to the present, specimens from the following extra-European countries, the specimens answering the standard description of head-lice and body-lice, but some showing variations rendering exact determination impossible. In the latter case they are attributed to *capitis* if found on the head, and to *corporis* if found on the body:

Capitis: *Africa*: from Arabs, Algeria; from Dinkas, Anglo-Egyptian Sudan; from negroes, S. Ashanti and Uganda. *Asia*: from Chinese,

[1] The investigations herein described were carried out at the request of the Local Government Board, the expenses entailed being partly met by grants from the Board.

[2] With the exception of the matter contained in my previous paper: "On the copulatory apparatus and process of copulation in *Pediculus humanus*," *Parasitology*, IX. 293–324. The anatomy and histology will be treated in a future paper which will include some details regarding the mechanism of feeding and process of digestion, etc., matters which cannot be dealt with conveniently here.

Tientsin, China; from Chinese pony (mixed with *corporis*, see p. 112), Szechuen, W. China; from Tamils, Malaya; from Persia; from natives, India. *America*: from Eskimos, Frobisher Bay, Baffinland (mixed with *corporis*); from natives, Mexico.

Corporis: *Africa*: from Arabs and negro, Algeria; from negroes' clothes, N. Nigeria; from natives' axilla, the hair of the head, blankets, and from tame pig, Nyasaland; from natives' clothes, Kibondo, Belgian Congo. *Asia*: from man and pony, Szechuen, W. China; from man, Wai-Hai-Wai, China; from Japanese, Yokohama. *America*: from the United States; from natives, Mexico; from East Indian, Turkeyen, British Guiana.

As it is desirable to obtain further information regarding the distribution and variation in human lice, I shall be much indebted to any reader who will kindly supply exact data, if possible accompanied by specimens of lice (*Phthirus pubis* included) from different parts of the world.

N.B. The names *corporis* (syn. *vestimenti*) and *capitis* are used in a descriptive sense only in this paper, body-lice and clothes-lice being regarded as at most merely racial forms of the species *Pediculus humanus* Linnaeus, for reasons that will be stated elsewhere.

Part I.

PREVALENCE AND MODES OF DISSEMINATION.

The Prevalence of Lice amongst the Poorer Classes.

Under this heading, both *Pediculus humanus* and *Phthirus pubis* must be included because of the lack of classified statistics. Judging from memory of what I have seen in Mexico, and parts of Italy, and from random examinations made some years ago on a tour in Algeria, I am convinced that nowadays almost the whole poorer population in some countries is permanently infested with *Pediculus*. Historical evidence points to lousiness having been very general in all classes of European society in former times, but to-day it is largely confined to the poorer classes and to the soldiers in the field.

Statistics regarding the prevalence of lice are only given in a few papers. Thus in the United States, Greenough (1888, cited by Blanchard, 1890, p. 445) reports that of 15,551 patients admitted to hospital in Boston, Massachusetts, during the years 1878–1886, there were 914 (5·5 %) found to be verminous. In other towns in the United States and Canada, 1·5 to 3·3 % of the patients were verminous.

Figures from Germany are supplied by Kisskalt (13. v. 1915, p. 579), who records the monthly returns for January–December 1914, of the number of persons whose clothing required de-lousing[1] in the night refuges of Berlin. The refuges are under the direction of the Berliner Asylverein für Obdachslose, and between 13,000 and 15,000 persons pass through the institutions per month; the refuges are well organized and had steam-sterilizers working regularly every night to destroy vermin when I visited them some twenty years ago. The proportion of admitted persons whose clothes had to be de-loused in 1914, according to Kisskalt, varied between 5·2 and 8·0 %; no seasonal incidence of pediculosis was observed, there being, for instance, 8 % in August and 7·3 % in January.

The Relative Frequency of Infestation with Different Lice.

That *capitis* occurs more frequently on females than on males, and that the reverse holds to a certain extent for *corporis*, is shown by the figures of Greenough (1888, cited by Blanchard, 1890, p. 445), who classified 864 verminous patients admitted to hospital in Boston, Massachusetts:

Capitis	was found in	81	men and	419	women;	*i.e.*	500	times
Corporis	,, ,,	196	,,	141	,,	,,	337	,,
Ph. pubis	,, ,,	26	,,	1	,,	,,	27	,,
Totals		303		561			864	

The Greater Prevalence of *Capitis* in Children and Old People.

Children. Head-lice are particularly prevalent in children of school age, girls, because of their possessing long hair, being much more frequently infested than boys.

In *England*, for instance, Raven (1907, p. 64) records the presence of *capitis* on 80 % of the girls arriving at a convalescent home at Broadstairs, whilst an Editorial (1909, p. 1427) states that at Willesden, Lower Place Council School, 60 % of the girls required treatment for head-lice.

Similar conditions are recorded from the *United States*; thus Greene (1898, p. 70) writes of a school in Boston, Massachusetts, visited by 756 children, aged 6–16 years, of which about 50 were boys. Only 200 of the children were free from nits, the remaining 74 % were in-

[1] The word "de-lousing" requires no apology; it was needed as a specific term in this war and it has come to stay. The French equivalent is *dépouillage*, the German *Entlausung*.

fested: 234 (31 %) bore few nits, 269 (35·5 %) had many, and 53 (7 %) harboured very many nits upon their heads. Of Kindergarten children, less than 50 % were infested, whereas five-sixths of the children aged 6–12 and of the girls aged 12–16 were infested. The children not attending the Kindergarten are supposed to "take care" of their own hair; a dozen or more of these children showed eczema of the face or scalp and enlarged glands due to pediculosis. The negro children were mostly clean, this being attributed to the liberal use of vaseline or pomade for the purpose of keeping their hair parted; those whose hair was dry had the usual proportion of pediculi.

Sobel (1913, pp. 656–664), in a valuable paper, based on eleven years' experience of pediculosis in the schools of New York, states that roundly 22–23 % of the children there are infested, some 150,000 to 185,000 cases a year having been recorded during the years 1909–1912 in the public schools of New York. In six boys' schools 1·5–6 %, in six girls' schools 10–28 %, of the pupils were infested. As the result of monthly examinations and instruction, there had been a decline in the severity and sequelae of pediculosis if not in the number of cases. The examination takes place rapidly; the hair is raised and the occiput inspected for lice and nits, the girls being instructed to braid the hair at school, to unbraid and comb it at home. Sobel, like Greene in Boston, also records that negroes are less infested than whites, thus of 28,791 children in 16 schools, 2579 were coloured (0·5 % lousy) and 26,212 were white (16·5 % lousy). The homes of the negroes are mostly cleaner than those of alien whites, and negroes appear to take more care of their children's hair. Dr W. L. Funkhouser, writing to Sobel, states that of 2600 children he examined in Rome, Georgia, 800 were coloured (0 lousy) and 1800 were white (33 lousy); he attributes this to the modern efforts to straighten the hair (to get rid of the kinks), many using hair cosmetics and spending much time in combing the hair. "They will neglect their bodies for their hair." In pale, partly white, negroes whose hair is merely wavy or straight, lice are found more frequently.

As Sobel correctly states, the occurrence of pediculosis capitis may be accidental but its continued presence is due to neglect.

Old people, next to children, are most affected by head-lice. This is proved by wide experience in many countries, the aged tending to become more neglectful and uncleanly in their persons with advancing years, this being particularly noticeable among the indigent poor.

The Number of *Pediculi* that may Infest a Person.

Corporis.

No enumerations have hitherto been made on highly infested persons. A medical friend, who attended confinement cases among the poorest classes in Edinburgh, once gave me a graphic description of the thousands of lice he beheld upon the body of a patient whose skin had a greyish colour owing to the huge numbers upon it.

Hase (1915, p. 13), who enumerated the lice on a very verminous Russian, was disappointed to find but 3800 in all stages of development, having expected a larger total. Peacock (1916, pp. 45–52) gives some interesting figures relating to British troops in the present war: of the infantrymen examined, 274 (95 %) were infested with an average of 20 lice per man after 6 months' active service; about 5 % harboured 100–300 lice apiece. The number in some cases ranged from 168 to 895 per man, and Peacock estimated that one shirt held 1355 lice and 4260 nits, whilst another shirt contained no less than 10,428 lice and 10,253 nits. To these cases I may add that in a shirt worn by an old woman on admittance to Lambeth Workhouse in June, 1915, we found ca. 600 lice in all stages coupled with innumerable nits (Lot 204).

Capitis.

The number of head-lice that may occur upon a person is enormous: no enumerations have hitherto been made in heavily infested persons.

In the case of a paralytic woman, aged 45, who was admitted to a Poor House Infirmary in May, 1917, and whose hair and vermin were removed in my presence, I enumerated the lice and found 1004 present of all stages (208 adults and 796 larvae), coupled with innumerable nits; in the opinion of the sister in attendance, the case represented a very mild degree of infestation compared to others that have been admitted to the same institution. The woman's clothes harboured a few *corporis* (8 adults and some larvae) in addition.

In June, 1917, Captain Orr of the Canadian Sanitary Corps, stationed in Surrey, sent me the pubic hair shaved from a soldier. The hair harboured 82 lice (76 adults and 6 larvae), 2544 unhatched and 2636 hatched nits. The number of nits was estimated from a count made of one-quarter of the hair mass. The soldier was not infested with lice other than *capitis*.

Seasonal Variation in the Number of Lice on Man.

On the ground that typhus is chiefly a disease which prevails in camps in winter, Kisskalt (13. v. 1915, p. 379) concludes that its increase at this season cannot depend merely upon the numerical increase of lice, for no seasonal variation in the number of lice was observable in Berlin. Several authors have sought to attribute the increase of typhus to a corresponding augmentation in the numbers of lice in winter.

Beginning with the year 1909, Dr W. H. Hamer, of the London County Council, conducted observations upon the prevalence of fleas, bugs and lice in the beds and bedding of common lodging-houses. The population of such houses is not stationary. Hamer's report for 1910 (p. 7, Diagram IV) illustrates the prevalence of the insects during the preceding year (1909). Inspectors examined the beds in 11 districts,

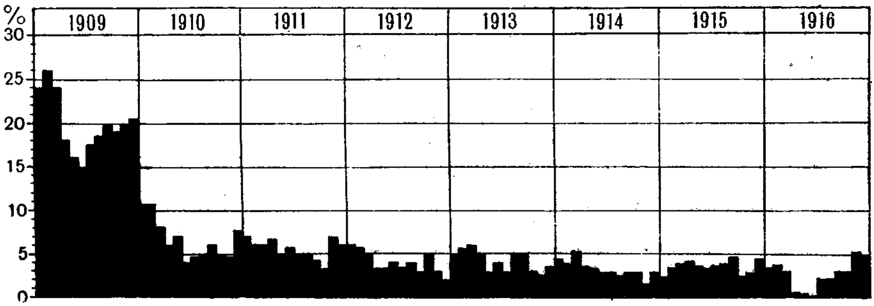

Fig. 1. Chart illustrating the variation in the percentage of louse-infested beds during the years 1909–1916, in London; the black columns represent the monthly records. The seasonal incidence is most clearly shown in 1909 and 1916. Curve constructed from data kindly supplied by Dr W. H. Hamer, of the London County Council.

"ten beds being examined daily on five days out of seven making a total of 550 beds weekly." The sheets of each bed were carefully scrutinized for lice. The louse-infested beds ranged from a maximum of 31 % to a minimum of 12 % in the first weeks of February and June respectively. The beds were found most frequently verminous in January–February; few were found infested in April–June, after which the curve gradually rose, attaining a fairly high point in August–October. The autumn rise appears partly attributable to the return to London, on the approach of winter (Sept.–Oct.), of hop-pickers who are frequently verminous, tramps and others coming later.

Dr Hamer has most kindly supplied me with data relating to the prevalence of lice in common lodging-house beds during the years

1909–1916, and the accompanying chart, which I have drawn, comprises the records for the whole period 1909–1916, the percentage of infested beds being shown in monthly columns. Dr Hamer informs me that he attributes the remarkable fall in the curve since 1909 to the undoubted improvement in the condition of the beds consequent upon the increased attention directed to them as the result of his investigation.

Hamer (1910, p. 7) refers the greater prevalence of body-lice in winter in London to the clothes being less frequently changed and washed at this season. Sergent and Foley (VI. 1910, pp. 337–373) observed a similar increase of lice during winter in Algeria, when the indigenous population wear their clothes continuously for weeks, few lice being found on their persons in summer when light clothes are worn, the children wearing hardly more than a shirt. Müller (1915, p. 53), in Austria, refers the increase of lice in winter to woollen clothes being more suited to lice than lighter fabrics. Klemperer and Zinn (II. 1915, p. 324), in Germany, attribute the subsidence of typhus in summer to the effect of heat in killing off the lice, probably basing their statement upon the observations of Anderson and Goldberger in Mexico (see p. 90). Hase (XI. 1915, pp. 160–163) attributes the much lessened prevalence of lice in the German army, during the preceding summer, to three causes having been in operation: (*a*) the heat, (*b*) increased personal cleanliness, and (*c*) greater experience in dealing with lice; he states (p. 158) that lice are more frequently encountered on the outer garments in warm weather. An increase of pediculosis capitis in winter has been observed in children by Pinkus (1915, pp. 239–241) owing to the hair being allowed to grow and its not being washed because of the cold (see the section on lice and disease, p. 68).

From the foregoing evidence, we may regard it as established that there is an increase in the louse population in the winter months and a decrease in summer. Kisskalt's figures (p. 87), showing that there is no special difference in the number of verminous persons admitted to Berlin refuges in winter and summer, do not disprove this general conclusion, since they fail to take into account the probably increased louse population per man and relate but to a very limited class of persons.

Leeuwenhoek (ed. 1807, p. 163) already noted that lice particularly trouble those who cannot change their apparel frequently; such persons are necessarily unclean. It is a matter of common knowledge that the poorer classes are more prone to wear their clothing continuously and that they are more unclean in winter than in summer. During the present war, the incidence of lice on troops who could not perforce change their clothing except at long intervals, and who could not keep themselves clean, proves how important these factors are in relation to the incidence of pediculosis. Moreover, in winter, in normal times, people congregate more in houses, and the chances of infestation spreading are greater because of increased personal contact and the increased shedding of lice by the more heavily infested individuals. In summer the clothing is lighter, either fewer garments are worn or they are of lighter material, people huddle together less, clothing is more often changed, and there is more personal cleanliness.

Apart from the factors above mentioned, which may influence the seasonal prevalence of lice on man, the *climatic conditions prevailing in clothing* deserve mention. Rubner[1], who uses the word "Kleidungsklima," writes of it only in relation to man, but it is of equal importance to the louse. The temperature of the skin, when comfortably clothed, usually ranges, according to Rubner, between 30° and 32° C., the air temperature between succeeding layers of clothing falling toward the exterior, being lowest in the outside layer. The nearer the skin, the higher the temperature and the drier the air; *the air is very dry near the body*, and it is more charged with water in the outer layers of clothing in proportion as the air grows cooler.

In the heat of summer, there is an increased amount of moisture given off from the skin, and with or without physical labour, there may be so much watery vapour given off as to render the innermost atmospheric layer almost or completely saturated, condensation taking place upon the clothing so that it becomes wet, with the consequence that the temperature of the skin rises. It has been observed in febrile conditions, that lice wander away from the host, and moreover, lice have been observed more frequently upon the outer garments in summer. Evidently the overheated body-surface and the excessive moisture are uncongenial to lice. Needless to say, active perspiration would lead to their being flooded out or driven away, especially from their usual haunts where the clothing lies most closely applied to the body-surface. It is these parts of the clothing that become wettest when active perspiration sets in. It appears to me a fair hypothesis, therefore, that the climatic conditions prevailing in clothing in summer are on the whole less suited to the body-louse than in winter. This hypothesis is, moreover, borne out by the following evidence.

That a few degrees higher temperature than that normally found

[1] Rubner, M. (1911), "Die Kleidung" in *Handbuch der Hygiene*, I. 600–606.

in clothing near the surface of the body is deleterious to *corporis* is shown, for instance, by the fall in the number of eggs that hatch at 37° C. (ca. 54 %) as compared to 30° C. (ca. 70 %) in the thermostat (see p. 152).

I have, however, obtained striking evidence of the deleterious effect of a *slight increase of warmth* on lice maintained on the person by the wristlet method (p. 107). Whilst raising *capitis*, a number of adults died prematurely, their early death being attributed to the advent of warm weather (p. 132). The heat was sufficient to cause me some discomfort at night. The wristlet, worn on the arm or knee, was covered by bedclothes and it was noticed that the adults on warm nights invariably wandered to the chiffon beneath the lid of the box, the temperature near the body accompanied by slight perspiration evidently being unpleasant to them. The lice were found dead in the box especially after warm nights. The effect of the excessive warmth in bed not only affected the adults, it increased the mortality among the hatching larvae to 27 %, whereas previously the mortality had only been 2 %.

Influence of Climate on Lice.

Anderson and Goldberger (ii. 1910, p. 183), who studied typhus fever in Mexico, observed cases on the Plateau at an altitude of 1500–1800 metres or more. The disease does not occur at lower altitudes. On enquiry, they found that body-lice are practically unknown at Tampico (Coast of Gulf of Mexico, subtropical) though head-lice are common. This is "so well known among the natives that when peons from the plateau, in search of work, arrived infested with body-lice, they declined to take any special measures for the destruction of the parasites on the ground that lice could not live there more than a few days, and such he (Dr Rolph, the authors' informant) actually found to be the case."

Apart from the higher temperature and increased atmospheric humidity prevalent at lower altitudes in Mexico, the slight rise of body temperature, amounting to about 0·5–1·0° C., which may occur, according to Plehn, in persons on first going from a cold to a hot country, may also contribute to rendering the proximity to man unpleasant, thus driving the lice to the outer clothing, starvation and death. This appears to me worth mentioning in referring to the observation above described.

It would be of interest to know if similar evidence to that emanating from Mexico is forthcoming from other parts of the globe. I have noted elsewhere (p. 82) the occurrence of body-lice in the tropics. Mr F. M. Howlett informs me that *corporis* occurs in colder parts of India and *capitis* both in cold and hot parts, but the distribution of lice requires to be studied before a decided opinion can be expressed.

THE DISTRIBUTION OF *CORPORIS* UPON MAN'S CLOTHING AND PERSON.

It is commonly stated that *corporis* is confined to the clothing, chiefly the underwear, that it lays its eggs solely on clothing and only goes upon the body to feed. Of recent authors, Pinkus (1915, p. 239), Fasal (1915, p. 225), and Sergent and Foley (VI. 1915, p. 378), may be cited as expressing this view, although Fasal adds, that if an infested man is stripped rapidly, lice are occasionally found on his body. We shall see that this view is incorrect, for *corporis* occurs on the body and it may oviposit upon the body hair.

In considering the distribution of pediculi upon the person and clothing, it is well to bear in mind that lice possess very active locomotory powers. I have seen a female *corporis* travel at the rate of 1 metre in under 3 minutes across sateen (see p. 100), and it is evident that they can run a distance equal to the length of a man's body in a few minutes. This activity of lice should not be obscured by their marked tendency to haunt or assemble on particular parts of the clothing or person.

We shall first consider the distribution of *corporis* upon the clothing of infested persons.

DISTRIBUTION UPON THE CLOTHING.

Railliet (1895, p. 827) states that *corporis* mainly infests the clothing that is closely applied to the body, *i.e.* on the back of the neck, shoulders, lumbar region, waist, wrists, thighs and external surface of the buttocks.

Legendre (1915, p. 280), writing from experience with French soldiers in the present war, states that most adult lice are found on the underclothes in contact with the body, a certain number occur on the outer garments where the nits are specially found; nits are rare on underclothes but numerous inside the tunic, trousers and neckcloth-folds, whereas there are few in puttees and usually none in the cap.

In connection with German soldiers, Uhlenhuth (1915, p. 533) states that he has seen lice on soldiers' suspenders and at the entrance to the trousers' pocket; Hase (XI. 1915, p. 158) notes that lice often occur on the outer garments in warm weather; Trappe (1915, p. 1266) states that the nits are chiefly found inside the collar; in trousers about the waistband, seams and fork, whilst many are discoverable beneath the lining.

Although precise statements are lacking regarding the distribution of lice upon the clothing of British soldiers, I gather that the condition is much the same as that described by Legendre in French troops, with the addition of the Scotch kilt which has become a notorious depository for nits, its many folds, accessible only to lice, affording an ideal place for peaceful oviposition; outer garments, made of fur, may also become heavily infested. The statement of Peacock (1916, pp. 45 et seq.) that clean shirts, issued to troops in the trenches, attained the usual degree of lousiness in two days, the lice migrating thither from the trousers, indicates already that the shirts showed most lice and that the necessity of de-lousing other garments was not at first recognized by those in authority. The renewal of one garment like a shirt is clearly of little avail if all the other clothing remains infested. German soldiers told Hase (XI. 1915, p. 158) that they preferred keeping on their dirty old greasy underclothes because these were a better safeguard than clean ones, stating that "if one puts on a clean shirt the lice are there at once."

If necklaces may be classed as clothing, it may be mentioned here that Brumpt (1910, p. 550) has seen large numbers of *corporis* upon the necklaces of naked aborigines in Africa.

DISTRIBUTION OF *CORPORIS* UPON THE BODY.

Although, as previously stated, it has been denied that *corporis* may live upon the body and deposit its eggs upon human hair, there is clear evidence to the contrary. I am convinced that *nits will be found much more frequently upon the body hair if inspection is made less casually.* The nits upon the body hair are inconspicuous objects and may well escape notice. The matter is of considerable practical importance in its bearing on the efficacy of measures directed against lice, for the measures may be vitiated if lice and nits remaining on the body are not considered. I have seen *corporis* upon the hair of the breast and axilla. The evidence of the following authors, moreover, appears conclusive:

Nysten (1858, p. 1180) states that in cases of heavy infestation, *corporis* oviposits on the body hair, mainly on that of the chest and armpits. Girard (1885, p. 1084) writes that lice occur in these situations and upon the hair of the legs, besides in the clothing and its seams; he cites some of the well-known instances of so-called phthiriasis or "maladie pédiculaire" in which *corporis* has been seen to occur in vast numbers upon the body (see p. 69). Boral (1915, p. 645) cites Flusser of the Military Hospital at Mährisch-Weisskirchen, to the effect that they shave all patients there because *corporis* nits occur on the pubic and axillary hair. Brauer (1915, pp. 561–562), in Germany, writes that contrary to what is stated in the text-books, *corporis* does occur on the body; he attributes to this the failure of prophylactic measures directed solely against lice in clothing. He states that most people harbouring these lice in their clothing have lice also on their bodies; at times large numbers of their nits are found on the hair of the pubic, peri-anal and axillary regions, and he has seen the nits on the hair of the thigh and leg. He saw *corporis* (not *Phthirus pubis*) hatch from such nits, and concludes that prevailing conceptions regarding the habits of so-called clothes-lice will have to be altered. Müller (1915, p. 52), in Austria, like Brauer, has found nits upon the hair of the pubis and axilla. Finally Heymann (18. VIII. 1915, p. 304) states that in severe infestations *corporis* occurs all over the body and clothing, citing Hase and a personal communication to this effect from Wodermann. In the note on the geographical distribution of *corporis* (see p. 83) I have already mentioned specimens collected from the axilla and the hair of the head of negroes in Africa.

Apart from the last mentioned instance, there are no cases apparently recorded of the occurrence of *corporis* upon the hair of the head. Denny (1842, p. 17) never saw or heard of a case and I can find no record of a similar case in the literature. There seems to me no valid reason why they should not occasionally invade the province of *capitis* and they may be found more frequently on careful examination.

The foregoing instances of the parasitism of *corporis* upon the body should suffice to convince the reader, since they emanate from independent eye-witnesses. It will doubtless take some years before the fact is mentioned in text-books, some of which appear to take pains to perpetuate errors, merely because the authors will not consult original sources.

The Distribution of *Capitis* on Man's Body.

As a rule *capitis* occurs on the head, mostly about the occiput and about the ears (see Plate III, and its legend). A number of authors state that it only occurs upon the head, but this is incorrect. Pinkus (1915, p. 239) writes that it is "strictly limited" to the head, but contradicts himself in the same paper by mentioning that it occasionally occurs on the body hair, extending to that of the pubis; he adds, however, that it does not proliferate there and that it has no significance in this situation. Several authors record the presence of *capitis* on the body. Denny (1842, pp. 14, 17) states that it doubtless prefers the head, yet it will stray over every part of the body, and he cites an observation of his own made at Leeds (see mention thereof on p. 96). Piaget (1880, p. 622) writes that it occasionally occurs on any part of the body and has consequently been at times confused with *corporis*. Brauer (1915, p. 561) finds that *capitis* not unrarely occurs on the body. Heymann (18. viii. 1915, p. 304) states that in heavy infestations it spreads all over the body and clothing, according to an observation communicated to him by Wodermann. Lydston (cited by Brumpt, 1910, p. 550, no reference) records its occurrence on the pubis. I describe a case of pure pubic infestation (see p. 86) wherein *capitis* proliferated actively in this situation.

We may conclude that *capitis* usually occurs upon the head, that it may spread over the body, establishing itself on other hairy parts, and that it may be confined to the pubic hair and proliferate there as my case demonstrates.

Modes of Infestation and Dissemination of *Pediculus*.

In considering the modes of infestation, it is well to bear in mind the power possessed by lice of clinging to hair and cloth. This clinging power constitutes an essential factor in their dissemination. If pediculi, especially when hungry and agile, are placed in a glass dish, they promptly cling to a piece of cloth or camels' hair brush, or to a single human hair that is brought in their vicinity; in fact this is the quickest way of collecting them out of the dish. Numberless *capitis*, under these circumstances, will cling in line upon a single hair, and they are not readily removed by forceps, for, if the grip of a leg upon the hair is loosened, another leg or two at once grasps the hair. If head-lice, thus attached to a hair, are dropped into 70 % alcohol, the insects will all die *in situ*; they appear to excel *corporis* in point of tenacity.

In the case of *corporis*, the nature of the external clothing must play an important part in respect to its liability to pick up lice that are brought in contact with it. The rougher the surface the better it is for lice to cling to. A somewhat similar instance is afforded by certain ticks which infest long-haired dogs much more readily than those that are smooth-haired. The slightest effort only is required of the louse to cling to rough cloth, one might almost say that no effort is needed, for dead lice can be readily picked up with a piece of rough cloth, because the six long and sharp claws on the feet penetrate among the fibres like so many fine curved needles. On the other hand, owing to the structure of the louse's feet, it is incapable of clinging to smooth surfaces, and a knowledge of this has led to the very general use of smooth overalls (oilskin, rubber) and foot wear for those who are exposed to louse infestation. In the laboratory, we often keep the lice we are raising in wide-mouthed unstoppered bottles, knowing that they cannot escape because they are unable to creep upward on clean glass, and, even when it is horizontal they tumble about on it and make no headway.

When corporis *are once established in clothing* they are but moderately influenced by its character. Clothing composed of rough woolly fabrics, especially where there are numerous folds and seams, affords the best protection to them. The use of *silk* underwear has been much advocated as being a protection against lice, on the assumption that it affords them a poor foothold and that they are less prone to oviposit upon it. There is no doubt, relatively speaking, that silk is not as suited to the louse as woollen materials, but it affords no safeguard against continued infestation. Lice oviposit upon silk without difficulty (see p. 132) and they cling well to silk fabrics, especially tricot. Pinkus (1915, p. 24) states that he once saw a lousy rabbi in Warsaw who was clothed in silk.

The main influence in permitting infestation to attain a severe character consists in *the continuous wearing of clothing.* This has been brought home to everybody in the present war. In former times, when lousiness pervaded all sections of society from king to beggar, it was observed that lice "especially trouble persons who cannot change their linen or other apparel frequently"; thus wrote Leeuwenhoek in the seventeenth century, at a time when most people ordinarily harboured a few lice. The frequent change of apparel was the agency which kept the numbers of the vermin down to a normal standard, for the louse population, clinging chiefly to the clothing, was removed periodically, thereby reducing the number upon the person sufficiently for practical purposes.

Man may become infested by pediculi directly or more or less indirectly. Infestation may occur in the following ways:

(1) *Contact with healthy verminous persons.* In individuals infested with pediculi, especially when these are numerous, the insects frequently stray away from their habitat. No doubt the scratching and restlessness induced by the presence of lice promote the wandering of the parasites. In common with others, I have frequently seen head-lice wandering on the hair and body-lice upon the clothing of verminous persons. Such wandering lice may pass readily from one person to another by contact. Thus the contact of children's heads at play may suffice to spread *capitis*, or merely brushing past an infested person may suffice to pick up an occasional *corporis*. Prolonged contact or close association with verminous persons is certain to lead to infestation sooner or later. Such close association is afforded in poor tenements, but this war has brought better examples in billets, dug-outs, military prisoners' camps and the like, where soldiers have huddled or been herded together, thus affording the best possible means for the dissemination of lice. Peacock (1916, p. 44) has observed that body-lice tend to wander when men's surroundings are warm and comfortable, for instance when men are sleeping closely crowded together[1]. If the present general prevalence of pediculosis in the fighting forces could be traced back to its sources it would certainly be found to be due to the introduction of lousy recruits among those that were clean. The former came from the slums and distributed their surplus lice to their companions who were handicapped by having to wear their clothing continuously.

(2) *Contact with the sick, dying, and verminous dead.* When an infested person is dying or has died, the insects wander out from their retreats in the clothing or hair. This behaviour of lice in abandoning the dead or dying recalls that of fleas and some ticks under similar circumstances. The scattering of the lice upon and about the body, is a phenomenon that has frequently been observed by those that have visited verminous individuals upon their deathbeds, or who have handled them when dead. As examples may be cited the following: Denny (1842, p. 14) saw *capitis* wandering in myriads all over the body of an old man who died in a much neglected condition at Leeds; many of the lice congregated about the nostrils, eyes, and corners of the mouth.

[1] I cannot confirm the statement by Warburton (1911) that *corporis* larvae are more prone to wander than the adults, for I find that both wander equally when hungry and the temperature is suitable. A fertilized female or two once established on a person would soon establish a flourishing colony, the conditions being suitable

Perroncito (1901, p. 596) records that in acute and chronic diseases, especially on the approach of death, *capitis* scatter from the scalp in large numbers over the face and body; the Italian hospital attendants describe the condition as an explosion of lousiness: "scoppiata la pidocchieria."

In the case of *corporis*, the scattering of the insects is perhaps less striking, because many encounter a mechanical obstacle to their wanderings outward from the clothing, nevertheless they frequently wander away from persons in fever and they scatter themselves about the bedding of those that have died. They have been seen in large numbers upon the sheets and blankets, crawling about for a couple of days in the vicinity of the dead, as credible eye-witnesses inform me. The wandering in such cases is due to hunger, or, in febrile conditions, it is apparently owing to the high temperature and possibly the repellant degree of moisture of the patient's skin. The danger of sitting upon the beds of typhus and relapsing fever patients was pointed out long ago when it was not known that these diseases were conveyed by lice (see p. 47).

(3) *Contact with the clothing, bedding, brushes, etc., previously used by infested persons.* This is a common way in which lice are disseminated. To put on verminous clothing[1] or to sleep in infested blankets or bedding, is a certain method of becoming infested with *corporis* or *capitis*. Sobel (1913, pp. 656–664), writing from a large experience of *capitis* in school children of New York, states that the problem of infestation is largely a home problem, reinfestation occurring there frequently through members of the household and bedding, clothes, towels, combs, brushes, etc., all of which are often in common use. Efforts at eradication in schools only are consequently bound to fail, because direct infestation there is relatively uncommon although it of course occurs. The beds of common lodging-houses (see p. 87) and similar institutions in various countries, are constantly being infested by vermin dropped by transitory lousy occupants. In one of the best hotels in Berlin, the proprietor told me some years ago that he always sought to exclude even the highest nobility among the travellers from some countries because they so frequently infested his guests' beds, thus necessitating a formidable process of de-lousing which took away much of the profits their sojourn entailed.

In our armies at present in the field, much blame has been attached

[1] Galewsky (III. 1915, p. 285), who was in medical charge of prisoners at Königsbrück, reports that 5000 French prisoners who were almost louse-free were mixed with 9000 Russians who were almost all lousy; the prisoners exchanged clothing with the result that the French became infested.

to *dug-outs* as centres of infestation. Peacock (1916, pp. 48–54), who has had a large practical experience of the louse problem at the western front, considers that dug-outs *per se* are wrongly blamed, for, although the men constantly assert that "the dug-outs are lousy" he failed to find lice there. The dug-outs that hold the most men have the worst reputation. He found that soldiers in open trenches, where they could not change clothes, and men in dug-outs, where they huddled together, were infested to an equal degree. Peacock does not believe that infested blankets play an important part in disseminating lice, for in a regiment with an average of 31·4 lice per man, the average per blanket was only 0·8 lice; many blankets contained no lice, others 20–60 or more apiece; in the latter case, however, the men were very unclean. In short, if I properly seize the author's meaning, the chief cause of dissemination does not lie in dug-outs and blankets, but in the men themselves and their huddling together, especially when one or more are infested, as I have previously indicated. Jeanneret-Minkine (1915, p. 130) states that lice occur in the straw sacks (*paillasses*) used by French soldiers, the sacks being made of loosely webbed fabric, and, like German observers, he rightly denies that lice lay eggs in straw.

(4) *Contact of clean persons' clothing, blankets, hats, etc., with similar articles belonging to infested persons.* In the case of *capitis*, Harding (1898, p. 95) in Boston, Mass., points out, that having found lice in school-girls' hats hung beside each other in the racks of school halls, he regards it as probable that the lice wander from hat to hat and are thus distributed. Experience with the transportation of soldiers' kit-bags in the Boer war, showed that *corporis* may wander out of bags containing infested clothing and that they may stray on to clean clothing in adjacent bags. Jeanneret-Minkine (1915, pp. 128, 130) describes how he saw Austrian grey-blue uniforms of infested men from the trenches, being piled up in a courtyard; after a few minutes they were so covered by lice as to appear of a *café-au-lait* colour when viewed at a distance of a few yards. He, moreover, saw lice wander away in large numbers from infested clothing placed on the floor; the lice migrated toward the door of a room which had been darkened. Peacock (1916, pp. 42–44) has also observed that lice congregate on the upper surface of discarded verminous clothing. It is therefore evident that clean apparel may become infested by proximity to that which is verminous.

(5) *Infestation through stray lice.* It is obvious from the foregoing that lice may be disseminated by being dropped by infested persons or

from verminous clothing and effects. It has long been known that stray lice may be picked up in public conveyances and railway carriages, particularly those that are upholstered and used by unclean persons. Like many others, I was always warned, when a child, against leaning *my head against the backs of the seats, especially in some southern* countries where *capitis* is prevalent.

LOCOMOTORY POWERS OF LICE ON CLOTH AND HAIR.

(*a*) *On Cloth.*

When placed on cloth in a window, *corporis* will usually walk away directly from the light with more or less speed, according to the prevailing temperature, the degree of light, and the nature of the fabric. When it is cool, they progress more slowly than when it is warm, and they traverse a relatively smooth-surfaced fabric more rapidly than one from which numerous fibres protrude, having fewer obstacles to encounter in attaining their goal. It is due to these several factors not having been sufficiently taken into account that the locomotory powers of lice have not hitherto been appreciated.

Several observers record the speed with which *corporis* may walk across a surface: Hase (1915, pp. 41–42, cited by Müller, 1915, p. 73) has apparently made detailed observations; he states that unfed lice walk more rapidly than those that have fed, and that large specimens walk faster than small. Over a horizontal surface of filter-paper, they walked a distance of 6·5–22·7 cm. a minute; their progress up an inclined surface was somewhat slower, and beneath rough fabrics they averaged 10 cm. a minute; the pace when walking on dirty glass, leather, plastered walls, sand, etc., was also determined. Sikora (VIII. 1915, p. 533) placed lice upon cloth inclined at 80° and found that they walked upward a distance of 10–16 cm. in a minute. Peacock (1916, p. 42), without specifying the nature of the surface, saw two lice wander a distance of ca. 150 cm. in one hour, and he notes that lice have been seen to climb 90 cm. up the wall of a room. Gerwin (1915, p. 802), apparently impressed with the migratory powers of lice, suggests that wooden gutters filled with fluid should be placed on the floor about the beds of typhus patients. None of the foregoing authors mention the temperature at which their observations were made nor the intensity of the light to which the insects were exposed[1].

[1] Galli-Valerio (9. v. 1916, p. 37) has published tracings showing the aimless meanderings of lice upon a surface without stating particulars about the experimental conditions in respect to light and temperature, etc.

A few experiments, carried out by me in sunlight, show that the locomotory powers of lice have been greatly underestimated, judging from the records above cited. Thus two *corporis* females (Lot 212) that had gorged three hours previously and had been maintained at 30° C., were placed upon a large piece of cloth on a window bench upon which the sun shone. The air temperature registered 18° C. in the shade, and a thermometer placed beneath the fabric rose to 24·5° C. The insects walked very rapidly over a distance of 30 cm., as follows, as timed in minutes and seconds by a stop-watch:

Female	Time	Material traversed	Direction
a	1′ 37″	black sateen	horizontal
a	49″	,, ,,	,,
b	1′ 40″	,, ,,	,,
b	1′ 41″	,, ,,	,,
b	2′ 53″	,, ,,	angle of 45°
b	2′ 53″	,, ,,	,, ,,
a	2′ 51″	rough cloth	horizontal
a	2′ 10″	,, ,,	,,

These records show that ♀ *a*, in her second run, actually travelled at the rate of 1 metre in 2′ 43″ on black sateen. The rate of locomotion in ♀ *b* went like that of a clockwork in four successive runs, only a difference of 1″ occurring in two horizontal runs, whilst the two runs at 45° agreed exactly in point of time (2′ 53″). The records show clearly that it takes lice longer to ascend at an angle of 45° than to traverse a horizontal surface, *i.e.* about as long as to traverse rough cloth horizontally.

(*b*) *On Hair.*

As it seemed to me of interest to determine the speed with which pediculi may climb along human hair, I constructed a simple apparatus for the purpose. This consisted of an oblong bent glass frame to which a ruler with centimetre scale was attached by crossed rubber bands; two long human hairs were stretched between the bands, and the frame was clamped to a stand which held it in any position desired. The two hairs were ca. 1 mm. apart and parallel, but they could be readily separated still further by an intervening object. When gently handled with fine forceps, the head being pointed in the desired direction, the insects promptly climbed along the hairs behind which the scale could be read. The timing was done with a stop-watch.

When climbing two hairs, the louse uses all its legs, grasping both hairs with the legs of each side, whereas in climbing a single hair, *capitis* especially used the three legs of one side, occasionally the third leg of the other side being used to right itself; after using let us say the three right legs for a while, these were replaced by the three left legs; in each case the foreleg on the side away from the hair waved about rapidly as if in search of something to grasp, whilst the insect steadily progressed. Of the legs grasping the hair, the first appeared to do most of the work, its movements recalling that of the human arm in the effort of climbing a rope. In this way, the louse climbed along the single hair, swinging from side to side as it alternately brought the left legs and then the right legs into play upon the hair. The following climbing records are those of different individuals that were tested within 24 hours of their having moulted.

Records of the Rate at which Pediculus climbs Hair.

(*a*) *Capitis*. (Lot 210.)

Apparatus placed in a window. Time given in minutes and seconds. The distance travelled was 20 cm. All the insects had fed moderately and were removed shortly before from the person. Bright diffused light from the north.

Temp.	Stage	Time	No. of hairs	Direction
17–18° C.	♀	1′ 25″	2	vertically upward
	♀	1′ 50″	2	,, ,,
	♂	1′ 50″	2	,, ,,
	♂	1′ 50″	1	,, ,,
	♀	2′ 4″	1	,, ,,
	♂	2′ 20″	2	,, ,,
	♂ [1]	2′ 25″	1	,, ,,
	♂ [1]	2′ 46″	1	vertically downward
	♂ [1]	2′ 12″	1	angle of 45° upward
	♂ [1]	3′	1	,, ,, downward
	♂	3′ 10″	1	,, ,, ,,
	♀	2′ 42″	1	,, ,, upward
	♀	1′ 32″	2	horizontally, away from light
	♀	2′ 13″	1	,, ,, ,,
	3rd st. L.	2′ 45″	1	vertically upward
	2nd st. L.	3′	1	,, ,,
	1st st. L.	8′ 57″	1	,, ,, (unfed; refused to climb when fed)

[1] The brackets denote records relating to the same individual.

(*b*) *Corporis*. (Lot 212.)

Apparatus as before. All the insects had gorged 6½ hours before and still contained a considerable amount of food; they were transferred directly from the thermostat at 30° C. They climbed so slowly that only one was allowed to climb 20 cm. The distance actually travelled is stated, but, for comparison with *capitis*, the rate of progress is given as for 20 cm.

Temp.	Stage	Time	No. of hairs	Direction	Actual distance travelled in cm.
17–18° C.	[1] {♀	5′ 54″	2	vertically upward	20
	{♀	8′ 12″	1	,, ,,	10
	♂	12′ 42″	1	,, ,,	10
	3rd st. L.	11′ 6″	1	,, ,,	10
	2nd st. L.	14′	1	,, ,,	10
	{♂	15′ 48″	1	horizontally (unfed)	10
	{♂	10′ 54″	1	,, (fed)	10
	3rd st. L.	11′ 16″	1	,,	10
	2nd st. L.	11′ 34″	1	,,	10

When the apparatus was placed in the (glazed) thermostat at 30° C., the same insects made better records. The experiments demonstrate the effect of temperature on their activity, and they now climbed the full 20 cm.

Temp.	Stage	Time	No. of hairs	Direction
30° C.	♂ unfed	2′ 13″	2	vertically upward
	[1] {♀ ,,	4′ 15″	2	,, ,,
	{♀ ,,	5′ 56″	1	,, ,,
	{♀ gorged	2′ 40″	2	,, ,,
	{♀ ,,	5′ 43″	1	,, ,,
	{♂ ,,	2′ 21″	2	,, ,,
	{♂ ,,	7′ 54″	1	,, ,,
	{♀ unfed	6′ 16″	2	horizontally
	{♀ ,,	5′ 30″	1	,,
	♂ ,,	8′ 9″	2	,,
	♂ ,,	7′ 18″	1	,,

Whilst at first sight these observations may appear trivial, they really afford striking objective evidence of the relative activity of *capitis* and *corporis* under like conditions, and of the influence of temperature on the agility of lice as evidenced in *corporis*.

The ease with which *capitis* clings, and the speed with which it travels upward along a single hair, indicates sufficiently how girls with

[1] The brackets denote records relating to the same individual.

long hair may pick up lice, the insects soon reaching the root of the hair and finding refuge near the scalp. The greater activity of *capitis* at a temperature of 17–18° C., as compared to *corporis*, is clearly demonstrated; the latter only attains a full measure of activity at a higher temperature approximating to that close to the human body. At 30° C., *corporis* is about as active as *capitis* at ca. 18° C.; it is torpid at lower temperatures.

Lice on hair climb as rapidly upwards as they do horizontally; they climb downward more slowly. *Capitis* climbs a single hair about as rapidly as it does two parallel hairs, whereas *corporis* climbs more rapidly along two parallel hairs. In short, these climbing records demonstrate a biological difference between the two races of *P. humanus*.

DISSEMINATION OF LICE BY THE WIND.

Under favourable circumstances lice (*corporis*) may be distributed by the wind. Schilling (1916, p. 1176), who records the first observation of the kind, states that Turkish officers had previously insisted that lice were carried through the air; some officers even supposing that the insects flew. Schilling reports that when examining Turkish soldiers in a valley in the Taurus, the soldiers stripped to the waist at a distance of 50–100 metres, and then walked up to be examined by a physician, behind whom stood a Commission of officers and engineers. The wind, of medium velocity, blew towards the Commission from the spot where the men undressed. Only the physician actually touched the men. After a short time, an officer observed a louse on his hand, a second officer found one on his coat, a third found one on his sleeve. After two hours, five out of six members of the Commission had captured 1–4 lice apiece, all of them occurring upon the outer garments or hands. The captured lice were about 2 mm. long and filled with fresh blood, so that they had undoubtedly been wafted over from the men, being carried far because of their small size. Subsequently thrice as many men were similarly examined, the wind being stronger, but blowing across the path pursued by the soldiers in approaching the Commission; on this occasion no lice were captured on members of the Commission. Still later, ten examinations of men on a large scale were made on a windless day and these also gave negative results. Schilling dwells on the importance of this observation in relation to the possible conveyance of typhus and relapsing fever by lice carried from a distance. Schaefer (1916, p. 1507), moreover, states that he had occasion to examine some Russian workmen prisoners; he did so in a wind, and, as a prisoner undressed before him, he saw a louse blown on to himself from the man who stood two feet away from him. Schaefer was wearing a rubber coat, consequently the louse slipped off and fell to the ground. He frequently saw lice drop from men whilst they removed their clothing, and, in consequence of the experience he narrates, always examined men afterwards whilst standing to windward of them.

DISSEMINATION OF LICE BY HOUSE-FLIES.

Calandruccio (1890, p. 135) states that he has seen *capitis* and *corporis* conveyed from place to place and person to person by flies, the insects being most prevalent in Sicily. Bohne (1915, p. 358) also refers to house-flies as carriers of lice, in the title of his paper which I have been unable to consult. Galli-Valerio (1916, p. 41) put two flies in a vessel with lice and subsequently found a louse clinging to a fly. Swellengrebel (1916, p. 13) doubts that flies carry lice about because he never saw gorged lice cling to flies that walked upon his arm whilst he fed lice thereon; as this author, however, states elsewhere that it is the hungry lice that cling promptly to passing objects, his negative opinion is somewhat invalidated. I have no doubt that Calandruccio's observation was correct; nevertheless, in the presence of the many other ways in which lice are conveyed, it seems that fly carriage can but play a very subordinate part and this under particular circumstances only.

Part II.

METHODS.

Methods of Raising Lice Experimentally.

There are various ways of raising lice experimentally, the best being those which afford conditions approximating closely to the natural.

(*a*) Raising methods whereby unlimited opportunities of feeding on man are provided together with normal or almost normal surroundings.

Anthony van Leeuwenhoek (ed. 1807, pp. 163–169) appears to have been the first to raise lice with the object of studying their life-history, and it seems appropriate to quote his description of how he proceeded to do so.

Leeuwenhoek's Raising Experiment. This astute observer determined to carry out the experiment on himself "at the expense only of enduring on one leg, what most poor people are obliged to suffer on their whole bodies during all their lives." Instead of the white stocking usually worn, he used "a fine black stocking, choosing that colour, because I considered that the eggs and the young lice thence proceeding, would be more easily distinguished upon it. Into the stocking I put two large female lice, and cutting another black stocking into long strips, I bound it over the first above the knee, to prevent their escaping. After wearing this stocking six days, I took it off, and found one of the lice in the same place where I had put it, and that it had laid fifty eggs, and in another part of the stocking the other had laid about forty eggs, but the parent I could not find. I opened the other which had laid fifty eggs, and found in its body at least fifty more, and who knows how many eggs it had laid before I put it into the stocking, and how many more eggs it might then have in its body which my sight could not reach?"

After a further period of ten days, he found some 25 lice of different sizes in the stocking; he judged that they were freshly emerged and 1–2 days old, and one egg was about to hatch. "But I was so disgusted at the sight of so many lice, that I threw the stocking containing them into the street; after which I rubbed my leg and foot very hard, in order to kill any louse that might be on it, and, repeating the rubbing four hours afterwards, I put on a clean white understocking."

Wilder (1911, p. 87) followed Leeuwenhoek's method, but placed the stocking and the contained lice upon a patient's leg. He allowed many females to oviposit and let the eggs hatch *in situ*, but did not continue the experiment. No further experiments of the kind have been carried out to my knowledge.

The Felt Cell Method.

The method used by me for raising *corporis* through its life cycle upon the body was as follows: A thick (0·5 cm.) oblong piece of dark blue felt was made into a cell, an oval aperture, measuring 5 × 4 cm., being cut in the centre. The felt cell was laid upon the forearm, and folded strips of felt and cloth were laid into the oval space, so as to afford interstices corresponding to the seams in clothing, into which the introduced lice could retreat at will. A small piece of black sateen was next laid upon the cell, and the whole covered by a thin black stocking, the foot of which had been cut off. Beneath both ends of the stocking,

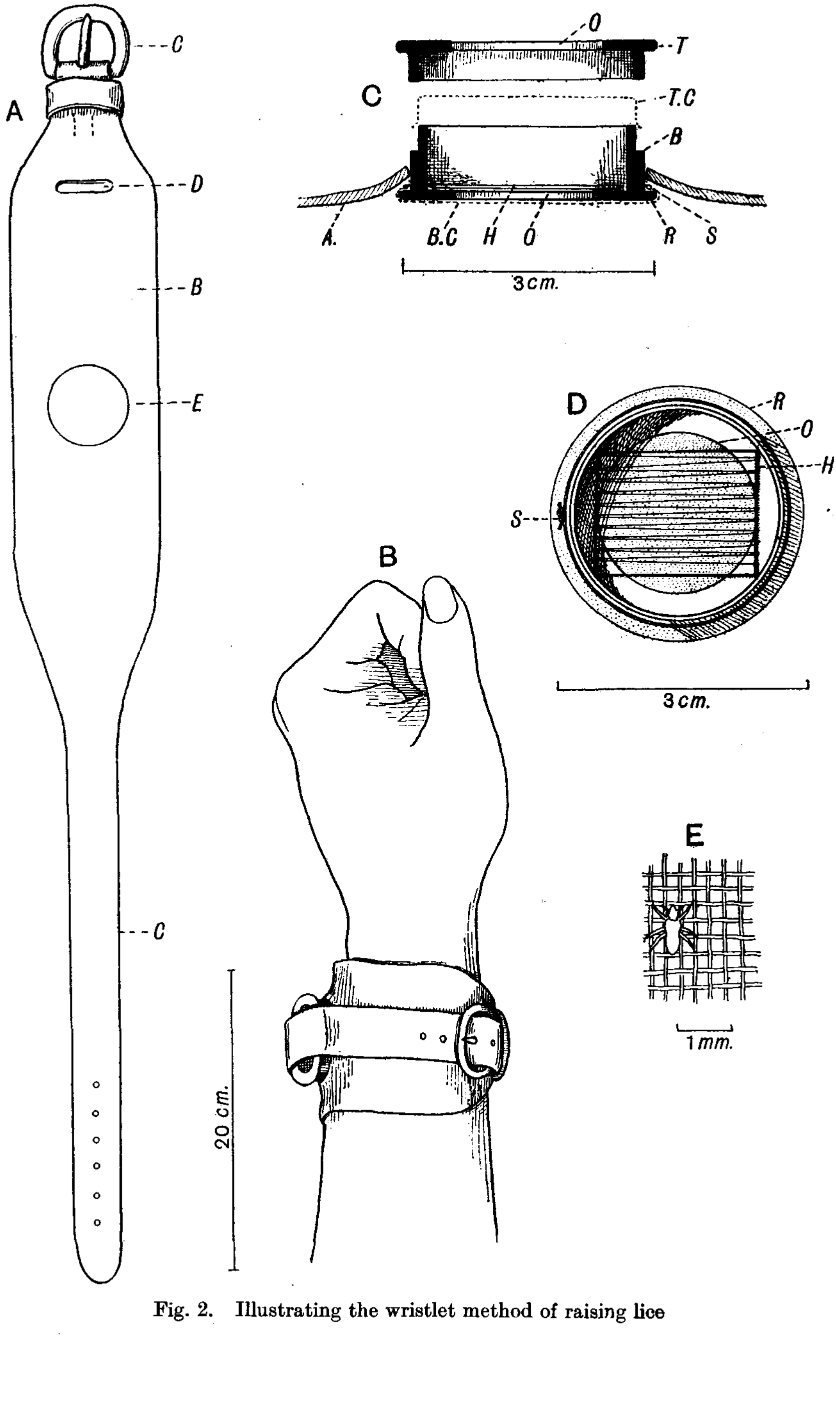

Fig. 2. Illustrating the wristlet method of raising lice

near the elbow and wrist, a narrow strip of absorbent cotton surrounded the arm, and light elastic bands held the stocking down on the skin immediately beyond the two cotton barriers. A light bandage was now applied firmly to the forearm and fixed with safety pins. With this arrangement, it was found that the insects rarely escaped from the cell; if they did so they could but escape into the stocking, the cotton barriers and elastic bands effectually blocking further progress. The contents of the cell were inspected daily, the exposure lasting but a few minutes, during which counts of eggs and moults were made and the arm cleansed.

The Wristlet Method.

After numerous failures in attempting to raise *capitis* satisfactorily, by the usual method employed for *corporis* (see p. 109), I obtained excellent results by the following method (Fig. 2 A—E). Some small pill-boxes were obtained at trifling cost from a druggist. A circular hole was punched in the pasteboard lid and floor by means of a wad punch hammered down sharply upon a sheet of lead. A layer of fine chiffon, such as Bacot has used, was placed beneath the floor and tied with a silk thread above the rim of the box. Another piece of loose chiffon of circular form was held firmly in place between the lid and box when the latter was shut. The chiffon on the floor of the box

Fig. 2. A. Wrist-strap with broad portion (*B*) tapering abruptly toward the buckle (*C*) and tapering to a narrow strap (*C*) at the opposite end. The aperture (*E*) is cut to fit the sides of the pill-box tightly, when, without its lid (as shown in C), it is pushed outward through the opening. The narrow strap (*C*) slips through a second aperture (*D*) to return to the buckle when the strap encircles the arm as shown in the succeeding figure.

B. Wrist-strap with pill-box as worn on the arm. Carried on the left arm by day and on the right arm by night. A and B are drawn to the same scale as indicated below.

C. A screened pill-box as seen in cross section; the solid parts of the box in black. (*A*) the strap; (*T*) the top; (*B*) the bottom; (*O*) the circular aperture in the lid and bottom. (*T.C.*) the top chiffon which slips in between the lid and box rim when the latter is closed. (*B.C.*) the bottom chiffon gummed to the under surface around the central aperture, and tied by (*S*) a thread of silk above the rim. (*H*) the hair-grid.

D. Lidless pill-box showing (*H*) the hair-grid at the bottom, resting directly over the screened aperture (*O*) in the floor. (*S*) the silk thread which holds the chiffon firmly in place. (C and D natural size.)

E. Magnified portion of shellacked chiffon, with thirty-six strands per cm., showing the relative size of an unfed first stage larva of *capitis* to the openings in the screen.

was fixed to it by gum arabic, and, after this had dried, the whole of the chiffon with its silk thread, as well as the top chiffon, were impregnated with shellac varnish, the object being to cement the fibres of the chiffon to each other at their points of crossing, thus strengthening the grating and ensuring against the escape of small lice through the apertures of the fabric whose fibres may otherwise become displaced. Fig. 2 E illustrates the size of the grating in the shellacked chiffon in relation to an unfed first stage larva, showing that the apertures are too small to permit of the escape of the louse whilst not obstructing its movement when it desires to feed. Upon the floor of the pill-box was laid a small snugly fitting frame of fine soft steel wire about 0·5 mm. thick, the frame being wound round with a long hair (as shown in Fig. 2 D) knotted to the frame at both ends, and firmly fixed to the crossings with the wire by means of shellac applied with a feather. The frames were removed and replaced by others every day or two according as they became charged with eggs. The different frames in a series were distinguished by small coloured glass beads strung on the wire, and the eggs laid on each day were spotted by means of a fine camels' hair brush with different coloured inks, thus permitting accurate registration of when they were laid. The rest of the apparatus will be readily understood by reference to Fig. 2, and the descriptive legend accompanying it. The lower part of the box is first placed in the round hole in the wrist strap (A), the lice are put in the box, the top chiffon is then placed in position and the lid closed down upon it; the strap is then applied to the arm as shown at (B). The strap is of the ordinary form used for sprained wrists. The looping of the strap upon itself holds the lid of the box down firmly in place, and the bottom chiffon is pressed down upon the skin, the pressure being regulated by suitably tightening the strap.

Both my Laboratory Assistant, Mr C. Harpley, and myself wore the strap on the wrist day and night for weeks whilst raising broods. The box was shifted periodically from one wrist to the other, up the arm, or from the front to the back of the arm. After three weeks the biting of a hundred lice repeatedly upon the same spot produced increasing irritation and I transferred the strap to the knee, wearing it like a garter. The temperature between the box and skin varied but slightly day and night (32–34° C.). That the box shifted little was shown by the impress it left upon the skin and the corresponding circular pattern made by the bites inflicted by the lice. The method here described will be referred to as the *wristlet method* in subsequent pages to avoid needless repetition in detailing the conditions under which insects under experiment were kept[1].

(b) Raising methods where the opportunities of feeding on man are limited and the surroundings but moderately normal.

Raising Corporis.

Warburton (1911, pp. 23–37), after unsuccessful attempts to raise *corporis* away from the body, succeeded as follows: he placed the insects on pieces of cloth in a cotton-plugged tube which he carried in his pocket. The lice were fed twice daily, by removing the cloth with the vermin clinging to it and placing it upon the back of the hand where they fed without leaving the cloth. Fantham (1912, pp. 513–515) appears to have merely followed Warburton's method.

Nicolle, Blaizot and Conseil (1912, pp. 110–192; 10. VII. 1912, p. 1636, and III. 1913, p. 210), in Tunisia, kept lice alive for 3–4 weeks by feeding them twice daily on man, and, between feeds, keeping them in a damp atmosphere in the thermostat at 28° C. They state that few lice died under these conditions.

Hindle has raised many generations by this method and so have I, the temperature ranging from 28–37° C., the best temperature being about 30–32° C. As I have stated elsewhere (p. 89), body-lice dwell normally in a very dry atmosphere, and we, in England, have found it unnecessary to render the air moist in the thermostat. The lice may be kept in open bottles or tubes containing a piece of cloth for them to cling to; we have used bits of black sateen as they afford a good contrast for eggs and small larvae. For some purposes I prefer small hair frames to cloth; they are more convenient for accurate inspection: but for ordinary purposes cloth is better; the lice cling to the cloth or hair, before, during, and after feeding. Lice are most conveniently fed upon the bared left forearm. It is best to sit facing a window in a good light, as young lice are small objects which may otherwise escape notice. A fine camels' hair brush or very finely pointed soft-springed forceps are used for picking up the insects that may wander or such as are required for examination.

[1] Zupnick (v. 1915, p. 564), who failed to raise *corporis* under different conditions in the laboratory, finding that at best only a few nits hatched, recommends gumming cells of dark cloth or linen upon a man's back for the purpose of raising lice. He illustrates the method by photographs, but records no observations made with the aid of it. It would be difficult to imagine a more cumbersome and unpractical method of raising lice.

Patton and Cragg (1913, p. 552) raised lice by feeding them but once a day and keeping them at room temperature, 30° C., in India. Kinloch (VI. 1915, p. 1038) fed lice upon the finger on which they were confined by a finger stall; he kept the lice at 24–37° C. in an incubator between feeds; this method, however, is unsuited for feeding lice in numbers. Legroux (VII. 1915, p. 470) attempted to raise lice by applying them once a day to the skin in a cupping glass, maintaining them between feeds on muslin in dishes at 16–18° C.; this temperature is too low for development. Heymann (18. VIII. 1915, figs. 2–3) devised cylindrical or flat metallic boxes of wire gauze for confining lice. The boxes were placed in a flat silk container sewn so as to form 50 pockets which were closed by safety pins; the silk container was worn under the clothing. He observed the development of lice in the boxes at intervals of 24 hours or more, up to four weeks; he does not state how he fed the lice.

Sikora (VIII. 1915, p. 523) confined lice in cotton-plugged tubes or screened boxes which were carried in the pocket by day, at ca. 24° C., and near the person at night, at ca. 35° C. The lice were usually fed twice a day upon the hand and forearm. Threads or hair were placed inside the containers for the lice to cling to and oviposit upon. Sikora found that larger lice would bite through silk gauze having 12 holes per centimetre, the gauze serving to enclose the insects in containers which were periodically applied to the arm, thus enabling the lice to feed. Larval lice could not feed through the gauze, because they failed to reach the skin. Larvae were confined in corn rings attached to the skin and covered over, or the feeding area was circumscribed by smearing a line of fat about it. Very few nits were laid on the gauze. Rocha-Lima (IX. 1916, pp. 1381–1383) illustrates an apparatus, devised by Sikora, for feeding lice upon the arm. It consists of an oblong wooden box about 8 cm. long, with perforated lid and bottom covered by coarse gauze, and held on the wrist by two straps. The apparatus appears clumsy, and the box, if not accurately made, might well permit lice to escape; besides it is entirely unsuited for work with small larvae. The illustration, however, gave me a useful hint which led to my devising the simpler and better wristlet method already described.

Bacot (II. 1917, pp. 229–230, Figs. 1 and 2) kept lice in glass-bottomed entomological boxes lined with cloth, the top covered with chiffon, through which the lice fed. It was an adaptation of the method he had previously devised for feeding fleas. The boxes were arranged in lots of twelve, in a pasteboard frame, whereby they were held against the skin for 6–7 hours by night. The boxes were carried in the clothes' pockets by day. In some experiments the eggs were allowed to hatch at 31° C. in the thermostat. By using a fine quality of chiffon as a screen to the boxes, Bacot was able to deal effectively with larvae. In raising *capitis*, Bacot placed hair loosely in the boxes above described instead of folded bits of cloth.

Relative advantages of the foregoing methods.

For obtaining a true picture of the biology of *corporis*, my felt cell method is the best since it places the insects under natural conditions where they at all times have direct access to the skin for feeding; they are, moreover, provided with retreats similar to those afforded by seams in clothing, and the climatic conditions are normal. The objection to the method lies in the necessity of bandaging and unbandaging the arm for inspection.

Failing this, the next best is the wristlet method as used for my experiments with *capitis*. The chiffon screen on the top and bottom of the box prevents the condensation of moisture within that inevitably takes place where glass-bottomed boxes are used as in Bacot's method. The pill-boxes can, moreover, be much more rapidly opened, cleaned and inspected, and, being shallow and the chiffon fine, a great deal of what is going on in the boxes can be seen through the chiffon with a hand-lens or binocular microscope without disturbing the inmates. It is a great safeguard against the escape of small larvae if the chiffon is impregnated and stiffened with a varnish like shellac. Successive batches of eggs, laid on hair grids, can be removed to other boxes that are carried in a bag about the neck prior to hatching. For examination, the boxes, when opened, are best placed in glass dishes. The lice stay upon the chiffon floor and hair grid, occasionally upon the chiffon lid, laying nearly all their eggs on hair. The method will work equally well with *corporis*.

To lay their full quota of eggs per day lice must have unlimited opportunities of feeding. This is demonstrated by protocols which follow (see p. 127). *There is not room in the female's body for more than a small feed, oft repeated, when she is laying ten to twelve eggs a day.* Those who have fed lice but once or twice a day have therefore reached false conclusions regarding the egg-laying capacity of lice.

Whereas *corporis*, maintained at 28–32° C., dry, in the thermostat, can be raised successfully when taken out and fed twice, or even at times once a day, they do not thrive so well as when they feed at their list. The rare feedings cause the lice to gorge themselves in an abnormal manner, which leads to a certain mortality, nevertheless they have remarkable powers of adapting themselves to such artificial conditions.

Attempts to Raise Lice by Feeding them on Animals, with Notes on their Occasional Occurrence on Animals.

In view of experimental work on typhus and relapsing fever, and the difficulties involved in finding persons willing to submit themselves to the discomfort of being bitten by lice, even when these are not suspected as possible carriers of infection, it is natural that repeated attempts should have been made to raise the insects by trying if they would feed upon different animals.

That human pediculi occasionally stray on to other animals, is well known. According to Cummings (1915) the British Museum possesses specimens collected from monkeys, cats, dogs and pigs, all of which, we may add, may live in close contact with man. I have even seen specimens stated to have been collected on a fowl. This occurrence of human pediculi on different animals, has, however, no more significance than if they were found on a hearthrug or chair unless it can be shown that they breed upon other hosts than man. Müller (1915, p. 52) investigated the reported occurrence of *corporis* upon horses, but on several occasions found that *Haematopinus asini* had been mistaken for the human parasite; on the other hand I possess both *capitis* and *corporis* collected for me from a pony in Szechuen, Western China; I have, however, little doubt but that they emanated from lousy native riders.

According to a review of a paper by Noeller (1916, p. 778), which I have been unable to consult in the original, it would appear that this author found human lice "capable of living and breeding on pigs"; it remains to be seen if this is true or not. With this questionable exception, then, there is no record of human pediculi having been raised successfully on animals.

In the following list, I have grouped the various observations in the order of the animals upon which attempts have been made to *feed* lice by different authors:

Monkey ......*corporis* feeds, but not so well as on man (Nicolle, Blaizot and Conseil, III. 1913, p. 210)[1].

Dog ....*capitis*, 20 large larvae placed on a dog, failed to feed and died on the animal (Nuttall).

Rabbit ......*corporis*, tried, but were unable to feed (Sikora, VIII. 1915, p. 531).
capitis, feed on shaved rabbit (Galli-Valerio, 1916, p. 37)[1].

Guinea-pig...*corporis*, when starved, they feed to repletion, but mostly die afterwards (Nicolle, Blaizot and Conseil, *loc. cit.*).
,, feed on young animals with coaxing, but die in 24–48 hours (Heymann, 18. VIII. 1915, p. 307).
,, feed (Sikora, *loc. cit.*; Musselius, XI. 1915, p. 170). The latter author shaved the hair or used depilatory powder[1].
,, live a short time (review of Noeller, 1916, p. 778)[1].
capitis, feed (Galli-Valerio, *loc. cit.*)[1].

Rat...........*corporis*, feed, but die (Warburton, 1911, p. 23).
capitis, feed on shaved rat (Galli-Valerio, *loc. cit.*)[1].

Mouse.........*corporis*, feed badly (Prowazek, I. 1915, p. 67).
,, refuse to feed (Fiebiger, VII. 1915, p. 645).
,, feed (Toyoda, 1914, p. 313; Sikora, *loc. cit.*)[1].
,, feed with much coaxing, on skin treated with depilatory powder; feed readily when they get accustomed, but must prick several times to draw blood (Widmann, 18. VIII. 1915, p. 290).
,, refuse to feed on young naked mouse and on shaved white mouse (Nuttall, Expt. VII. 1916).

Fowl ....*corporis*, feed under experimental condition (Brumpt, 1910, p. 550)[1].

Pigeon ......*capitis*, refuse to feed (Galli-Valerio, *loc. cit.*).

Swallow......*corporis*, tried hard to feed on naked skin of young bird but failed because of the slippery skin affording no foothold (Nuttall, Expt. VI. 1916).

Collecting, Forwarding and Preserving Lice.

Lice are best collected from the clothing and human body or hair by means of fine pointed forceps, care being exercised to grasp them gently. Hair with attached eggs should be cut off near the root without touching the eggs. For transportation alive, the insects should be placed in corked glass tubes with hair or bits of cloth to which they can cling; cotton wool is to be avoided as the insects become entangled in it. Most of the lice collected in this manner will live 2–3 days, unfed, at usual temperatures. For ordinary purposes of preservation, they should be dropped alive into 70 % alcohol.

[1] No particulars are given as to how long the lice lived after having fed, or if the feeding was ever repeated. We must presume that the lice were fed but once and that no attempt was made to raise them on blood other than human.

Part III.

SPECIAL BIOLOGY.

The Relative Numbers of Males and Females in *P. humanus*.

A few authors have noted that there appear to be more females than males present upon the infested host. For instance Harding (1898, p. 95) states this of *capitis*, and Sikora (viii. 1915, p. 528) of *corporis*. To my knowledge no actual enumerations have been made hitherto of all the lice or of an adequate number collected from persons with a view of determining if this is merely a subjective impression or not. Personally I believe that many males, especially when small, may be mistaken for third-stage larvae and thus lead to a false impression of their numbers. Moreover, when specimens are collected by inexperienced persons or assistants, there is a natural tendency to collect the largest specimens, most of which are likely to be females.

As yet, I have only been able to make one enumeration of what constituted practically all the *capitis* that were present on one person. The specimens were taken from a woman's head which was shorn in my presence. By a curious coincidence there were exactly 104 ♂ and 104 ♀ present upon the scalp. It is evident that further enumerations of the kind, both of *capitis* and *corporis*, are required to determine the proportion of the sexes upon the host, since this observation is in direct contradiction with what has hitherto been stated. In any case, Sikora's explanation that the females appear more numerous because they live slightly longer, is one that scarcely throws light on the problem.

Raising Experiments.

The proportion of the sexes, as determined by raising experiments, has yielded contradictory results. Owing to the marked disparity in the proportion of the sexes constituting the broods of certain pairs, as first discovered by Hindle (ii. 1917, p. 259), the figures obtained are specially liable to fallacious conclusions when these are based on limited observations. Mr Harrison has calculated from Hindle's ms. notes, that the latter raised (from 1590 first stage larvae) a total of 944 *corporis* to maturity of which about 40 % were ♂ and 60 % ♀, the actual numbers being 392 ♂ and 552 ♀. These figures would tend to support the view that the females are more numerous than the males. On the other hand, if we total up the progeny of Bacot's hybrids (*vide infra*) between *capitis* and *corporis*, we find that he raised 882 ♂ and 624 ♀. Assuming that it is permissible to combine the figures of both authors we obtain a grand total of 1274 ♂ and 1176 ♀, indicating that perhaps in nature the sexes balance out in equal proportions. On the other hand, of 100 insects, the progeny of 4 ♂ and 6 ♀ *capitis* (Lot 210) raised by me on man, 43 were ♂ and 57 ♀, these figures harmonizing with those of Hindle for *corporis*. My figures, however, appear to afford better evidence of the true sex ratio (in a mixture of six broods) than those of Hindle or Bacot, because the mortality among the individuals raised by me was practically nil[1]; Hindle's figures especially indicate a great mortality, which might have affected the males more than the females[2]. As previously stated, however, further enumerations of a large number of lice from a number of persons, coupled with more raising experiments, are required before final conclusions can be reached as to the relative numbers of both sexes.

THE DISPARITY IN THE PROPORTION OF THE SEXES IN DIFFERENT BROODS.

As previously stated, the results of raising experiments, especially on a small scale, may be very contradictory. Sikora (VIII. 1915, p. 528) raised two broods which yielded respectively (*a*) 10 ♂, 14 ♀, and (*b*) 5 ♂, 6 ♀. The only authors who have raised lice on a large scale are Hindle (II. 1917, p. 258) and Bacot (II. 1917, p. 253).

Although Hindle raised descendants of many pairs of *corporis*, the number of adults of each brood was usually small. Nevertheless a striking disparity in the proportion of the sexes was observable in some of these partial broods, in that a number yielded only ♂♂, others only ♀♀, and still others ♂♂ and ♀♀ in varying proportions. He raised one stock of lice through several generations, the insects being fed twice daily on man and maintained during the intervals at 30° C. in the thermostat. Excluding details that are irrelevant to the problem under discussion, I append some of his results in condensed form.

[1] Of 106 eggs, four were sterile and 102 hatched, only two larvae failing afterwards to reach maturity.

[2] *Vide* Doncaster, L. (1914), *The Determination of Sex*, Cambridge Univ. Press, pp. 73-89 (Sex-ratio).

Table showing the Disparity of the Sexes.

(*a*) In the offspring of 25 isolated pairs (Hindle).

Corporis pair	Progeny raised ♂	Progeny raised ♀	*Corporis* pair	Progeny raised ♂	Progeny raised ♀
1	9	0	14	0	9
2	12	0	15	13	18
3	10	5	16	0	2
4	26	0	17	28	2?
5	0	4	18	2	9
6	0	36	19	38	0
7	17	8	20	0	6
8	14	3	21	0	24
9	0	34	22	0	64
10	0	48	23	2?	27
11	27	0	24	8	2
12	0	45	25	0	26
13	1?	31			
			Totals	206	383

(*b*) In the offspring of mixed pairs (selected examples from Hindle).

Parents ♂ ♀	Progeny raised ♂	Progeny raised ♀
13+15	13	15
6+ 4	54	0
6+ 4	28	0
6+ 4	0	42
6+ 8	12	8
8+ 4	0	32
10+ 4	0	37

On the other hand, the following protocol from my own experiments shows greater uniformity in the proportions of the sexes (raised at 31° C.):

Parents ♂	Parents ♀	Progeny raised ♂	Progeny raised ♀	Total adults raised from 1st stage larvae
2	4	25	13	37%
4	4	17	12	34%
3	5	16	14	35%
4	4	8	16	38%
13	17	66	55	Average 36%

Bacot's observations relate to hybrids of (*a*) *capitis* ♂ + *corporis* ♀ and (*b*) *corporis* ♂ + *capitis* ♀, the progeny of fewer pairs having been reared than in Hindle's experiments but the respective broods being larger. The proportion of the sexes is seen to vary considerably; in some broods the sexes are nearly equal in numbers, in others especially the males predominate.

Table showing the Relative Numbers of the Sexes.

(*a*) In the offspring of *capitis* ♂ + *corporis* ♀ (from Bacot).

Parents		Progeny raised ♂	Progeny raised ♀
Pair 1	... ...	71	25
„ 2	... ...	130	22
„ 3	... ...	51	49
„ 4	... ...	76	35
2nd generation.	Progeny of pair 1 ...	211	181
3rd generation.	Descendants of pair 1 ...	93	110

(*b*) In the offspring of *corporis* ♂ + *capitis* ♀ (from Bacot).

Parents		Progeny raised ♂	Progeny raised ♀
Pair 1	... ...	27	22
„ 2	... ...	17	7
2nd generation.	Progeny of pairs 1 and 2	143	109
3rd generation.	Progeny of pairs 1 and 2	63	64

The cause of the variation in the proportion of the sexes in the offspring of different pairs remains to be determined. Further experiments under varying conditions may perhaps serve to explain the interesting phenomenon. The occurrence of male and female broods doubtless prevents excessive interbreeding among the descendants of a given pair, and, by insuring cross fertilization, promotes the maintenance of the species.

OVIPOSITION.

Oviposition in *P. humanus*, under favourable conditions, commences 24—36 hours after the emergence of the female from the third larval skin; it is delayed or inhibited by a low temperature. The number of eggs laid by a female is dependent upon the food supply and the temperature at which she is maintained. A few eggs may occasionally be laid by females some days after they have been fed, thus Hase (1915, p. 75, cited by Müller, 1915) saw female *corporis* lay after fasting 2—3 days, in one case even after fasting for 5 days. I have moreover seen 3 ♀♀ *corporis* (Obs. v. 16), after one feed, lay no eggs until 48 and

96 hours had elapsed, the temperature having risen from ca. 15° C. to 22—23° C. in the last 48 hours; they then laid 8 eggs.

A careful survey of the literature on lice has only revealed a single reference bearing directly upon the manner in which the louse oviposits, but it throws no light on the process. Widmann (VIII. 1915, p. 292) states of the cement with which the female fastens her eggs, that it has the property of drying quickly, for he saw a freshly laid nit adhere to the leg of a louse that climbed over a female as she was ovipositing and it was found impossible to remove it from the leg without injuring the limb. I have once seen a male to whose leg an egg was similarly cemented, and doubtless this arose in a like manner.

Before describing the act of oviposition in *P. humanus*, I would refer the reader to *Parasitology*, IX. p. 312, wherein the copulatory organs of the female are described and figured.

When viewing some living lice upon a hair-frame, of which a description follows, it struck me that the "gonopods" might well serve as graspers for the hair upon which the female is desirous of ovipositing[1]. On reflection, it appeared certain that for the female to lay an egg in proper alignment upon a single hair, she must in some way hold her abdomen accurately in a line with the hair. Not only is the hair exceedingly pliable but the abdomen of the female louse is very pendulous especially when weighted with eggs and a full meal of blood. It is well that this hypothesis of the possible function of the gonopods was formed before the act of oviposition was observed, because the function of these organs might otherwise have been overlooked. The function of the outwardly directed chitinous spines lining the vagina and of certain muscles in connection with oviposition, has already been indicated (loc. cit. p. 316).

The Process of Oviposition.

To observe the act of oviposition, I constructed small frames of bent glass or copper wire, winding a knotted line of long hairs about them in the manner depicted in Fig. 6 C (p. 123). The hair was held in place by occasional knots and gum arabic lightly applied on the outer margin of the frame. The frames were then placed in cells of suitable size and shape to fit the frames (Fig. 6 A), being constructed in a simple manner out of glass plates held together by strips of gummed paper.

[1] In vol. IX. p. 301, I stated that the so-called gonopods took no part in the act of copulation as Peacock (1916, p. 39) has assumed.

The lidless cells prevented the escape of the insects and confined them to an area corresponding in size with that of the hair-frame. Shortly after being fed, the female insects were placed upon the hair-frame in the cells and transferred to the stage of a binocular dissecting microscope placed at ca. 30° C. in a Nuttall microscope-thermostat. Until one of the females showed evidence that she was about to oviposit, only a minimum of light was allowed to enter the window, the latter being screened. Lice are very sensitive to light and care is necessary in regulating the degree of illumination required to see the insects well and not disturb them by an excess of light. The females which occasionally wander off the frame should be gently returned thereto with a fine brush. Incidentally I would mention that lice viewed under such circumstances are infinitely more active creatures than might be supposed from ordinary observation.

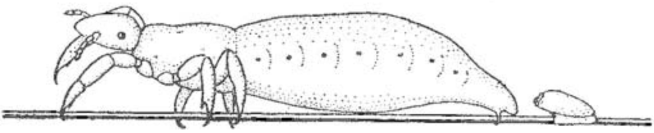

Fig. 3. Illustrating the process of oviposition upon a hair in *Pediculus humanus* (*corporis*), the insect being viewed through a microscope placed vertically. Drawing made from memory with the aid of dead specimens. The egg, a little under 1 mm. long, may serve as a scale. The female has just deposited the egg and is walking away with her gonopods still grasping the hair which is about to be released.

The females (*corporis*) walked about a good deal at first but presently slowed down in their movements. One female was observed to bend the posterior portion of her abdomen downward so that it appeared somewhat concave in profile. She maintained this posture whilst relatively quiet, for a period lasting perhaps a minute. She then walked backward along a hair which was seen to glide within the fork formed by the posterior lobes of the last abdominal segment. The gonopods were flexed away from the body and against the hair; suddenly they were seen to slip around the hair and grasp it, almost at a right angle. Whilst gripping the hair with the gonopods the female retreated still further along the hair for a distance about equal to half her body length; she then came to a stop. What appeared to be a minute drop of hyaline fluid now appeared at the sexual orifice and after a few seconds the insect walked forward, the egg being completely freed by her and cemented to the hair in the fraction of a second (Fig. 3). The female now released the hair from the grip of the gonopods, and, wandering off slowly to adjoining hairs, she came to rest. The whole act of oviposition, timed by a stop-watch, did not last over 17 seconds, counting from the time the female began to slide back along the hair until she again moved forward abandoning the egg. The latter remained cemented upon the hair with the operculum

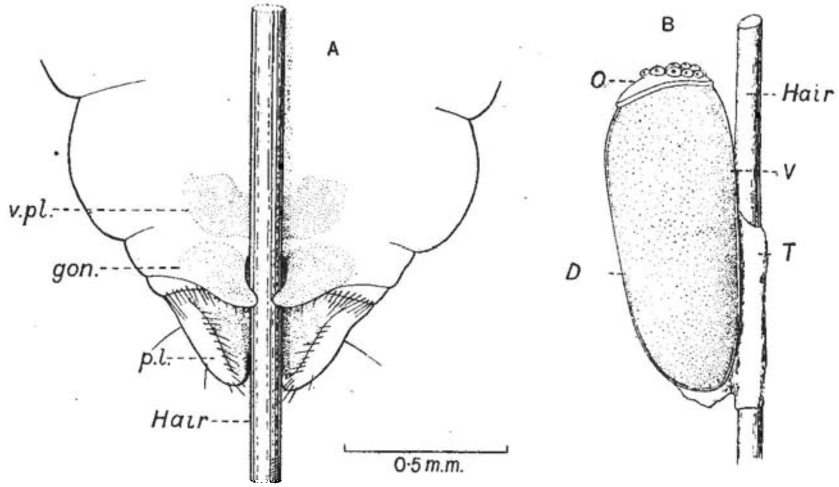

Fig. 4. (A) Posterior ventral portion of the abdomen of *Pediculus humanus* (*corporis*) ♀, illustrating the function of (*gon.*) the gonopods as claspers of human hair, whereby the insect is able to lay its eggs in alignment with the hair. At rest, the gonopods are directed backward or somewhat dorsally; when grasping a hair they are flexed downward as shown in Fig. 3. The hair passes backward between the (*p. l.*) posterior lobes of the last abdominal segment which are shaped for the purpose. Anterior to the gonopods lies the (*v. pl.*) ventral plate, the structures being pigmented and rigid, the pliable integument between them functioning like an interarticular membrane. The space between the gonopods and between the posterior lobes is adjusted to the calibre of human hair; they may, however, separate and have been seen to grasp two hairs.

(B) An egg of *Pediculus humanus* (*corporis*) cemented upon a fine human hair and seen in profile; otherwise it is orientated in relation to the adjoining figure A, the pointed end being directed backward as the egg issues from the female; (*D*) the dorsal and (*V*) the ventral surfaces of the egg, (*T*) the cement tube surrounding the hair.

Both figures drawn to scale with the aid of a camera lucida.

directed toward the female as she walked away. Dr Keilin, who immediately afterwards confirmed my observation here described, was unable to time the act because it took place too rapidly. Whereas the female I observed was seen in profile, the female observed by Dr Keilin was viewed in ventral aspect during the act of oviposition. I subsequently observed the act on two occasions. The posterior abdominal lobes were seen to be retracted and protruded several times during the process and to approach and separate from each other in the median line as if feeling and then grasping the hair. The appearance of the pointed end of the egg was preceded by a flow of cement and the egg was rapidly extruded. The females quickly released the hair from the grip of the gonopods after the egg issued, and they walked away from it. A third female made repeated and violent efforts to void an egg but failed to do so; between the throes she remained hanging to the hair by the gonopods whilst she rested.

In this connection I may mention that a hair can be readily passed either from in front or behind through the circular space between the gonopods in dead and living females; the manipulation recalls that of passing a thread through the eye of a needle. I threaded the insects under a low magnifying power; my Laboratory Assistant succeeded in doing so with the naked eye (!) after I had shown him the manipulation on specimens long preserved in alcohol. Insects thus treated remained hanging to the hair by their gonopods. When at rest, the pincers formed by the gonopods being closed, the circular interspace coincides with the calibre of ordinary fine human hair; where the hair is broader or two adjoining hairs have to be grasped the gonopods readily adapt themselves by becoming more or less separated (see Fig. 4 A). That the gonopods aid in fixing the eggs on fabrics is evident from the position of the eggs on the fibres; in an alcohol specimen I once found fibres between the gonopods, these having emanated from the felt on which the female had laid.

The Orientation and Mode of Attachment of the Egg.

Whilst the egg is in the ovary, its operculum is directed toward the head of the female, and it maintains this orientation when it issues from the sexual orifice.

The position of the female when she oviposits is the factor determining the orientation of the egg when it is laid; thus, when she lays an egg on a hair, say on the scalp, she usually walks away from the scalp, and the operculum is consequently directed toward the distal end of the hair, the egg being cemented near the hair root. On moderately infested heads as a rule only one nit per hair is found, but a considerable number of eggs may be laid one behind the other upon a single hair, all of them pointing in one direction. Fig. 5 shows them similarly placed on *pubic* hair. This latter appearance is commonly seen on the heads of persons heavily infested with head-lice and it may be observed under experimental conditions both with *capitis* and *corporis*. From the fact that the latter often oviposit deep down in the interstices of felt or in seams of clothing (in soldier language they "dig themselves in" according to Peacock), it is evident that they must also walk backward and then forward on fabrics when about to oviposit, in the same way that we have seen them do on hair.

It is worthy of note that most of the eggs laid on hair in my experiments were orientated in one way. On the hair-brush (Fig. 6 D) used for experiments with *corporis* and *capitis* all the eggs (23 and

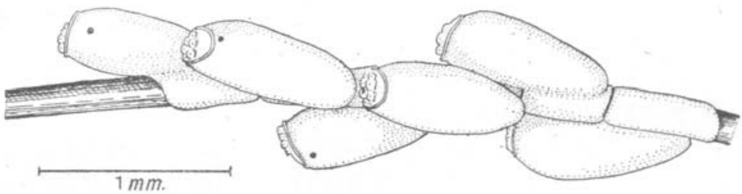

Fig. 5. *P. humanus* (*capitis*) eggs on pubic hair shaved from a soldier; the base of the hair having been cut through very close to the base of one egg. The hair bears six unhatched eggs all pointing to the distal end of the hair with their opercula; some eggs show the eyespot of the developing larva. All the lice on the soldier were confined to the pubis (see p. 86). Drawn from living specimens with the aid of a camera lucida.

33 respectively) were laid with the operculum directed toward the free end of the hair exactly as on the human head. On hair-frames, in the eggs laid *near* the glass or copper frame, most of the opercula pointed away from the frame, thus in two experiments *corporis* laid (*a*) 52 eggs directed in this way and only 4 reversed, and (*b*) 44 directed in this way and 8 reversed. The females usually go to rest near the artificial base of the hair (corresponding to the scalp) and as they lay they walk away along the hair in the manner observed by me in life.

When laid upon cloth, their orientation is almost always the same, the ventral surface of the egg being attached along its posterior half to the substratum; in this respect it is indifferent whether the egg is fixed to hair or cloth. The ventral surface of the egg corresponds to the ventral side of the female whence it issues and the egg appears to issue invariably with the ventral side directed toward the substratum to which the female clings. Already in the ovary, the egg shows asymmetry; this is clearly seen in eggs attached to hairs where they can be viewed in profile (Fig. 4 B). Thus viewed, the ventral contour appears relatively straight, the dorsal curved and slightly shortened to where it joins the operculum; the egg is broadest a short distance behind the operculum, whence it gradually tapers basally. The orientation of the egg is such that when the young larva emerges, it is able to grasp the hair or fabric directly it issues, the operculum

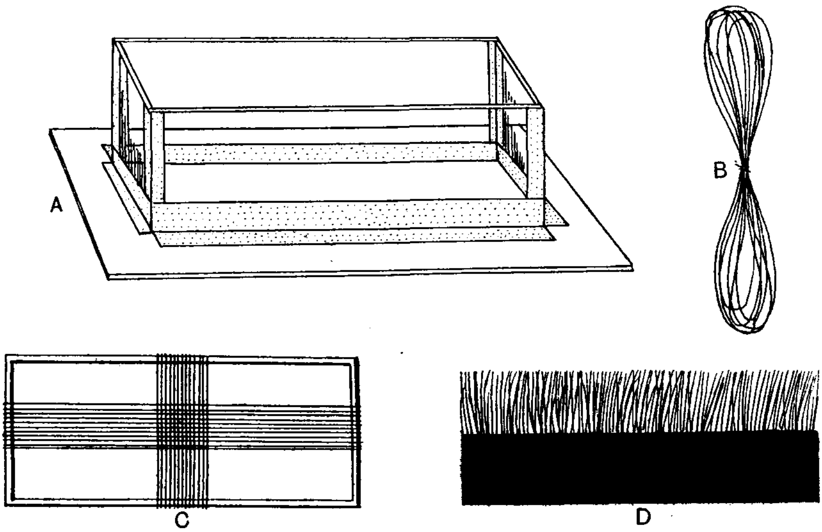

Fig. 6. (A) Glass cell used for confining lice under experiment. (B) Skein of human hair as used in experiments on oviposition. (C) A hair-frame, consisting of copper wire or glass with hair wound about it and interlaced where the hairs cross. (D) Hair brush with strip of cloth of corresponding superficial area laid upon its base. (All figs. $\frac{2}{3}$rds natural size.)

mostly springing open on the ventral side; the mechanism of hatching will, however, receive consideration elsewhere (see p. 148).

The cement that serves for the attachment of the eggs is secreted by large glands opening laterally into the uterus; it flows about the hair and base of the egg and is drawn between them by capillarity; its flow ceases before the broader opercular portion of the egg has issued, and this explains why it is always the posterior part of the egg which is cemented to the substratum; moreover, if the cement continued to flow out after the egg it would occlude the pores of the operculum.

When an egg is laid at the point of intersection of two or more hairs or fibres, these may be cemented together. The cement issues as a fluid having great wetting properties, for it forms a tube completely surrounding the greasy hair or adhering to the fibres of cloth, besides investing the posterior half of the egg, upon which it hardens rapidly as a transparent structureless membrane[1]. The latter is best seen in hatched eggs; it shows at most some irregular longitudinal ridges where it has dried in a layer of unequal thickness, the ridges converging toward the base of the tube surrounding the hair. I have but once seen a nit laid without sufficient cement, the appearance recalling in a moderate degree that seen in the pedunculated eggs of *Chrysopa*: a small amount of cement surrounded the hair, and from it a very delicate cement filament, about two-thirds the length of the egg, ran to the egg-base forming its only connection with the hair.

The rapid hardening of the cement may be fatal to a female that fails to extrude her egg promptly after the cement flows; I have seen a female so firmly held to a hair by a filament of hardened cement that she could not tear herself loose and died attached to the hair.

The hardened cement is exceedingly resistant to chemical agents, behaving like chitin in this respect; no solvent will remove it without first destroying the hair or fibre to which the egg is attached. When treated with mineral acids, acetic acid, or caustic potash, the cement tubes and eggshells remain after the hair or fabric has been dissolved, except perhaps for the detritus which may remain enclosed mechanically within the cement tubes[2].

When lice oviposit under experimental conditions upon cloth or felt resting on glass, they show a marked preference for laying their eggs on the under surface of the fabric, even when they are constantly kept in the dark. In their efforts to crawl beneath cloth resting on glass, the insects may move the fabric about considerably provided its weight is not excessive.

If narrow strips of felt are placed on end in flat-bottomed tubes with lice, the latter will lay most of their eggs underneath the small

[1] Some authors figure the cement covering the posterior half of the egg so that it recalls an egg-cup, an anterior margin or rim of cement being sharply defined as a line running round the egg; I have not seen this appearance and an attempt to stain the cement failed.

[2] Lelean (1917, p. 141), apparently on the authority of Austen, makes the erroneous statement that the cement is soluble in 10% acetic acid. Nits on hair or cloth may soak for days in the fluid but the cement does not dissolve.

end where it rests upon the glass. Thus, in ten tubes containing felt strips, some females laid 131 eggs of which 87 were attached to the bottom of the strips, 36 at the lower edge, and 8 at the sides within 0·5 cm. from the bottom. This observation led me to make the following experiments:

Expt. 1. A felt strip (Fig. 7 A) from the bottom of which a pin projected to a distance of 1·5 mm., was placed pin end down in a tube. The felt therefore did not rest directly on the glass. Lice placed in the tube laid 12 eggs at the bottom of the strip and 2 eggs near the lower edge.

Expt. 2. As lice are prone to hide in the seams of clothing it was thought that by pinning two strips of felt together like an inverted V (resting the ends on two pins to prevent the contact between the glass

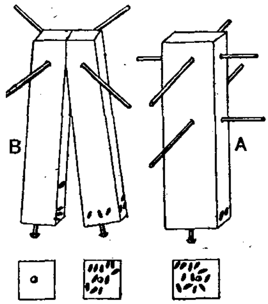

Fig. 7. Illustrating the arrangement of the felt strips used in experiments 1 and 2. The strips rest on pins projecting below, the strips being maintained vertically in the tube by pins traversing the felt crosswise. Natural size.

and felt, see Fig. 7 B) the insects would perhaps prefer to lay in the cleft. Contrary to expectation the females laid 11 eggs at the bottom of one strip, 6 near by at the sides, and only 3 in the cleft but near the bottom of the second strip. That the eggs were laid at the bottom of one strip only, serves as a good example of the "homing instinct" presently to be described.

Expt. 3. A felt strip was placed horizontally about 2·5 mm. away from the bottom of a tube, a few pendant filaments permitted the insect to climb up on the felt from below. A female laid 4 eggs, all on the more filamentous sides of the felt.

Expt. 4. A felt disc accurately fitting a tube was inserted as a floor and a strip was pinned horizontally above it at a distance of about 3 mm. Some pendant filaments extended from the strip to the floor. Three females laid 4 eggs on the sides and top of the strip and 18 on the floor.

Expt. 5. Two felt discs were placed in a tube, the one served as a floor, the other as a slanting roof to the space in which the lice were confined. The upper disc touched the floor on one side and was only slightly slanted. The lice confined in the space laid 9 eggs under the roof and 14 on the floor. Most of the eggs were laid where the discs approached each other to a distance of about 2 mm.

These experiments show (*a*) that lice prefer to lay on horizontal as against vertical surfaces; (*b*) that they greatly prefer to lay on the underside of fabrics resting on or near glass; (*c*) that when confined between two surfaces (roof and floor) of felt, the interspace allowing of free movement, they lay about equally well on both.

The Influence of Temperature on Oviposition.

The temperature at which females are kept markedly influences oviposition. For instance in one of my experiments (13—14, v. 16) 65 ♀♀ *corporis* were placed at 22° C. and only laid 3 eggs during 46 hours. When 35 of these females were placed in a thermostat at 30° C. they laid 188 eggs in 24 hours. In a second experiment 10 ♀♀ laid no eggs at 21° C. during 24 hours but when placed at 22—23° C. for a similar period they laid 8 eggs. They lay rapidly at 37° C. although this temperature shortens their lives under experimental conditions.

Sikora's statement (VIII. 1915) that lice cease to lay at 25° C. is inaccurate; the author has, however, corrected it, having since found (XI. 1915, p. 164) that eggs may occasionally be laid at 20° C. According to Hase (1915, p. 75, cited by Müller, 1915) lice do not oviposit at 12° C.

We may conclude therefore that *corporis* cease to lay at temperatures beneath 20° C. Infested persons who remove their clothing at night will consequently become less heavily infested than those who wear their clothing continuously—this being in accord with practical experience. The periodic cooling of the clothing and of the therein contained lice necessarily leads to their progeny being materially reduced.

ON THE NUMBER OF EGGS LAID BY *P. HUMANUS* UNDER DIFFERENT CONDITIONS.

OBSERVATIONS BY PREVIOUS AUTHORS.

I. *Corporis.*

The literature on lice contains statements of very unequal value in respect to the number of eggs which a female may lay. The text-books repeat the same misstatements from edition to edition and greatly underestimate the fecundity of the insect. For instance Railliet (1895, p. 827) states that they lay 70–80 eggs, and Eysell (1913, p. 48) gives the figure as 80. Recent writers, Heymann (8, VIII. 1915, p. 253; 18, VIII. 1915, p. 306), Fiebiger (VII. 1915, p. 645) like many others, merely cite from text-books without acknowledging the source of their information.

Relatively few authors contribute original observations on the subject and the data they supply are frequently imperfect, either because the conditions under which the observations were made are not stated or because the lice were only kept under observation for a few days.

The total number of eggs laid by a single female.

(*a*) *Under natural conditions.* Leeuwenhoek (ed. 1807, pp. 163–169) placed 2 ♀♀ in a stocking on his leg, and after 6 days he killed and examined the ovaries of one of the insects. From the condition of the ovaries and the egg-counts he had made, he estimated that the female would have been capable of laying at least 100 eggs.

(*b*) *Under artificial conditions.* Warburton (1910, pp. 23–27), who fed an isolated female twice daily and carried her on cloth in a tube on his person in the intervals, records that she lived 25 days and laid a total of 124 eggs. Sikora (VIII. 1915, p. 528), in an experiment conducted under similar conditions to Warburton's, found that 6 ♀♀ lived 21–45 days and laid 88, 81, 175, 194, 198 and 197 eggs respectively. Swellengrebel (1916, p. 12), without recording the conditions, saw a female lay 107 eggs. Bacot (II. 1917, pp. 236–239) records the total number of eggs laid by 6 ♀♀ which lived 23, 29, 30, 32, 32 and 34 days respectively and laid 118, 102, 180, 123, 172 and 150 eggs apiece. In his whole series the number laid ranged from 55 to 295 (maximum); the numbers I cite are the highest figures in his protocols. The average per female was 177. Bacot kept the females confined in cloth-lined entomological boxes and they were afforded an opportunity of feeding through chiffon (covering the orifice of the box) during 6–7 hours in the 24.

The number of eggs laid per day by a female.

(*a*) *Under natural conditions.* There are only two observations to record from the literature under this heading. Leeuwenhoek (loc. cit.) allowed the two females with which he experimented to remain 6 days under the stocking on his leg, and found that they had laid 40 and 50 eggs respectively during that period (average 6 and 8 eggs per day for each female). Wilder (1911, p. 87), like Leeuwenhoek, placed lice in a stocking, but he used a patient's leg instead of his own; 70 ♀♀ with 70 ♂♂ were left beneath the stocking for two days and during that period laid 1000 eggs (average ca. 7 eggs per day for each female). In both of these observations the period of observation was limited, so that the figures do not represent a true average, for the whole laying period.

(*b*) *Under artificial conditions.* Warburton (loc. cit.) records of 1 ♀ that she laid 124 eggs in 25 days under conditions already referred to (average 5 eggs per day). Fantham (1912, p. 514) following Warburton's method (?) states that a female lays 4–5 eggs per day; Widmann (VIII. 1915, pp. 292–293) saw females lay 5–6 eggs per day for 12–14 days; Swellengrebel (1916, p. 12) gives 3 eggs as the daily average. The last three authors do not state the conditions under which their observations were made. Sikora (VIII. 1915, p. 528), under conditions similar to Warburton's, found that a female laid 2–4 eggs daily for 3–4 days, then 5–7–8 daily; one female laid 20 eggs in two days; on the approach of death only 2–4 eggs were laid per day. Bacot (II. 1917, pp. 243–244), under conditions already described above, found that females laid 3·5–6·4 eggs per day, averaging 5·1 during the whole oviposition period; whilst during a limited period of 8 days ca. 5 females laid an average of 4·5–6·3 eggs per day. When they were given an opportunity of feeding for ca. 10 hours instead of 5–6 hours out of the 24, they laid an average of 8 eggs per day during a period of 8 days.

Finally, I append the result of an unpublished observation by Mr L. Harrison in my laboratory. He fed 10 ♀♀ twice a day and maintained them isolated with as many males, at 30° C. in the thermostat between meals. During a period of 10 days they laid a total of 312 eggs, the averages per day per female ranging from 1·9 to 4·1. 98 records of the number laid per day by each female show that 8 eggs a day were only laid once, and that 7, 6, 5, 4, 3, 2, 1, and 0 eggs daily were laid respectively on 3, 5, 20, 18, 16, 11, 11, and 13 occasions. The observation, though incomplete, since it does not cover the whole oviposition period, shows the combined influence of limited nutrition and moderate temperature on the number of eggs laid.

II. *Capitis.*

Our information regarding head-lice is slight in respect to the number of eggs they lay. Railliet (1895, p. 825) states that a female laid about 50 eggs in 6 days (an average of 8·3 per day). Harding (1898, p. 95), Eysell (1913, p. 47) and other authors give the total at 50–60. No observations are recorded of the total number of eggs a female may lay under natural conditions.

Bacot (II. 1917, pp. 246–248) kept the records of 20 ♀♀ maintained by him under conditions similar to clothes-lice but for the addition of hair in the boxes; of 20 ♀♀, 8 laid between 101 and 138 eggs, the others less; the daily average was 3·7. In one instance a maximum total of 141 eggs was attained.

The number of eggs laid by head-lice under the foregoing experimental conditions is less than in the case of clothes-lice; but this affords no proof that they are less fertile.

THE NUMBER OF EGGS LAID BY *CORPORIS* UNDER NATURAL CONDITIONS. DAILY AVERAGE AND TOTAL.

In the following experiment, 2 ♂♂ and 2 ♀♀, on the day of their emergence from the third larval stage, were confined in a thick felt cell bandaged to my Laboratory Assistant's arm as described on p. 105. The lice were the offspring of adults similarly confined upon the arm, and raised in the cell from the egg to the adult stage. Throughout the experiment, the insects were only disturbed for a few minutes each day so as to permit of an inspection and count of the number of eggs or moults and a periodic removal of cast skins and filth.

The adults moulted on 17. II. 1916, Day 1 of the following protocol:

Day	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
♀ *A* laid ...	0	2	10	11	12	11	12	9	11	10	10	10	9	8	11
♀ *B* laid ...	0	3	11	11	11	10	11	9	12	9	11	10	9	8	11

Day	16	17	18	19	20	21	22	23	24	25	26	27	28	29
♀ *A* laid ...	8	11	10	10	10	8	9	1	—	—	—	—	—	—
♀ *B* laid ...	9	11	9	11	10	9	9	12	12	11	11	9	8	5

On the 23rd day ♀ *A* was found dead and crushed. Total eggs 203. Average 9·6.

On the 29th day ♀ *B* died. Total eggs 272. Average 9·7 per day.

As the two females *A* and *B* were confined together, the eggs laid by each are apportioned equally in the protocol up to the death of ♀ *A*; the day of death, in the case of the latter, is excluded in computing the daily average.

One ♂ was lost on Day 7; the second ♂ was found dead on Day 28.

As far as I am aware this is the only experiment of the kind that has hitherto been carried out. The daily inspection showed that the adults fed frequently, imbibing small quantities of blood at each meal; the insects never gorged to repletion as they do when fed but twice or thrice a day. It is probable that lice which feed at frequent intervals assimilate their food better than others which gorge after more or less prolonged starvation. This, combined with the uniform conditions of temperature and moisture, explain the high total and average number of eggs they laid per day. Only one of Bacot's results shows that a female may lay up to 295 eggs, otherwise the highest totals recorded by Sikora and by Bacot are 197 and 180. Both of these authors allowed the adults but limited opportunities of feeding, and although Bacot's method is ingenious it is imperfect. The highest average numbers of eggs laid per day hitherto recorded for limited periods are those of Leeuwenhoek (8) and Wilder (7) in lice confined in a stocking worn on man; the highest average for one female recorded for the whole oviposition period by Bacot (6·4) is distinctly lower, and does not compare favourably with the average of 9·7 per day obtained by me with ♀ *B* under natural conditions. I would add that an examination of the latter female soon after death revealed the presence of three small eggs in her ovaries.

We may therefore conclude that under optimum *natural conditions* 275–300 eggs represent the normal number of eggs which a female *P. humanus* is capable of laying, and that during the greater part of her oviposition period she lays 9–12 eggs a day, or an average of 9·7.

The Number of Eggs Laid by *Capitis* in a Wristlet.

Although the wristlet method (see p. 107) cannot be stated to afford natural conditions, it has yielded results in striking contrast to those previously obtained in repeated attempts to raise *capitis* experimentally. The number of eggs laid per day by a female, as will be seen from the appended protocols, is considerably greater than has previously been recorded, and it is to be attributed to the insects having had unlimited opportunities of feeding.

The parents (1st generation)[1] of the lice experimented upon, when received from Mr Bacot, 2. vi. 1917, were placed in a wristlet where they laid eggs which yielded larvae that were raised to maturity in the wristlet.

Expt. 1. 5 ♂♂ and 7 ♀♀ (2nd gen.) that emerged 18. vi. 17 (Day 1 of the protocol) were isolated in a wristlet worn by my Laboratory Assistant (C. H.). The insects copulated on Day 1 and began to lay the day following:

Day	1	2	3	4	5	6	7	8	9	10	11	12	13	
No. of eggs laid by 7 ♀♀	0	1	42	57	53	50	55	65	58	39	42	38	13	Total 513

On the night of the 12th day of the experiment, my Laboratory Assistant unfortunately slept in bedding that contained naphthalene, with the result that the adult lice were found dead on the morning of the 13th day, only 13 eggs having been laid prior to the death of the insects during the night. In 10 days (Days 3–12) the females laid 499 eggs; about 71 apiece or an average per day of 7·1. The apportioned numbers laid per day per female during the 10 days were roundly 6, 8, 7, 7, 8, 9, 8, 5, 6, and 5. All the eggs found on the morning of the 13th day hatched out normally, showing that the naphthalene, whilst killing the parents, had no effect upon the nits.

Expt. 2. 2 ♂♂ and 3 ♀♀ (2nd gen.) that emerged 23. vi. 17 (Day 1 of the protocol) were isolated in a wristlet worn by me. The insects copulated on Day 1 and began to oviposit next day as follows:

Day	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
No. of eggs laid	0	4	13	17	16	18	20	20	23	17	20	26	17	13	11	14
by	3 ♀♀ (Days 1–12)												2 ♀♀ (Days 13–16)			

Day	17	18	19	20	21	22	
No. of eggs laid	5	6	5	5	4	1	Total 275
by	1 ♀						

Whereas in the previous experiment all the adults died on the same day by accident, in this experiment the deaths occurred in succession, the two males died on the 10th and 12th, the 3 ♀♀ on the 12th, 16th

[1] Lot 210, obtained from a girl's head, London.

and 21st–22nd day. During the first 12 days 3 ♀♀ laid roughly 1, 4, 6, 5, 6, 7, 7, 7, 6, 7, and 9 eggs apiece; during days 13–16 two ♀♀ laid about 8, 7, 5, 7 eggs apiece; and during the following 5 days the 1 ♀ laid an average of 5 per day. It is unfortunate that the adults did not live longer. Their early death is attributed by me to the advent of warm weather. Although in a sense a failure, this experiment is of interest in its bearing on what is stated on pp. 87–90 regarding the seasonal incidence of lice. A further trial of the wristlet method of raising *capitis* during cooler weather is in contemplation, as it seems reasonably certain that it will yield a larger total of eggs, the adults living longer.

The Preference shown by *Corporis* for Laying on Certain Fabrics.

That lice prefer certain fabrics to others as a habitat has been repeatedly stated. Thus Hase (cited by Müller, 1915, p. 72) is reported to have made observations showing that they prefer rough felt-like woollen fabrics, and, next in order, loosely woven cotton and flannel; tightly woven linen, cotton, and silk being avoided unless no other fabrics are available. Hase (1915 *a* cited by Friedmann, 1916, pp. 321–338) is also stated to have shown that lice definitely object to silk, since, under otherwise similar conditions, they lay eggs on wool in 24 hours but only after some days on silk. Friedmann (1916, p. 325) placed lice in dishes containing strips of various fabrics and reported that the insects always sought wool in preference to silk; and, given the choice between silk and wool, they always oviposited on wool. In view of these statements it appeared desirable to make further experiments.

To test the behaviour of female lice with regard to their preference for certain fabrics to the exclusion of others for the purpose of oviposition, a simple mode of experimentation was devised. Pieces of the different fabrics to be tested were cut of uniform size (ca. 2·5 × 1 cm.) and laid radially, like the numbers on a watch dial, upon the floor of a glass dish 10 cm. in diameter. The pieces of fabric were surrounded on all sides by an area of glass. The lice, after being fed, that is, twice a day, were put in the centre of the dish upon the glass, whence they wandered about at will in the darkness of a thermostat maintained at 32° C.

Expt. 1. Four females with males were placed in the dish with five pieces of fabric. After 72 hours they had laid

24 eggs on blue felt,
9 ,, ,, white silk tricot,
6 ,, ,, smooth white silk (old handkerchief),
4 ,, ,, glossy black silk tricot (thin stocking),
0 ,, ,, black sateen.

The last fabric on the list, the black sateen, has been used for some years in the laboratory for lice to oviposit upon: they lay readily upon it in the absence of other fabrics.

Expt. 2. A similar number of lice were placed in a dish with seven pieces of fabric. After 48 hours they had laid

15 eggs on	blue felt,	
7 ,, ,,	white silk tricot,	
5 ,, ,,	thick shaggy blue cloth	woollen,
5 ,, ,,	,, ,, grey cloth	woollen,
5 ,, ,,	thin brown cloth	woollen,
1 ,, ,,	smooth blue cloth	woollen,
0 ,, ,,	smooth white silk.	

Expt. 3. Five females were placed in a dish, 12 cm. in diameter, containing 10 pieces of fabric, five of which were smooth and five more or less rough; the rough and smooth fabrics were arranged alternately. After 24 hours they had laid

19 eggs on	white flannelette bandage	rough fabrics,
2 ,, ,,	thick bright green baize	rough fabrics,
0 ,, ,,	dark blue cloth, shaggy	rough fabrics,
0 ,, ,,	thin grey flannel	rough fabrics,
0 ,, ,,	cotton tricot, black stocking	rough fabrics,
0 ,, ,,	,, drill, thick and smooth	smooth fabrics.
0 ,, ,,	,, loosely woven	smooth fabrics.
0 ,, ,,	linen, coarse, unbleached	smooth fabrics.
0 ,, ,,	,, finely woven, smooth	smooth fabrics.
0 ,, ,,	silk, smooth white, thin	smooth fabrics.

Nearly all the eggs were laid on the flannelette from which most fine fibres projected; next in order came the baize with many coarse fibres projecting; the shaggy blue cloth was the same used in Expt. 2, where it attracted but few lice; the lice missed this and the thin flannel, and no eggs were laid on the rest, five of these fabrics being smooth.

The colour of the fabrics exerted no influence, for the insects were kept in the dark. The essential factor governing selection is apparently the *texture* of the fabrics, the ones selected being those affording the best foothold combined with interstices and irregularities of surface and especially the presence of numerous fibres to which and amongst which the eggs can easily be cemented. Felt and flannelette were the most preferred, whereas silk is by no means avoided; in fact silk tricot stands second on the list. Smooth materials are as a rule not selected, but lice will lay even on black sateen and smooth silk, especially when choice is limited.

The Number of Eggs Laid on Hair as compared to Cloth by *Corporis* and *Capitis*.

That clothes-lice may lay on hair was first recorded by Sikora (VIII. 1915, p. 524); although I had established this before in experiments with artificial scalps made of hairs planted in hard paraffin and had found eggs laid on hair most convenient for testing the effect of insecticides upon them.

Bacot's Observations.

The statement of Bacot (II. 1917, pp. 231–232) that *corporis* and *capitis* behave differently, when given a choice between cloth and hair upon which to oviposit, is of interest as indicating a biological difference between them.

According to Bacot *corporis* seldom if ever lays eggs on hair if cloth is available: (1) In one experiment, 2 or 3 ♀♀ were confined in a breeding box containing hair 2–3 cm. long, but no cloth; during a period of 3 days they laid 35 eggs of which 21 were attached to two or more hairs, especially (in 60 %) where hairs crossed each other; 4 were fixed to single hairs; 9 were fixed to the gauze cover, and 1 was attached to the hairs and box. (2) In a second experiment with flannel and hairs contained in a box, the females laid 44 eggs on flannel and 56 eggs on hair; Bacot refers this result to the matted arrangement of the hairs in the box. Bacot subsequently reported (IV. 1917, p. 63) that when *corporis* are given a choice between flannel and hair, they will lay 80 % of their eggs on flannel. He gives the protocols of two experiments (III, IV) made with two lots of 12 ♀♀ in a box containing flannel and hair. Box (A) contained females bred from eggs laid on hair, and box (B) such as had been raised on flannel. The result, after five days, was as follows:

	Box A contained	Box B contained
No. of eggs on flannel	320 (89 %)	340 (99 %)
„ „ hair	38	0
„ „ gauze	1	4
	359	344

The results with *capitis* were different. Bacot (II. 1917, pp. 231–232) states that the latter will sometimes lay eggs on cloth in the presence of hair; a fact I had also established. (1) In one experiment, he placed some females in a box with hairs only; they laid 36 eggs in 3 days, all on hair: 28 on single hairs, 6 on two hairs, and 2 on three hairs. (2) In a second experiment some females were placed in a box with hair and flannel; they laid 92 eggs on hair and 8 on flannel. Bacot subsequently (IV. 1917, p. 63) stated that given a choice of hair and flannel, *capitis* will lay 80 % of her eggs on hair. He reports two experiments (III, IV) in which two lots of 12 ♀♀ were put in boxes containing hair and flannel. Box (A′) contained females bred from eggs laid on hair, and box (B′) such as had been raised on flannel. The result after 5 days was as follows:

	Box A′ contained	Box B′ contained
No. of eggs on hair	259 (95 %)	332 (98 %)
„ „ flannel	14	4 (2 "near flannel")
„ „ gauze	1	4
	274	340

Bacot (II. 1917, pp. 231–2) has moreover stated that *corporis* females "appear to be less skilful in cementing, or careful in getting the long axis of the egg into alignment with the hair. When forced to lay on hair they not infrequently attach the egg at an angle to the axis of the hair." He cites an observation wherein of 25 eggs laid on hair in a box, 21 were "cemented to two or more hairs, the females having apparently searched for positions where the hairs crossed or ran parallel to each other so as to avoid attachment to single hairs." It will be seen that my results do not agree with those of Bacot in this respect[1].

These experiments appeared to me to call for repetition under somewhat modified conditions to be more precisely defined especially with regard to the arrangement of the test hair and cloth and the equalizing of the proportions of each.

[1] For observations on oviposition in hybrids of *corporis* and *capitis*, see Bacot, II. 1917, pp. 253 et seq.

The Author's Observations.

The following experiments were designed to control those of Bacot above described. The lice were fed twice daily and kept at 32° C. Stated briefly, Bacot's conclusions were (*a*) that *corporis* seldom if ever lays eggs on hair in the presence of cloth; (*b*) that *capitis* almost invariably lays eggs on hair in preference to cloth; (*c*) that *corporis* is less expert than *capitis* in the manner of ovipositing on hair. These statements will be considered in the same order as follows:

(*a*) *Does* corporis *lay on cloth in preference to hair?* Three experiments were carried out to answer this question:

Expt. 1. A thin brush of human hair was constructed by gumming a row of hairs between strips of paper fixed upon a piece of glass measuring $3 \times \frac{1}{2}$ an inch, the hairs projecting half an inch. A piece of woollen cloth measuring $3 \times \frac{1}{2}$ an inch was laid upon the paper on the glass, consequently the surfaces of cloth and hair, viewed from one side, possessed the same superficial area (see Fig. 6 D, p. 123). Two lots of *corporis* ♀♀ were placed respectively on two of these apparatus, and after 48 hours they had laid (A) 18 eggs on cloth and 12 on hair; (B) 10 eggs on cloth and 11 on hair.

Expt. 2. A long knotted thread of human hair was wound around three fingers and knotted in the centre (Fig. 6 B). The skein of hair was laid on the floor of a cell (Fig. 6 A) and a piece of felt the size of a slide laid upon it. Several *corporis* ♀♀ were placed in the cell and after 24 hours they had laid 9 eggs on felt and 18 on hair.

Expt. 3. A hair-frame (Fig. 6 C) was placed in a cell with a piece of cloth resting upon it. Several *corporis* ♀♀ after 5 days had laid 9 eggs on the cloth and 86 on hairs.

Taking the total number of eggs laid in the three experiments, there were 46 deposited on cloth or felt and 127 on hair. The relative number deposited on cloth and hair differed considerably in each experiment, nevertheless the results do not confirm Bacot's statement that *corporis* seldom lays eggs on hair in the presence of cloth; in fact they preferred hair to cloth.

(*b*) *Does* capitis *lay on hair in preference to cloth?* Three parallel experiments to the foregoing were performed:

Expt. 1′. The ♀♀, after 48 hours, had laid 33 eggs on hair and 4 on cloth.

Expt. 2′. The ♀♀, after 24 hours, had laid 10 eggs on hair and 0 on felt

Expt. 3′. The ♀♀, after 5 days, had laid 114 eggs on hair and 10 on cloth.

The total for the three experiments was 157 eggs laid on hair and 14 laid on cloth or felt. This result strongly bears out Bacot's contention that *capitis* shows a very marked preference for laying on hair.

(*c*) *Does* corporis *attach her eggs to hair in a different manner to* capitis? The statement by Bacot (26. II. 1917, pp. 231–232) that *corporis* lays its eggs on hair less skilfully than *capitis* is contrary to my experience during the last two years; I had failed to notice any difference of the kind in hundreds of eggs laid on hair. From what has been said of the function of the gonopods which serve to bring the egg into alignment upon a hair, it seemed to me incredible that there should be such a difference. I had also failed to observe any greater tendency in *corporis* than *capitis* to oviposit on two or more hairs at once or at the intersection of hairs, and therefore concluded, on reading Bacot's paper, that he was misled by a subjective impression. To exclude this source of error some counts were made of eggs laid on hair, the result being as follows:

(1) *Regarding the alignment of the eggs on hairs:* (*a*) Some hairs bearing eggs of *corporis*, dating from older experiments, were reexamined. The females had laid the eggs on fine ladies' hair placed in small quantity, haphazard in a tube containing the insects. Out of a total of 79 eggs, only 4 were not in perfect alignment and one of these was misplaced through contact with a previously laid egg. (*b*) In Expts. 3, 3′, previously described as conducted on hair-frames, *corporis* laid 86 eggs of which 2 were out of alignment, and *capitis* laid 114 on hairs of which 2 were out of alignment. (*c*) In another case, *corporis* laid 61 eggs, 9 thereof being out of alignment.

The slight differences observed would appear at first sight to support Bacot's view, but closer inspection showed that eggs laid out of alignment were usually placed alongside of others that had been laid previously. Out of 11 *corporis* eggs out of alignment only one was not in contact with other eggs; of 2 *capitis* eggs one was in such contact and one isolated. When an egg is laid in contact with others whose cement has hardened, it may well be misplaced to one side without this being due to any fault of the insect. In the experiment with *capitis*, the eggs were laid somewhat further apart than with *corporis*, which circumstance also explains why fewer were out of alignment. A subsequent examination of 476 *capitis* and 356 *corporis* eggs, laid on hair-grids, gave concordant results, and it was again noticed that *corporis* laid its *eggs somewhat more closely aggregated. I therefore conclude that there* is no difference in the matter of alignment of eggs deposited by the lice.

(2) *Regarding the laying of eggs on two or more hairs and at the intersection of hairs: Bacot (loc. cit., Fig. 4) states that corporis lays* more eggs at the intersection of hairs than does *capitis* under experimental conditions. A count of eggs laid on hair-frames and skeins of hair in my experiments showed no such difference. Thus out of 110 eggs laid by *corporis* there were 6 laid where hairs crossed; out of 117 eggs laid by *capitis* there were 7 laid where hairs crossed. On looking over nit-bearing hairs preserved from old experiments as examples of the oviposition of *corporis* on hairs, placed haphazard in a tube, a count revealed that of a total of 79 eggs, 57 were laid on single hairs, 14 upon two fine hairs which lay closely in contact and 4 at the intersection of two hairs. The haphazard arrangement of hairs in boxes would therefore appear to have misled Bacot. To test the matter the arrangement of the hairs should be strictly comparable. When hairs are placed loosely in a vessel, they will continually shift about owing to the movements of the insects, and uncontrollably irregular results must follow. When two fine hairs happen to lie closely apposed they are grasped by the gonopods as if they were one hair, this (Bacot, loc. cit. Fig. 3), like the occasional deposition of eggs on the glass surface of the cell, may happen with *capitis* as well as *corporis*.

The "Homing Instinct" in respect to Oviposition.

Whereas I have frequently observed that *corporis* lays eggs about one spot on a piece of cloth, the subject received no particular attention until the appearance of Bacot's paper (II. 1917, p. 232) wherein he refers to this tendency. Finding it difficult to enumerate the eggs laid by a female when they were ranged close together, Bacot sought to persuade the female to lay elsewhere by shifting the piece of cloth about within the breeding box in which she was confined. He states that as a rule he was unsuccessful, "there seemed to be some attraction which led to the deposit of fresh eggs where others were already laid." Although he does not specifically state that he observed the tendency in isolated females, it may be assumed that he did so. The tendency is said to be less marked in *capitis*.

As the presence of such an instinct in lice is of interest, I resolved to repeat Bacot's experiment under somewhat altered conditions in so far as a larger piece of cloth was chosen, and an isolated female (without a male) was allowed to wander about upon it.

(A) *Corporis.*

Expt. 1 (20–24. II. 1917). A square of thick dark blue woollen cloth, rough on one side and smooth on the other, measuring 7·5 × 6 cm., was placed rough side up upon the bottom of a circular glass dish of corresponding size. A small platform of glass, measuring ca. 1 × 1·5 cm., was laid in the centre of the cloth and the orientation of the latter noted.

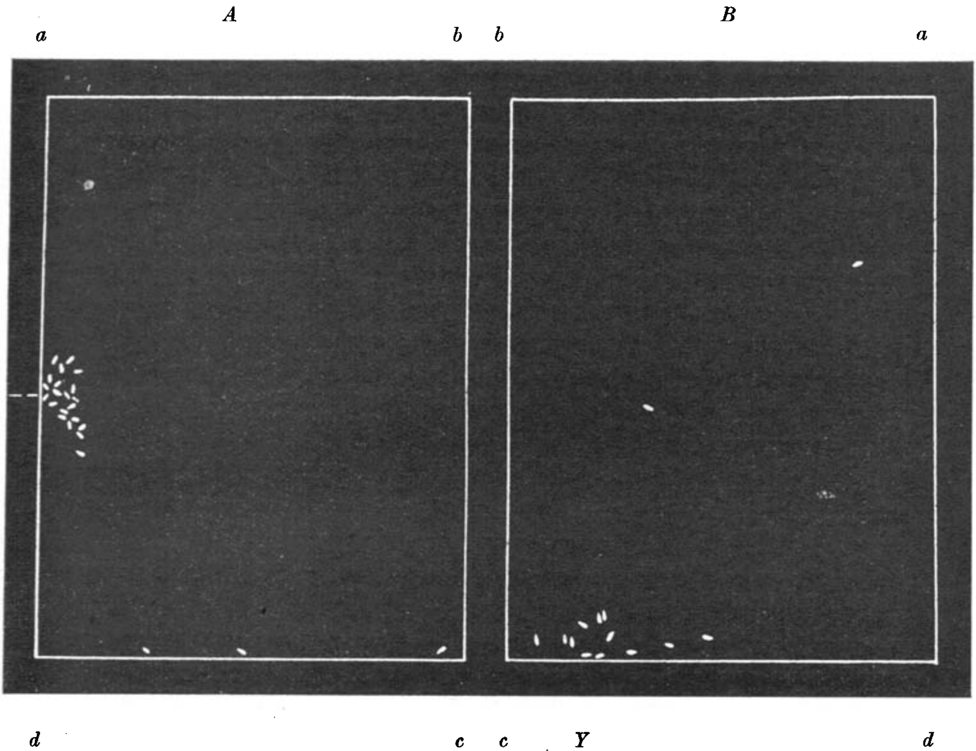

Fig. 8. Illustrating the experiment on "homing instinct" in regard to oviposition in *Pediculus humanus* (*corporis*) described in the text. (*A*) the smooth and (*B*) the rough side of the cloth. Natural size.

In the accompanying figure (Fig. 8) the smooth underside of the cloth is indicated by the letter *A*, the rough upper side by the letter *B*. The female was fed twice daily, being removed from the cloth for the purpose. After each feeding she was replaced upon the platform and returned to the thermostat maintained at 32° C. The cloth, whose corners are marked *a*, *b*, *c*, *d* in the figure, was inspected twice daily whilst the female was being fed.

The result was striking. During the first 24 hours, although replaced three times upon the platform, she laid 6 eggs in succession at one spot midway along the under margin of the cloth, at *X*, along the side *a—d*. In the second 24 hours she laid 7 more eggs at spot *X*, the area dotted with eggs being about 0·5 cm. across; 2 eggs were laid apart close under the edge of the cloth along the side *d—c*, and 1 was laid near the middle of the upper surface *B*. The cloth was now reversed, the rough side *B* being undermost, whereby the eggs at *X* appeared uppermost. In the third 24 hours, one more egg was laid at *X* (making a total there of 14), 4 were laid on the (now) under surface of the cloth *B* along margin *c—d* in an area denoted by *Y*. In the fourth 24 hours 7 more eggs were laid at *Y* and 1 was laid on surface *A* near *c*.

Expt. 1 (*continued*). The female having been removed from the cloth, the latter, with only the eggs upon it, was returned to the thermostat for two days. Beginning on 26. III. 17, the rough side (*B*) of the cloth being uppermost, another female was placed on the platform; during the following 24 hours she laid 1 egg at *X* and 1 egg at *Y*. A third female was now placed on the platform and during the following 24 hours she laid 6 eggs at *X* (underside) and 1 near the platform on the upper surface *B*.

At the end of the experiment, out of a total of 38 eggs, 21 had been laid at *X*, and 12 at *Y* along margin *c—d*, 3 along margin *d—c* on the surface opposite to *Y*, and only 2 were scattered elsewhere.

It is certain, therefore, as Bacot indicated, that *corporis* females show a marked tendency to return and oviposit on the same spot where eggs have been laid by themselves. My experiment shows, that a female will select a spot previously chosen by another female, and the reversal of the cloth showed that the tendency to creep beneath a cloth to lay to a great extent overcomes the tendency to return to the same spot if the spot is put uppermost.

B. *Capitis.*

Bacot (loc. cit.) states that the "homing instinct" with regard to oviposition is less marked in *capitis* than in *corporis*. I have subjected the statement to the test of enumeration in two comparative experiments. I. (*a*) Some *capitis* laid 114 eggs on a hair-frame; nearly all were aggregated in two areas at one side and at one end of the frame, 71 eggs being laid on 4 adjoining parallel hairs alone. (*b*) In a parallel experiment with *corporis*, 95 eggs were laid, mostly in one area, 81 being attached close together on 6 parallel hairs. II. (*c*) Some *capitis*, in a wristlet, laid 476 eggs on 8 hair-grids, chiefly on certain hairs, but the eggs were mostly separated by distinct intervals. (*d*) Some *corporis*, in the thermostat at 31° C., laid 356 eggs on 4 hair-grids, many of these were in close aggregations, but many were scattered as in *capitis*.

It would appear therefore that *corporis*, under experimental conditions, tends to lay its eggs more closely aggregated than does *capitis*. Nevertheless, as shown in Fig. 5 (p. 122), *capitis* at times packs its eggs very closely under natural conditions, therefore the difference is inconstant.

The Laying of Unfertilized Eggs.

That lice lay unfertilized eggs has been repeatedly observed; in the absence of a male they will lay numerous eggs which soon shrivel up. Oviposition continues, therefore, irrespective of fecundation as Bacot has also observed. The number of unfecundated eggs laid by a female is governed by the same conditions affecting fertile eggs; unfertilized or fertile eggs may be laid beginning about 24 hours after the emergence of the female from the third larval skin.

Hindle, Harrison and myself have failed to obtain any evidence of the existence of parthenogenesis in lice.

SUMMARY REGARDING OVIPOSITION.

1. The temperature at which lice are maintained greatly influences oviposition. They do not lay at a temperature below 20° C.; the optimum lies at about 32° C., although they will lay at 37° C. Infested persons who remove their clothing at night, as practical experience has shown, become less heavily infested than persons wearing their clothing continuously, because the periodic cooling of the clothing and the therein contained lice necessarily leads to the insects' progeny being restricted.

2. The fertility of *Pediculus humanus* (*corporis*) has been greatly underestimated. Under optimum natural conditions a female may lay 275 to 300 eggs; the average number laid per day during the whole oviposition period being about 10.

Two experiments made with the wristlet method (see p. 107) indicate that *capitis* may lay more eggs than has hitherto been supposed, the females having laid up to 8 and 9 eggs apiece on some days.

3. Oviposition usually begins 24–36 hours after the adult female emerges from the third larval skin. The eggs may be either fertilized

or unfertilized, and the number laid in either case is equally influenced by the conditions of temperature and nutrition affecting the female.

4. Lice that are confined continuously on the body do not gorge as they do when fed at longer intervals; by partaking of frequent small meals of blood they will doubtless assimilate their food better and this may account for their laying more eggs.

5. It may be mentioned incidentally that there is no evidence of the occurrence of parthenogenesis in lice. Unfertilized eggs, in my experience, invariably shrivel up soon after they are laid.

6. The process of oviposition in *P. humanus* is described for the first time in this paper. (This is extraordinary considering the length of time the insect has been known to man!) It is shown that the gonopods, whose function has not hitherto been known, serve to clasp human hair upon which the insect oviposits; without these organs she could not lay eggs on hair in proper alignment, such alignment being an important safeguard in preventing injury to the eggs and thus maintaining the species in nature; the gonopods constitute a special adaptation to a phase of its parasitic life.

The egg, whilst in the ovary, has its operculum directed toward the head of the female; it issues from the vagina with its pointed end first. The egg is asymmetric, its ventral contour, seen in profile, being flattened. The ventral surface of the egg glides out upon the ventral wall of the vagina and thence upon the hair or other support upon which the insect oviposits. To bring the gonopods into play, the female walks backward along the hair, flexing the gonopods upon it; the latter then slide down about the hair to whose dimensions they are closely adapted. The expulsion of the egg follows a few moments after the gonopods have clasped the hair; the expulsion taking place in the fraction of a second, after which the female promptly walks forward, away from the egg, releases the hair from the grip of the gonopods, and seeks a place of rest. The gonopods facilitate the deposition of eggs on filamentous fabrics, but necessarily function imperfectly on fabrics, being primarily organs for the performance of oviposition on human hair. The cement, which attaches the hair to its support, issues before the anterior broad portion of the egg has emerged, and, flowing about its posterior end and the hair, or fabric, hardens rapidly. The cement behaves like chitin in its resistance to the effects of chemical agents, the latter destroy the hair or fabric before affecting the chitinous eggshell and its cement. The orientation of the egg upon the hair or substratum is such that the young louse in issuing readily seizes the hair or cloth as it emerges; the ventral surface of the larva coincides with the ventral surface of the egg and the operculum usually springs open ventrally.

7. Lice prefer to lay on horizontal than on vertical surfaces of cloth; they greatly prefer to lay on the under surface of fabrics resting on or near glass; when confined between two approximately horizontal layers of fabric, the interspace between these allowing the insects the freest movement, they lay about equally well on the upper and under surfaces.

8. *P. humanus* (*corporis*) shows a marked preference for laying on felt and rough filamentous fabrics such as wool or flannelette. They will, however, lay readily on silk tricot. They can oviposit on the smoothest fabrics (sateen, silk, etc.) but on the whole avoid them because they afford an imperfect foothold.

9. Under experimental conditions, when given a choice between cloth and hair, *corporis* preferred to lay on hair than on cloth, this being contrary to the result of Bacot's experiments; *capitis* on the other hand, in one lot tested, showed a more marked preference for hair. The difference observed was only one of degree and it appears premature to draw final conclusions either from Bacot's or my experiments; a larger series of experiments upon a number of different strains of *corporis* and *capitis* should be carried out under the more exact conditions laid down in this paper. If such a series of experiments proves that there is a constant difference, which I am inclined to doubt, it does not follow that such a difference is specific.

10. Contrary to Bacot, my experiments reveal no difference between *corporis* and *capitis* in the mode of oviposition on hair, in so far as concerns (*a*) the alignment of the eggs on hair and (*b*) the laying of eggs at the intersection of hairs or on several hairs at a time.

11. The observation of Bacot, that *corporis* shows a marked tendency to oviposit where eggs have been previously laid, is confirmed. Experiments with *capitis* indicate that this tendency is perhaps a little less marked than in *corporis*, but it is inconstant.

HATCHING.

THE TIME AND TEMPERATURE CONDITIONS REQUIRED FOR THE HATCHING OF THE NITS.

(*a*) *Corporis*.

There is no evidence that eggs maintained at 22° C. or under are capable of hatching. Eggs kept at the following temperatures have failed to hatch: 8–10° C. (Hindle MS.); 10° C., observation period of

53 days (Nuttall); 15° C. (Hindle and Harrison MSS.); 16° C., constant (Sikora[1]); 15·6–18·4° C., dry, observation period 24 days (Bacot[2]); 6–10° at night and 20° C. by day (Sikora[1]); 12–20° C., observation period 21 days (Hase[3]); 22° C., observation period 54 days (Nuttall); 22° C. (Hindle MS.).

The observations recorded by the following authors are therefore erroneous, namely, that eggs hatch at 20° C. in 7 days, tested on 3 eggs (Widmann[4]); at 20° C. in 10–12 days (Heymann[5]); at "room temperature" in 4–6 days (Wulker[6]); at 16–18° C. "they rarely hatch" (Legroux[9]).

The following table records the observations of different authors, arranged in accordance with the temperatures at which the eggs were maintained prior to hatching being observed:

Temperature at which eggs were kept, ° C.	Eggs hatched after	Authority and remarks
After 13 days at 10°, they were placed at 26–30°	10 days	Widmann[4] (6 nits)
After 2 days at 0°, they were placed at 26–30°	13 „	„ (5 nits)
25°, constant	16 „	Sikora[1]
25–28°	8–10 days	Legroux[9] (said to be optimum)
25–30°	8–10 „	Hase[3]
28°	6½–7 „	Widmann[4]
28°, damp	7 days	Nicolle, Blaizot and Conseil[7]
? 28°	7–15 days, mostly 11–15 days	Swellengrebel, 1916, p. 4
30°, constant, dry ...	7–14 days, mostly 11–13 days	Nuttall
In coat pocket	8 days	Nocht and Halberkann[8]
32°, constant, dry ...	7–8 days usually	Nuttall
In tube near body ...	8 days	Warburton, 1911, p. 25 (8 nits)
35°	7½ „	Widmann[4] (3 nits)
35°, on man's body ...	6 „	Sikora[1]
ca. 35°, on man's arm ...	7 „	Nuttall (the first of many)
In stocking on leg ...	6–8 days	Wilder, 1911, p. 87 (many)
Near the body	5 days	Nocht and Halberkann[8]
In bag under armpit ...	6–8 days	Peacock, 1916, p. 39 (6 nits)
36·1°, dry	4–8 „	Bacot[2] (143 hatched)
37°, damp	5–6 „	Nocht and Halberkann[8]
37°	5–7 days, rarely 5 days ...	Hase[3]
37°, dry, constant ...	4–7 days, mostly 5–6 days ...	Nuttall
38°	8 days	Widmann[4]
40–45°	died	Sikora[1]

[1] Sikora, VIII. 1915, p. 529. [2] Bacot, II. 1917, p. 248. [3] Hase, 1915, p. 22, cited by Müller, 1915. [4] Widmann, VIII. 1915, p. 293. [5] Heymann, 18. VIII. 1915, p. 305. [6] Wulker, 1915, p. 628. [7] Nicolle, Blaizot and Conseil, 1912, pp. 110–192; VII. 1912, pp. 1636–1638. [8] Nocht and Halberkann, 1915, p. 626. [9] Legroux, 1915, p. 470.

Some authors, without mentioning the conditions, state that eggs hatch as follows: In 3–8 days (Railliet, 1895, 827); 5–6 days (Fantham, 1912, p. 514); 6 days rarely in 4 (Jeanneret-Minkine, 1915, p. 126); rarely in 5 days usually in 6 (Hase, 1916, abstract); 8 days (Fiebiger, 1915, p. 657; VII. 1915, p. 645); Eysell (1913, p. 48) asserts that *corporis* eggs hatch in 3–4 days, and appears to be the not-cited authority for the similar statements of Prowazek (I. 1915, p. 67), Fasal (II. 1915, p. 225), Heymann (III. 1915, p. 253), Nocht and Halberkann (V. 1915, p. 626); Eysell is perhaps quoting from Railliet, but there is no evidence that either author made original investigations. I have only once seen an egg hatch in 4 days, at 37° C., and no recent observer has seen hatching in 3 days.

The following are the only detailed experiments that have been carried out to my knowledge on *corporis* eggs of accurately determined age:

No. of eggs that hatched	Temp. of thermostat in ° C.	Hatching occurred after days											
		4	5	6	7	8	9	10	11	12	13	14	
1283	30° damp	—	—	—	3	56	33	8	0·2%	—	—	—	Bacot, II. 1917, p. 248
160	30°, dry	—	—	—	—	—	9	46	92	11	2	—	Hindle MS.
105	30°, dry, constant	—	—	—	1	3	2	6	35	41	10	7	Nuttall Expt. II. 16
93	37°, dry, constant	1	36	54	2	—	—	—	—	—	—	—	Nuttall Expt. V. 16

The observations recorded in the foregoing table show that eggs laid on the same day may take a variable time to undergo development. This is also shown by my experiments on *capitis*. Incidentally they disprove the statement by Sikora (VIII. 1915, p. 529) that there is great uniformity in the hatching period of eggs of the same age.

(*b*) *Capitis*.

These lice were raised by the wristlet method, as described on p. 107.

No. of eggs that hatched	Temp. ° C.	Hatching occurred after days						
		5	6	7	8	9	10	
103	32–35° on wrist	4	23	60	14	2	—	Nuttall, Expt. VI. 17
244	30–33°, in bag on neck, warmer weather	—	23	166	51	3	1	„ Expt. b. VII. 17
			9·4 %	68 %	20·9 %	1·2 %	0·4 %	
500	Ditto, cooler weather	—	7	307	167	19	—	„ Expt. a. VII. 17
			1·4 %	61·4 %	33·4 %	3·8 %		

Without giving any particulars, Railliet (1895, p. 825) states that *capitis* eggs hatch in 5–6 days; Eysell (1913, p. 47), who perhaps intends to quote Railliet, gives 6 days as the hatching period. There is no evidence that either author made personal observations.

Delayed Hatching.

Under certain circumstances, the hatching of the eggs of *corporis* may be considerably delayed, and it is of practical importance to know this. The following observations serve as examples of delayed hatching:

Conditions affecting the eggs	Eggs hatched after	Authority
After 8 days in tube near body, 8 of 24 having hatched, the remaining 16 were kept in waistcoat pocket, worn by day, hung up at ca. 0° C. by night ...	over 4 weeks	Warburton, 1911
Alternately at 30° C. and 8–10° C. for periods of 24 hours ...	33 and 35 days ... ... (Only 4 hatched out of many; 3 hatched 33rd day, 1 on 35th day. None before or after)	Nuttall
Alternately at 30° and at ca. 10° C. for periods of 12 hours ...	26 and 27 days ... ... (Only 4 hatched out of many. None before or after)	,,
At 24·5° C., damp	a few hatched up to 23 days	Bacot, II. 1917, p. 248
Alternately at 37° C. and at ca. 8° C. for periods of 12 hours ...	only 2 out of many, in 16 days	Nuttall
Alternately at 37° and ca. 14° C. for periods of 12 hours ...	only 4 out of many, in 15 days	,,
After 2–3 weeks at 9° C., transferred to "favourable temperature"	15 days	Heymann, 18. VIII. 1915, p. 305
After 24 hours at −10°, transferred to 26–30° C.	17 days (6 eggs)	Widmann, VIII. 1915, p. 293

The following authors' records of delayed hatching do not state the conditions: 6 weeks (Fantham, 1912, p. 514); 18 days (Nocht and Halberkann, 1915, p. 626); 21 days (Zupnik, 1915, p. 564); 18–22–30 days (Swellengrebel, 1916, p. 4).

In Bacot's and my experiments the time is reckoned from the day the nits were laid.

Summary relating to the time required for Hatching.

Corporis eggs do not hatch at 22° C. or below; a favourable temperature is attained at about 25° C., but development is slow, lasting 16 days; at 30° C., hatching occurs in 7–14 days, mostly in 11–13 days; at ca. 35° C., the eggs being kept near the human body, hatching occurs in 6–8 days; at 36–37° C., hatching occurs in 4–8 days, mostly in 5–6 days; at 38° C., hatching is slightly retarded, and the eggs die without hatching when kept at 40–45° C. Eggs do not hatch before the 4th day under any circumstances. Most of the eggs laid on the same day hatch within 48 hours of each other, but they may hatch during 4–8 days, there is therefore no great uniformity in the hatching period.

Under certain conditions (specified in the foregoing table) hatching may be delayed up to 35 days.

Capitis eggs hatched on the wrist at 32–35° C. in 5–9 days, mostly (60 %) in 7 days. When carried near the body at 30–35° C., in warm weather, they hatched in 6–10 days, mostly (68 %) in 7 days; under the same conditions, in slightly cooler weather, they hatched in 6–9 days, mostly (61 %) in 7 days. The influence of slight variations in temperature is well brought out in the protocols (see p. 145).

DEVELOPMENT OF THE LARVA IN THE EGG.

The following description relates merely to the changes that can be observed with a low magnification. Certain details relating to histology will be considered elsewhere. The freshly laid egg, when viewed by *transmitted light, appears almost transparent and faintly yellow;* the contents fill the shell and are finely granular (Fig. 9, 1). Assuming that an egg is placed at a temperature which allows of its development so that it hatches in six days, the following changes can be observed to take place through the egg-shell when the nit is viewed in a living condition:

2nd day. Segmentation has begun. Round yolk-masses of variable size are formed and their number increases; they are best seen by oblique illumination (Fig. 9, 2 and 3).

3rd day. Slightly opaque milky areas appear along one side and basally (4) and the limbs begin to form (5), the yolk masses fade and the body becomes defined, a clear space appearing basally in the shell.

4th day. The body and limbs become more clearly defined (Fig. 9, 6), the eyes become visible as two irregular pinkish antero-lateral spots.

5th day. When closely viewed, periodic pumping movements of the pharynx are observable. The stigmata may be seen, the claws and eyes are darker. The egg as a whole appears more yellowish brown and the eyes reddish. There may be slight movements of the limbs (Fig. 9, 7). Occasionally bubbles may be seen in the fluid in which the larva floats; they at times escape upward along the venter of the larva and pass over its head toward the operculum. The shell shows shrinkage, there being two long shallow spoon-shaped depressions seen postero-laterally; this shrinkage is very different from the total collapse seen on the first and second day in sterile incubated eggs.

6th day. The shell appears more hollowed at the sides. The pharyngeal pumping movements are more frequent, and bubbles of air are seen passing back from a large bubble in front of the mouth into the pharynx (Fig. 9, 8) and onward into the gut. This air passes in by diffusion through the operculum. The air accumulates in the gut and is forced backward and out through the anus and accumulates to form an air-cushion behind the larva, pushing it more and more against the operculum. The play of the pumping muscles of the pharynx can be seen in the head. The eyes are now jet black and circular. The head is pressed against the operculum, and with the anterior part of the thorax, is strongly flexed ventrally, the palps lying between the basal segments of the forelegs. Fig. 9, 14, shows a larva at this stage drawn immediately after its removal from the shell; a bubble is seen in its pharynx, and another large bubble in its midgut to the right of the circular disc-like organ which lies in a depression of the ventral surface of the midgut.

The manner in which the Larva issues from the Egg.

When the larva is ready to emerge, it begins to pump in air very rapidly, the bubbles being distinctly seen through the transparent glassy shell as they pass backward into the gut. When the pumping begins the larva fills the upper three-quarters of the shell, and as the air accumulates inside the gut, the end of the abdomen extends downward and finally impinges upon the base of the shell. If the micropyle apparatus is occluded by means of glycerine or oil, the pumping ceases and the insect dies. As the air expelled from the anus accumulates behind, the larva is pushed against the operculum; this pressure of the air-cushion finally overcomes the resistance of the operculum and the latter springs open. The fore part of the larva, which has acted like a stopper to the air, is slightly extruded after the operculum has opened. The head of the larva now assumes the normal position, and the first pair of legs emerge. Meanwhile the pumping process continues actively, increasing the pressure from behind. The larva now protrudes its second pair of legs, and the third pair soon follows, hatching being completed (Fig. 10).

The first to study this highly interesting process was Sikora (VIII. 1915, p. 530), whose observations I gladly confirm and extend. Hase (1915, p. 25) attributed the springing open of the operculum to the pressure of the head of the larva, and, although he observed the pumping process, he failed to catch its significance. Müller (1915, Pl. III, Fig. 14), who cites Hase, illustrates the emerging larva.

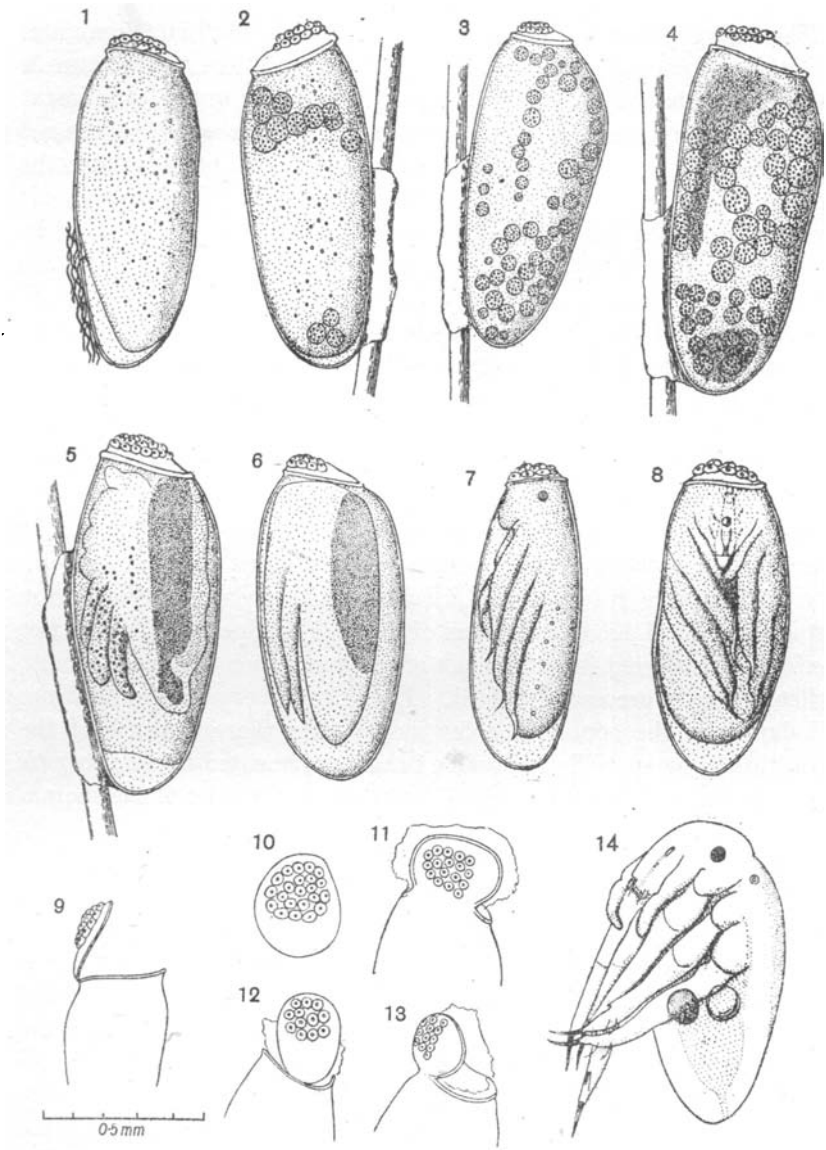

Fig. 9. *Pediculus humanus* (*corporis*). Development of the larva in the egg. As described in the text. Drawings from living specimens.

Note. A number of the points in this description have already been touched upon by previous authors; thus Wulker (1915, p. 628) gives five text-figures, tracing a development somewhat resembling that which I have figured; Jeanneret-Minkine (1915, p. 126), Widmann (18. VIII. 1915, p. 293) and Müller (1915, pp. 44–47, pl. III, coloured figs. 9–15) also devote a few lines of description to the development.

The young louse usually frees itself from the egg-shell in 2–5 minutes after the springing of the operculum. If, however, the temperature is too high, as I have frequently seen in eggs hatching in the thermostat or on the body, a considerable proportion of the larvae die in the act of hatching; death occurring at any stage of the process from the inability of the insect to free itself quickly, before the delicate and soft vitelline membrane hardens and the insect's moist body dries and sticks to the membrane. On the one hand, the larva may die without bursting the membrane which encloses it within the shell, in which case only the back of the head and thorax protrude from the orifice of the shell; or the larva may be unable to extricate the first, second, or third pair of legs, remaining stuck to the hardened and shrivelled intima, in the position depicted in Fig. 10.

We may add that when the pumping process begins, the larva appears pale, but as the moment of hatching approaches, it becomes markedly darker, especially in the region of the head, claws, etc. In other words the chitin hardens before the larva issues, and this explains why the insect is ready to feed at once on emergence, as Warburton first observed. I have, by means of a needle, helped a larva to free itself and transferred it to the back of my hand upon the needle point; it then instantly proceeded to feed. The chitinous exoskeleton becomes still darker in the course of a few hours after the emergence of the larva, this being specially noticeable in more pigmented forms of *capitis* where the larva shows well-marked dark lines at the sides of the thorax.

The Empty Shell.

The empty shell, when viewed by reflected light, presents a white pearly appearance to the naked eye. Under the microscope the shell is iridescent like a soap-bubble; and by transmitted light it is hyaline. The whitish appearance of empty shells is most striking to the naked eye when egg clusters are viewed in a good light upon a dark background of cloth or hair. The very thin and structureless vitelline membrane frequently protrudes out of the orifice of the shell like a funnel or cuff, this being the portion which has been pushed out and ruptured by the larva that has issued (Fig. 9, 11–13), and crumpled traces of it may be discovered within the shell or hanging like a sack in the aperture to whose margins it remains stuck. This membrane is purposely omitted from Fig. 10.

In describing the orientation of the egg in the section on oviposition (see p. 123) reference was made to the manner in which the operculum mostly springs open on the ventral side of the egg, hinging on the dorsal side (Fig. 9, 9 and Fig. 10), but it may spring laterally or dorsally, or be completely knocked off (Fig. 9, 10–13). There is therefore no constancy about the manner in which the operculum springs[1].

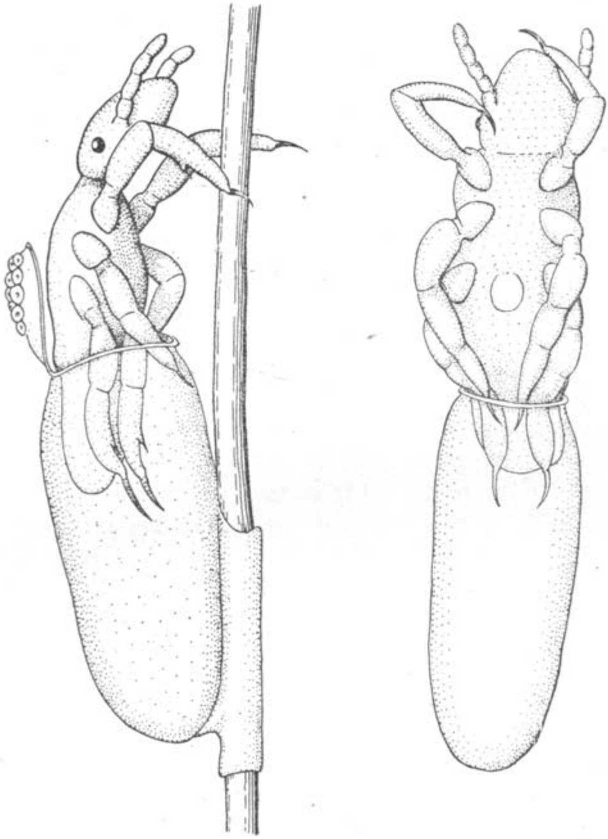

Fig. 10. *Pediculus humanus* (*corporis*). The larva in the act of issuing from an egg attached to a hair. The right-hand figure shows the ventral aspect of the same larva, sketched a few moments later, the hair being intentionally omitted. From sketches of the living insect.

[1] This appears from counts made on eggs to which the opercula still adhered: of 100 *corporis* eggs laid on cloth, the operculum had opened ventrally in 70, laterally in 27 and dorsally in 3; similar eggs laid on hair gave the figures 69, 21 and 10 respectively. Of 100 *capitis* eggs laid on hair, the operculum had opened ventrally in 43, laterally in 37 and dorsally in 20. The number of pores in the operculum is inconstant as shown in the figures.

The empty shells after a time break away anteriorly, but the basal portion surrounded by the thicker mass of cement, and the cement tube on the hair, remain unless mechanically removed. Rows of empty nits or tubes and fragments of eggs are frequently seen on hairs at whose bases there are unhatched eggs in different stages of development; this being due to the growth of the hair away from the scalp close to which the eggs were originally laid.

FERTILITY.

THE PROPORTION OF EGGS THAT HATCH AND THAT ARE FERTILE.

(*a*) *Corporis.*

According to Sikora (VIII. 1915), the first and last eggs laid by a female are equally fertile. This statement, however, requires qualification, for the fertility of the eggs depends upon copulation having taken place and the female having received a sufficient supply of spermatozoa to fertilize all the eggs she lays. There is no evidence that all the eggs laid by a female are fertile, in fact, as I have repeatedly seen, occasional infertile eggs are laid by fertilized females.

Bacot (II. 1917, pp. 241–244) states that usually but 33–65 % and at times 75–81 % of the eggs are fertile. In four sets of about four pairs (♂ ♀) observed for a period of some eight days, during the 12th–30th day of the females' lives, 91–97 % of the eggs were fertile. The greatest number of fertile eggs laid by a single female was 115. The following records relate to the percentage of fertile eggs, *as tested by hatching*, which were laid by many females of different ages. The first three records are extracted from Hindle's MS. notes, the last three are from my own more recent observations. The females were kept with males, were fed twice daily, and, like the eggs, were maintained in the thermostat.

Proportion of eggs that hatched.

Temperature at which eggs were kept, ° C.	No. of eggs that were laid	No. of eggs that hatched	%
30°	203	160	78·8
30°	322	238	73·9
30°	267	154	57·7
30°	*150*	*105*	*70·0*
30°	216	149	69·0
37°	161	87	54·3

Therefore out of 1158 eggs maintained at 30° C., 806 or 69·6 % hatched. In two observations, the figures are low, especially in that where the eggs were kept at 37°. Under constant temperature conditions in the thermostat at 30° C., we may therefore expect roundly 70 % of all eggs to hatch when laid by females to which males have access. Of the eggs that fail to hatch, some are sterile and others are fertile. In the latter case development may be arrested, or the larva may fail to issue. *Hatching alone is not therefore a true test of fertility* (vide infra and pp. 160, 161).

Peacock (1916, p. 41) records that of 291 eggs taken from a shirt, 82 % hatched. Swellengrebel (1916, p. 4) saw but 47 % of the eggs hatch under experimental conditions which he fails, however, to specify. The importance of the conditions under which the parents and eggs are maintained in relation to the proportion of eggs that hatch, is well brought out by the following records relating to *capitis*.

(*b*) *Capitis*.

The number of eggs of head-lice that hatch under ordinary experimental conditions is usually very low. At most a very few eggs will hatch in the thermostat at 30° C. under conditions where *corporis* yield an average hatching of 70 %. After repeated trials and failures to raise *capitis* satisfactorily in the thermostat with two daily feedings, etc., as applied to *corporis*, I concluded that the conditions were so obviously unfavourable as to render further efforts futile. The wristlet method (see p. 107) was therefore devised and remarkably successful results were at once obtained, merely because the conditions were as nearly normal as it was practically possible to obtain. The following three experiments demonstrate the difference between a good and a bad method in studying the biology of lice.

Expt. 1. Some ♀♀ were placed with ♂♂ in a wristlet, and laid 211 eggs on 2–4. VI. 17; 204 eggs hatched, two larvae showed arrested development and five eggs shrivelled up at an early stage, this indicating that they were sterile. Therefore at least 97·6 % of these eggs were fertile and 96·6 % hatched.

Expt. 2. Seven ♀♀ under the same conditions, the progeny of the foregoing, laid exactly 500 eggs on 19–29. VI. 17; of these six were sterile (ca. 1 %), whilst four larvae failed to complete their development. Therefore 99 % of the eggs were fertile and 490 or 98 % hatched.

Expt. 3. Three ♀♀ with two ♂♂, of the same generation as the last, were placed under the same conditions, and laid a total of 275 eggs during 21 days (24. VI.—14. VII. 17); the females died one after the other. Of these eggs, 28 were sterile (ca. 10 %) and three larvae (ca. 1·2 %) failed to complete their development. Therefore ca. 90 % of the eggs were fertile and 244, or ca. 88 %, hatched. The lower percentage of fertile eggs in this case was due to the death of the two accompanying males on the 9th and 15th days of oviposition, only four sterile eggs out of the 28 having been laid during the lives of the males.

The Length of Time a Female remains Fertile after Fecundation.

As copulation commonly takes place at frequent intervals, once a day, or oftener, and the female possesses no receptaculum seminis, it might be supposed that females would soon cease to lay fertile eggs after being isolated apart from the males. Whilst some observations show that certain females lay fertile eggs for but a brief period, others clearly demonstrate the contrary; fortunately there are a number of observations recorded by independent authors which elucidate the matter, and I have classified the data as follows:

(*a*) *Corporis.*

(*a*) *Brief periods of fertility* were observed by Harrison (MS.) in three batches of females, that only laid fertile eggs during two days after they had been isolated from males.

(*b*) *Longer periods of fertility.* Sikora (VIII. 1915, pp. 523–537) relates of two females: (1) that laid 64 fertile eggs during 12 days, after which she laid infertile eggs; (2) that laid 20 fertile eggs during nine days. Hindle (MS.) records that 20 females continued to oviposit for 20 days after isolation from as many males; for the first eight days after isolation 75 % of the eggs hatched, whereas after 9, 10, 11 and 12 days' isolation there hatched respectively 6/29, 4/32, 2/28, 1/27, in short only one out of 27 eggs laid on the 12th day hatched; the females were maintained at 30° C. and fed twice daily. Swellengrebel (1916, p. 12) saw an isolated female lay fertile eggs for a period of 15 days. The longest periods have, however, been observed by Bacot (II. 1917, pp. 240, 243, 251), who records isolated females as having laid fertile eggs for 12, 17, 18, 19 and 21 days respectively.

(b) Capitis.

Similar results have been obtained with head-lice. The longest period of continued fertility observed by me was five days. Bacot (*loc. cit.* p. 249), however, records periods of 7–12 days; one isolated female laid 70 fertile eggs.

In judging of these variable results, certain factors must be taken into account which do not appear to have been considered by some of the authors cited, although they are fairly obvious. These factors are: the age and potency of the copulating pair, the fact that hatching under experimental conditions is frequently an imperfect test of fertility since a variable number of fertile eggs may die under unfavourable conditions and be falsely reckoned as sterile. I have seen a male, after prolonged copulation with a female, separate from her and immediately seek a second mate, it being evident that he could scarcely fertilize the second female with full effect after such a short interval between the acts. The brief periods of fertility may therefore be explained either by the advanced age or exhausted state of the pairs, the longer periods by the pairs being younger or more potent. Finally, unless optimum conditions prevail for the development of the eggs, hatching affords a poor guide as to their fertility.

Fertilizing Power of the Male.

The only data relating to the fertility of the male are those recorded by Bacot (II. 1917, pp. 236, 239), who states that a ♂ *corporis* fertilized 18 ♀♀, and a ♂ *capitis* fertilized 10 ♀♀.

Development from the Larva to the Adult—the Moults.

There are three larval stages in the developmental cycle of *Pediculus*, and consequently three successive moults occur before the insect reaches the adult stage. The time required for development from 1st stage larva to adult depends greatly upon the temperature and food supply, factors whose importance few have recognized.

Swammerdam (1682 ed., p. 172) concluded that lice undergo 3–4 moults, and Warburton (1911) stated that there are "apparently" three, their number therefore remained in doubt until Patton and Cragg (1913, p. 552) in India, definitely established that there are three. This has been amply confirmed by different observers (Hindle, in England; Sikora, 1915, p. 523, in Germany; Müller, 1915, p. 47, in Austria; Swellengrebel, 1916, p. 4, in Holland, etc.).

The time required for lice to attain maturity, starting with the newly hatched larva, is variously given by different authors: two

	Period required for development from 1st st. L. to adult	Temp. ° C. and other conditions	Feeding	Authority
corporis	15–18 days	not stated	not stated	Railliet, 1895, p. 827
	11 „	near body	twice daily	Warburton, 1911
	11–12 „	not stated	not stated	Fantham, 1912
	15 „	25–28°	once daily	Legroux, 1915, p. 470
	17 „	not stated	not stated	Jeanneret-Minkine, 1915, p. 825
	9–10 „	35°, constant, 35 lice, *on person*	twice daily	Sikora, VIII. 1915, p. 523
	11–15 „	25°, constant, 4 lice	„ „	„ „
	8 „	on man's arm* ...	continuous	Nuttall
capitis	18 „	not stated	not stated	Railliet, 1895, p. 825
	14–21 „	„	„	Eysell, 1913, p. 47
	8–9 „	on man's arm † ...	continuous	Nuttall

* Felt cell method (p. 105). † Wristlet method (p. 107).

With regard to *corporis*, Railliet (1895, p. 827) is the unacknowledged authority used by Eysell (1913, p. 48), who in turn is cited by Prowazek (I. 1915, p. 67); whilst Fasal (II. 1915, p. 225) and Heymann (III. 1915, p. 253) cite Eysell also without acknowledgment. Fiebiger (VII. 1915, p. 645) appears to have borrowed Eysell's statement that *capitis* developes in 14–21 days, and to have applied it to *corporis*. These authors therefore only require mentioning in so far as concerns their method of procedure.

Relatively few authors mention the time that elapses between the different moults. Warburton states they moult every fourth day, but he left the number of moults in doubt. Swellengrebel (1916, p. 4) gives the duration of the 1st, 2nd, and 3rd larval stages as 7, 6, and 5 days respectively, without stating the experimental conditions.

The following records, which I have condensed and ordered for comparison, give much more accurate information on the subject; the timing starts from when the young larva had its first feed after hatching—Table A.

Protocols showing (*a*) the variation in the moulting periods of individual lice, and (*b*) the effect of a low temperature in retarding or impeding development (*corporis*)—Table B.

A similar individual variation in the rate of moulting has been observed by me in *capitis*.

The Act of Moulting.

The act of moulting takes place in all stages in the following manner. The old skin splits longitudinally along the length of the thorax and forward to the heavily chitinized vertex of the head along whose edge the split extends laterally to near the base of the palps. The insect's head

TABLE A.

No. of lice tested	1st moult occurred after	2nd moult occurred after	3rd moult occurred after	Developt. from 1st st. L. to adult took	Temp. ° C. and other conditions	Feedings in 24 hrs	Authority
11	3 days	2–3 days ...	3–4 days ...	8–10 days ...	35°, contin. on person	6	Sikora, VIII. 1915
—	5–6 days ...	4–6 „ ...	4–6 „ ...	11–15 „ ...	35° on person at night 24° in pocket by day	2	„
40	3 days (in 3 %) 4–5 days (in 97%)	4–5 days (in 72%)	4–5 days (mostly)	12 days in 50 %	In pocket by day, at ca. 31° at night	for 6–7 hrs	Bacot II., 1917, p. 235
—	4 days	6 days	6 days	16–17 days ...	30° in room	1	Patton and Cragg, 1913, p. 552

TABLE B.

No. of lice tested	1st moult occurred in	2nd moult occurred in	3rd moult occurred in	Developt. from 1st st. L. to adult took	Temp. ° C. and other conditions	Feedings in 24 hrs	Authority
15 out of 32 larvae raised to adults	3 after 5 days 23 „ 6 „ 4 „ 7 „ 1 „ 8 „ — 32	2 after 4 days 12 „ 5 „ 11 „ 6 „ 1 „ 8 „ — 30	1 after 4 days 9 „ 5 „ 3 „ 6 „ 1 „ 7 „ — 15	ca. 16 days ...	30° thermost.	2	Hindle MS.
12 larvae, all raised to adults	1 after 4½ days 7 „ 5½ „ 4 „ 6 „ — 12	1 after 3½ days 8 „ 4½ „ 2 „ 5½ „ 1 „ 6 „ — 12	2 after 4½ days 7 „ 5½ „ 3 „ 6 „ — 12	first adult in 13½ days, last in 16 days	30° thermost.	2	Harrison MS.
Not stated ...	9–20 days ...	11–16 days ...	not recorded ...	—	22° thermost.	2	Hindle MS.
None moulted	—	—	—	—	20° „	2	„
1 larva ...	—	24 days, died ...	—	—	16° „	2	Sikora
1 larva ...	did not moult, died 13th day	—	—	—	4° for 3 days, 10° for 10 days	1	„

is depressed whilst this is taking place. As in the process of hatching, described on p. 148, the louse, in the act of moulting, sucks up air into its pharynx, whence it passes into the gut, thus inflating the animal, and, passing backward, it escapes from the anus. At first the back of the thorax protrudes, then the first pair of legs, and these, pressing downward, help to free the head. As soon as the head issues it assumes its normal position and pumping ceases. The second and then the third leg-pair appear and help to remove the moult completely by

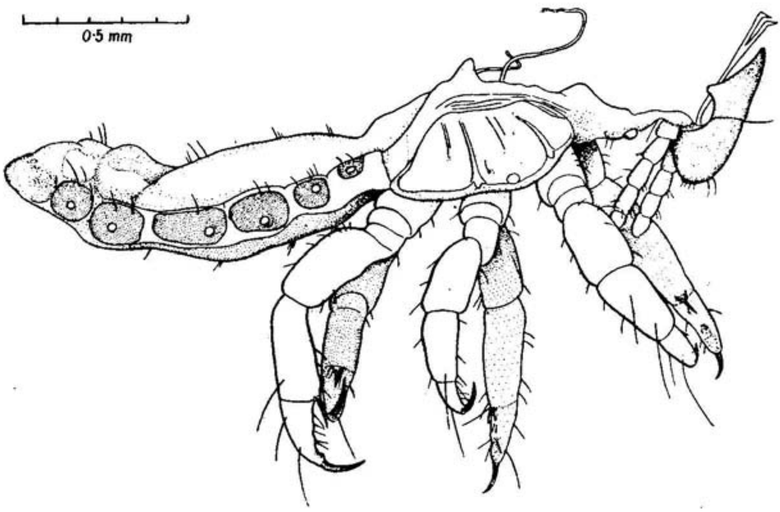

Fig. 11. *Pediculus humanus* (*corporis*). Empty second larval skin from which a third stage larva issued. Note the convergence of the legs which hold the hair or cloth on which the insect emerges. Dorsally the old tracheae are seen protruding. The anterior portion of the head is bent sharply downward as one piece; the forked structure emerging dorsally, represents a portion of the complex of the piercing organ. The longitudinal split starts at the vertex and extends backward to the end of the thorax; the antennae and eyes are turned downward ventrally.

pushing it backward. The first to observe the process was Sikora (VIII. 1915, p. 525) and this author's description is accurate if short; the process was seen to last 5 minutes, and 45 minutes later the louse, a 2nd stage larva, began to suck blood. The accompanying illustrations (Figs. 11, 12) show the appearance of the moult; Müller (1915, Pl. I, Fig. 5) figures a moult accurately as it appears in profile. Certain matters in relation to moulting will receive attention in the section on anatomy. I would note, however, that the legs of the moult remain clinging to the cloth or hair upon which the insect has emerged, as in the Mayfly; this anchoring of the moult insures against accidents during the act of emergence. When the adults issue, the abdomen appears

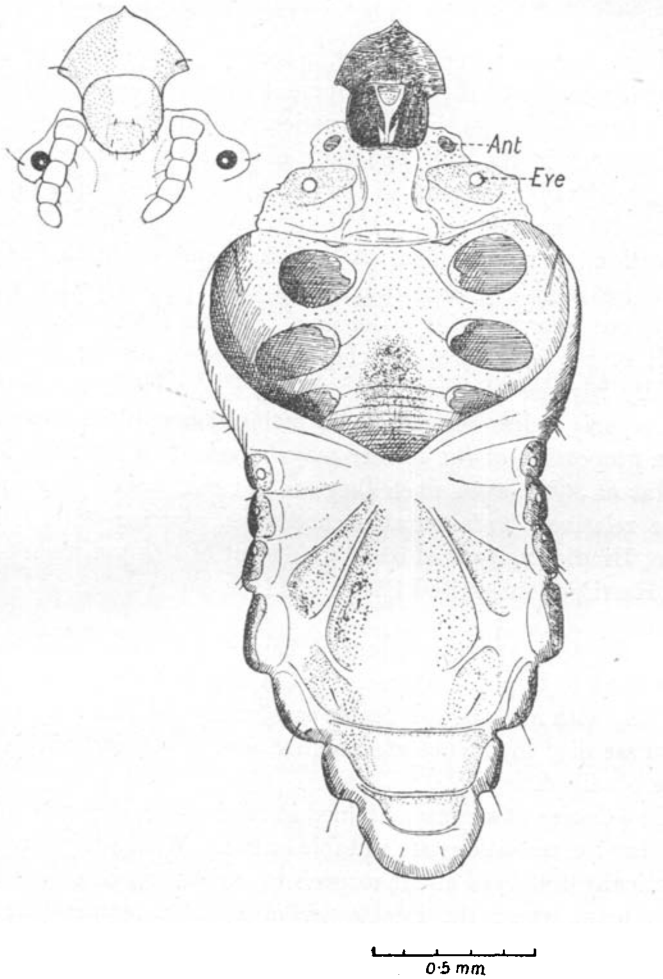

Fig. 12. *Pediculus humanus* (*corporis*).]
has emerged. Dorsal aspect, together with a frontal view of the head-parts of the moult showing the position of the eyes and antennae. The old tracheae are omitted.

short, broad, and curved dorsally behind; after a time they lengthen to out their normal dimensions and gradually darken.

Although Bacot (II. 1917, p. 235) states that the males undergo the act of moulting sooner than the females, I have failed to observe such a difference in over 100 *capitis* and many *corporis* raised to maturity, their ages being accurately recorded.

Loss of Life during Development.

When raised experimentally, a certain proportion of lice always die in the course of their development from the egg to the adult stage. Apart from accidents, in my experience, death may follow (*a*) arrested development in the egg, (*b*) failure of the larva to issue properly from the egg, (*c*) failure to cast off the old skin when moulting (a rare occurrence), (*d*) inability to feed from weakness probably due largely to starvation, (*e*) overfeeding. A common cause of death due to (*a–d*) is a too hot and dry atmosphere, coupled, in the active stages, with infrequent opportunities of feeding. Deaths from overfeeding are the result of too long intervals elapsing between meals; the insects may literally rupture themselves.

Corporis is less susceptible to artificial conditions than *capitis*. A large proportion of the former may be raised to maturity in the thermostat at 30° C. even when they are fed but twice a day: thus, under these relatively unfavourable conditions, starting with the 1st stage larva, Hindle (MS.) raised 59·3 % (944 out of 1590) of them to maturity, and Harrison (MS.) raised 12 out of 14.

Under the same conditions, I have repeatedly failed with *capitis*; they died in large numbers from the causes above enumerated (*a–d*). Starting with innumerable fertile eggs, many shrivelled up and hundreds of larvae died in the act of hatching, and in the end only a few adults were obtained.

The degree of success obtained in raising lice, depends entirely upon whether the conditions are suitable or not. With adequate precautions, practically 100 % of either *corporis* or *capitis* can be successfully reared upon man, where the insects find a suitable temperature, and most important, unlimited opportunities of feeding. In short, to obtain the best results, it is necessary as far as possible to imitate the natural conditions under which the insects live as parasites. By the methods described on pp. 105–109, wherein the lice were kept continuously upon the body, either in a felt cell or more conveniently in a wristlet, the results obtained are almost constant, loss of life being reduced to a minimum. *Capitis* affords the better test of the efficiency of the wristlet method. Thus, at the first trial, 100 were readily reared to maturity from 102 fertile eggs, the only two failures being due to an arrested development in the egg, and to a death in the second larval stage. A second trial with 104 fertile eggs yielded 103 larvae; five larvae died without feeding, and there was but one case of arrested development. A third trial, with a batch of 507 fertile eggs, gave 4 cases of arrested development whilst 4 larvae failed to free themselves from the egg-shell in hatching, consequently, at this stage, the loss of life was less than 2 %. In a fourth experiment, carried out during warmer weather, the result was not so favourable; thus of 247 fertile eggs, 3 showed arrested larval development and no less than 64 larvae died in the act of emerging, the loss of life therefore amounted to about 27 %. This observation is of interest as showing that in summer during hot weather there may be an increased loss of life in lice upon the human body, and it bears out what has been stated on p. 87 regarding the seasonal incidence of lice.

THE DURATION OF THE LIFE-CYCLE OF *P. HUMANUS* WHEN MAINTAINED CONTINUOUSLY UPON THE HUMAN BODY.

(*a*) *Corporis.*

The following experiment was carried out by the felt cell method (see p. 105), the insects being kept continuously on the arm and having direct access to the skin, as in nature.

On 2. II. 16, 5 ♂♂ and 5 ♀♀, received that morning from Dr W. H. Hamer in London, were placed upon the arm after being fed. On the afternoon of the following day (Day 1 of the protocol) the lice were removed, 25 eggs having been laid in the cell. Of these eggs 22 were fertile, all hatching normally at a subsequent date. The arm was inspected daily at 10–11 a.m. and the following results recorded:

	Day	
3. II. 16	1	22 fertile eggs laid on the felt
	11	4 more 2nd stage larvae found, making total 22
	12	13 2nd stage larvae and 9 *3rd stage larvae* found
	13	4 2nd stage larvae and 18 3rd stage larvae found
	14	22 3rd stage larvae found
	15	10 3rd stage larvae and 12 *adults* (2 ♂ and 10 ♀) found. All but 2 ♂ and 2 ♀ were now removed, copulation occurred, and the females oviposited as detailed on p. 129.
	16	first eggs laid

The time required to complete the life-cycle, from egg to egg, was therefore 16 days, made up as follows: Developmental period in the egg 8 days, 1st larval stage 2 days; 2nd larval stage 2 days; 3rd larval stage 3 days; adults' pre-oviposition period 1 day.

(*b*) *Capitis.*

The following experiment was carried out by the wristlet method (see p. 107), the insects remaining continuously on the arm and having unlimited opportunities of feeding through a screen of chiffon.

On 2. VI. 17, 4 ♂♂ and 6 ♀♀, received that morning from Mr A. Bacot in London, were placed in the wristlet and strapped to the arm; the females laid their eggs on the hair-grid. The daily record follows:

	Day	
3. VI. 17	1	31 eggs were laid before 10 a.m.
	7	24 eggs hatched, and as many *1st stage larvae* counted.
	11	19 *2nd stage larvae* counted
	14	— *3rd stage larvae* appeared
	16	16 *adults* (8 ♂, 8 ♀) counted; copulation occurred.
	17	first egg laid before 10 a.m.

The development from egg to egg therefore lasted 17 days, made up as follows: Developmental period in the egg 7 days; 1st larval stage 4 days; 2nd larval stage 3 days; 3rd larval stage 2 days; adults' pre-oviposition period 1 day. The remaining insects (also the case in *corporis*) developed more slowly.

These two experiments, as far as I am aware, are the only ones hitherto published which afford a true conception of the rate of development of body-lice and head-lice upon the human subject. Feeding the insects once or twice a day, and maintaining them in the thermostat between feeds under different conditions of temperature and moisture to those to which they are accustomed upon man, necessarily must lead to fallacious conclusions. Under natural conditions, lice feed at frequent intervals, and head-lice especially cannot be raised successfully unless fed frequently; this explains the repeated failures that attended my earlier efforts to raise *capitis*.

The Hypothetical Number of Descendants of One Female within a Limited Period.

Commencing with Leeuwenhoek (ed. 1807, pp. 163–169), who reckoned that a female *corporis* might have 5000 descendants in 8 weeks, a number of authors have referred to the possible number of the offspring within a limited period. Railliet (1895, p. 825) reckoned that a female *capitis* would have 125,000 descendants in 12 weeks, assuming that they escaped the accidents which destroy many of them in nature. Dore (1916, abstr. p. 630) calculates that a female may have 8000 descendants during her lifetime, and Alessandrini (1916, p. 96) also gives an estimate. Bacot (II. 1917, p. 258), writing of *corporis*, estimates the egg period at 12 days and the larva-to-adult period at 12 days; allowing an average of 8 eggs laid per day during 40 days, he computes that a female may have 4160 descendants during her lifetime.

The data obtained by me in raising *corporis* upon the body, differ from those of Bacot and other authors. The egg-to-egg period was found to be 16 days; the average number of eggs laid per day per female being 10, laid in 28 days. Taking the life of the adult female as lasting 30 days upon man; assuming that but 70 % of the eggs hatch and that only 60 % of the larvae attain sexual maturity, we allow a considerable margin for loss during development[1]; we must assume that the sexes are equally represented among the descendants. Given these data, Miss H. P. Hudson has kindly calculated for me that a female would have 1918 descendants during her lifetime, and that the offspring of her daughters, during their lifetime, would number 112,778. This offspring would include all stages of development from egg to adult. I may add that this large figure would be reached in 48 days from the date when the original female began ovipositing.

Judging from the enumerations that have been made of the numbers of lice that may be present on an individual (see p. 86), it is evident there must be a very great loss of life among the lice that infest a man, even when the clothing is worn continuously and no special measures are taken to destroy the vermin. A very large number are undoubtedly destroyed merely by the constant scratching of the person. When this combative action of the host becomes less active through debility or disease, it will be readily understood why enormous numbers of lice may occur on the individual as recorded in older reports on pedicular disease. We have parallel instances in animals which on becoming old or decrepit are super-parasitized by fleas, lice or ticks; the animal in health would have prevented this or, as the saying goes, would have "kept itself clean."

[1] No such heavy losses have occurred in my best raising results either with *corporis* or *capitis*.

Longevity of Lice (Different Stages) when Starved.

The first observation relating to the longevity of lice is recorded by Swammerdam (ed. 1682, p. 60) who states that lice soon die unless kept warm and moist. Recent publications contain many references to the subject because of its practical bearing, but the observations recorded are of very unequal value. Very few authors give the requisite data regarding (*a*) the number, age, and stage of development of the lice experimented upon, (*b*) the temperature and hygrometric conditions, (*c*) whether the insects had been fed or not prior to fasting, (*d*) whether the lice were kept in the dark or the light. All of these factors may materially affect the results obtained. In the following table I have sought to condense the information that is forthcoming from the writings of other authors and my own experiments:

Experimental Records relating to the Longevity of Starved Lice.

(*a*) *Corporis.*

(*a*) Records which state the temperature at which the lice were kept, and the stages that were experimented upon.

Experiments on 1st stage larvae.

The following records relate to experiments of mine, conducted with larvae (Lot 212) collected in batches of 10 for each test as soon as possible after hatching. Some larvae remained unfed, others were fed once immediately before they began their fast.

Temp. ° C.	Unfed or once fed at start	Conditions	Longevity when fasting (abbreviations: d. = dead; f. = feeble)				
33°	unfed	wristlet,	23 hrs.	27 hrs.			
		dark	7 d. 1 f.	2 d., last one dying			
33°	fed	ditto	9 d. 1 f.	last one dead			
20°	unfed	on cloth,	58 hrs.	71 hrs.	81 hrs.	95 hrs.	101 hrs.
		dark, dry	3 d.	4 d.	2 d., 1 dying	—	—
20°	fed	ditto	2 d.	1 d.	3 d.	2 d., 1 dying	1 d., last dying
12°	unfed	ditto, but	57 hrs.	72 hrs.	101 hrs.	120 hrs.	127 hrs.
		damp	1 d.	2 d.	2 d.	1 d.	4 dying
12°	fed	ditto	2 d.	2 d.	2 d.	2 d.	1 d., 1 dying

From this we see that some unfed and once-fed larvae at 33° C. lived up to 27 hours; at 20° C. some lived to 81 and 101 hours; at 12° C. some lived up to 127 hours. There is no material difference in the longevity of unfed and once-fed larvae; only at 20° C. did the fed larvae slightly outlive the unfed.

Other authors state that 1st stage larvae live: 1 day at 36·1° C., dry (Bacot[1])*; 1 day at 25–30° C. (Hase[6]); 1–2 days at 30° C. (Patton and Cragg, 1913, p. 552); at longest 4 days at 6° C. (Hase[6]). None of these authors state whether the larvae had fed or not.

Experiments on adults.

Temp. ° C.	Unfed or fed	Conditions	Longevity	Authority *
36°	not stated	dry... ...	3 days†	Bacot[1]
34°	„ „	not stated	1 day	Heymann[7]
25–29°	„ „	„ „	3–5 days	„
24°	„ „	damp ...	3 days	Bacot[1]
16–18°	„ „	dry ...	4–7 days	„
12–15°	„ „	not stated	7–9 „	Heymann[7]
15°	8 hrs. after ecdysis, fed soon before, 2 expts. with 10 lice	dry, dark, in tubes on cloth	3–4 „	Nuttall
15°	Several days old, fed soon before, 5 lice	ditto ...	5 days	„
10°	ditto	ditto ...	3 „	„
5°	8 hrs. after ecdysis, unfed, 2 expts., 10 lice	ditto, damp	3½ „	„
5°	ditto, except that fed shortly before	ditto, damp	3 „	„

* To avoid repetition, the references are arranged by numbers and given at the end of this section p. 170.

† A day is reckoned as 24 hours throughout.

I here append an unpublished experimental record of Hindle's relating to adult lice of unknown age:

"Eighteen pairs of lice were allowed to gorge, and then divided into three lots, each of six pairs, which were kept at different temperatures without further feeding, with the following results:

Days	30° C.	22° C.	8–10° C.
1	1 ♂ dead	—	1 ♂ dead
2	4 ♂♂ and 3 ♀♀ dead	—	—
3	1 ♂ and 3 ♀♀ dead	5 ♂♂ dead	—
4	All dead	1 ♂ and 5 ♀♀ dead	4 ♂♂ dead
5	—	1 ♀ dead	1 ♂ and 4 ♀♀ dead
6	—	All dead	1 ♀ dead
7	—	—	1 ♀ dead
8	—	—	All dead

The period of starvation that a louse can survive thus varies from about three days at 30° C. to seven days at 8–10° C.; but those which have been starved for three days at room temperature become so weak that they can only feed with difficulty, and there is little doubt that a louse, even if it survived a week without a meal, would not then be able to feed."

(*b*) Records which give the temperature but not the stages or age of the lice experimented upon. Presumably the lice were of very different ages and both fed and unfed.

Temp. ° C.	Conditions	Longevity	Authority*
40°	in thermostat	12 hours	Heymann[8]
37°	carried in axilla	1 day	,,
37°	41 lice in thermostat	1 day	Hase[6]
36·5°	not stated	1 day	Noeller[10]
35°	50 lice, moist	1½ days	Wilder[14]
29–33°	moist	5–7 days	Engelhardt[2]
30°	dry	50 % dead in 1 day, others lived 2–3 days	,,
30°	moist	3–5 days	,,
28–30°	carried on breast	30–36 hours	Heymann[8]
25–30°	85 lice	6 lice lived 2 days, none longer	Hase[6]
25–28°	carried on body	3–5 days	Heymann[8]
22°	not stated	2 days at most	Sikora[12]
20°	dry	2–4 days	Engelhardt[2]
20°	moist	3–6 ,, ...	,,
20°	several lice	5 days	Galli-Valerio[4]
16–18°	not stated	3 days at most	Sikora[12]
15–17°	dry	4–5 days	Engelhardt[2]
15–17°	moist	4–7 ,, ...	,,
10–20°	98 lice	only 1 lived 7 days† ...	Hase[6]
10–12°	not stated	occasionally lived 9 days	Heymann[8]
6°	100 lice	only 2 lived 9 days‡ ...	Hase[6]
5·5°	not stated	10 days	Noeller[10]
5°	,, ,, ...	occasionally 10 days ...	Heymann[8]
3·5–6°	on infested shirt exposed to wet weather	some lived 5 days ...	Peacock[11]

† There survived respectively 90, 67, 37, 10, and 2 lice out of the original 98 on days 2–6.

‡ There survived respectively 97, 93, 79, 54, 36, 18, and 11 lice out of the original 100 on days 2–8.

(*c*) Records which do not give the temperature, etc.

Records mentioning the stages experimented upon but not the conditions.

Stage	Longevity	Authority*
1st stage larvae	die in 36 hours	Warburton[13], Fantham[3], Girault (1912, p. 339)
,, ,,	2–4 days ...	Heymann[7]
Adults ...	4–5 days at most	Warburton[13]
,, ...	3 days ...	Fantham[3]

* To avoid repetition, the references are arranged by numbers and given at the end of this section p. 170.

Records which do not mention the stage, but state something regarding the conditions affecting the lice.

Conditions	Longevity	Authority*
In earth and sand	2–3 days ...	Hase[6]
In vitro	2–3 days, mostly	Fiebiger[15]
At "room temperature"	2–3 days ...	Galewsky[16]
"In open dishes," Russia	3–4 „ ...	Report, x. 1915, p. 53
"In the cold"	4 days at most	Sikora[12]
In moist sand	4 days	Hase[6]
In vitro	3–5 days ...	Müller[9]
Beneath 1 ft of dry earth or sand†	4 days	Noeller, 1915, abstr.
On single shirts in tins or paper parcels ...	5 „ ...	Peacock[11]
After removal from patient in Algeria ...	6 „ ...	Sergent and Foley[17]
Expt 1. On straw for 3 men infested with 535 lice; 3 men slept thereon, after 4½ days, on 3 successive nights, after which they harboured 18, 4 and 7 lice each	4½–7 days ...	Peacock[11]
Expt 2. As before, except that 1000 lice were used and the men slept on straw after 5½ days. Lice found: 2, 2, and 0, on 3 succeeding nights	5½–7 „ ...	„
Expt 3. On 3 palliasses infested respectively with 325, 500, and 500 lice	8 days	„
On soil in tin	7–8 days ...	„
On shirts stored in bulk	8 days	„
Kept "cool"	8 „	Hocht and Halberkann[18]
In clothing	6–10 days ...	Müller[9]

* To avoid repetition, the references are arranged by numbers and given at the end of this section p. 170.

† Noeller is reported as stating that the lice came up through 12 inches of earth or sand.

Furthermore, without stating any particulars, Bisset (1914, p. 114) in India, records a longevity of 5–6 days; Ragg (1915, p. 172) gives 6 days, and Prowazek (1915, p. 67) gives 2–4 days. Zucker (1915, p. 294) makes the absurd statement that gorged lice may live for weeks in soldiers' knapsacks.

(b) *Capitis.*

Without specifying the conditions under which the lice were kept, Galli-Valerio[5] states that head-lice at 30° C. lived 1–2 days, at 20° for 2–5 days, at 1–2° for 4–5 days, at 0–5° for 4 days.

The following records relate to experiments of mine carried out with larvae and adults (Lot 210) that had emerged within the previous 24 hours in a wristlet, where they had fed moderately; they starved subsequently.

Stage and No. of lice tested	Temp. ° C.	Conditions	Longevity when fasting (abbreviations: d. = dead; f. = feeble)				
1st st. L.	31°	on cloth, in dark	8 hrs.	24 hrs.	(similar results on body at 33° C.)		
10		thermostat, dry	4 d. 6 f.	all d.			
20	17°	ditto in room, dry	24 hrs.	33 hrs.	48 hrs.	54 hrs.	
			7 d. 3 f.	4 d.	4 d., 5 dying	all d.	
10	12°	ditto in damp refrigerator	48 hrs.	72 hrs.	77 hrs.	102 hrs.	121 hrs.
			1 d.	5 d.	1 d.	1 d., 2 dying	all d.
Adults							
2 ♂ 3 ♀	33°	on arm (wristlet)	23 hrs.	27 hrs.	30 hrs.		
			2 ♂ 3 ♀ d.	1 ♀ d., 2 dying	last ♀ d.		
2 ♂ 8 ♀	30°	on hair, in dark	23 hrs.		29 hrs.	47 hrs.	
		thermostat, dry	1 ♂ d. 1 ♂ dying		5 ♀ d.	last ♀ d.	
3 ♂ 7 ♀	20°	on hair, in dark	48 hrs.	58 hrs.	72 hrs.	78 hrs.	96 hrs.
		room, dry	1 ♂ 1 ♀ d.	1 ♂ d.	1 ♂ 3 ♀ d.	2 ♀ d.	last ♀ d.
6 ♂ 5 ♀	12°	on cloth in damp	96 hrs.	102 hrs.	120 hrs.	127 hrs.	143 hrs.
		refrigerator	1 ♀ d.	2 ♂ 1 ♀ d.	2 ♂ 3 ♀ d.	1 ♂ dying	last ♀ d.

Summary regarding the longevity of Starved Lice.

A selection confined to those of the foregoing records giving the longest spans of life observed under different conditions, gives the following general result:

	Greatest recorded longevity	Temperature ° C.	Authority
Corporis			
1st st. larvae, in the dark, unfed	27 hrs	33° dry	Nuttall
once fed	23 „	33° „	„
unfed	81 „	20° „	„
once fed	101 „	20° „	„
unfed	127 „	12° „	„
unfed	127 „	12° „	„
Various unspecified stages, not stated if fed or not, etc.	½ day	40° dry	Various authors cited in foregoing tables
	1 „	37° „	
	3 days	36° „	„ „
	3 „	30° „	„ „
	5 „	30° damp	„ „
	5 „	20° dry	„ „
	6 „	20° damp	„ „
	7 „	16–18° dry	„ „
	5 „	15–17° „	„ „
	7 „	15–17° damp	„ „
	9 „	10–12°	„ „
	9 „	6°	„ „
	10 „	5°	„ „
Capitis	Died within		
1st st. larvae, in the dark, unfed	24 hrs	31° dry	Nuttall
	54 „	17° „	„
	ca. 110 „	10° damp	„
Adults, in the dark, unfed	30 hrs	33° „	„
	47 „	30° „	„
	96 „	20° „	„
	143 „	12° „	„

Further experiments may give more accurate information, but the general result is conclusive in so far as it proves that lice live longest at a low temperature and that life is somewhat prolonged by a damp atmosphere under the conditions specified. The influence of feeding prior to a fast in *corporis* larvae was only apparent when they were kept at 20° C., otherwise there was no material difference in the longevity of the once-fed and unfed insects.

Longevity of Lice (Adults) when Fed.

In the following protocols, the age, in all cases, is reckoned from the last ecdysis.

(*a*) Longevity of *corporis* when gorged once daily.

No. of lice	Sex	Conditions	Longevity	Authority*
1	♀	? in tube on person ...	21 days ...	Fantham[3]
"some"	♀	? in thermostat at 28° C. whilst laying	30 ,, ...	Swellengrebel, 1916, p. 4

(*b*) Longevity of *corporis* when gorged twice daily.

No. of lice	Sex	Conditions	Longevity	Authority*
2	♂	on cloth in tube, near person	17 and ca. 21 days	Warburton[13]
1	♀	ditto (with ♂)	30 days ...	,,
"some"	♂	at 30° C. in thermostat	15–16 days ...	Hindle MS.
,,	♀	at 22° C.	24–28 ,, ...	,,
6	♀	at ca. 24° C. in pocket by day and at ca. 35° C., near person at night, whilst laying	respectively 21, 25, 36, 37, 37 and 45 days	Sikora, VIII. 1915, p. 528
5	♂	under same conditions as above	respectively 21, 28, 30, 31 and 35 days	,, ,, ,,

* To avoid repetition, the references are arranged by numbers and given at the end of this section p. 170.

(*c*) Longevity of *corporis*, *capitis* + *corporis* (1st generation of hybrids) and *capitis*, when fed by Bacot's method (see p. 110) during 6–7 hours out of the 24; carried next to the body at night, in the waistcoat pocket by day. The sexes were kept together and the females oviposited.

	No. of adults and sex	Longevity	Remarks	Authority Bacot II. 1917
corporis	1 ♂	32 days	whilst it fertilized 18 ♀	p. 236
,,	7 ♀	respectively 23, 29, 30, 32, 34, 44, 46 days (average 34 days)	—	p. 236
corp. + *cap.*	1 ♂ 1 ♀	45 days	female laid normally	p. 255
capitis	4 ♂	respectively 7, 12, 15, 30 days	—	pp. 246–247
,,	16 ♀	respectively 11, 14, 17, 20, 22, 25, 26, 29, 31, 31, 34, 34, 36, 37, 38 days (average 27 days)	—	pp. 246–247

(*d*) Longevity of *corporis* and *capitis* when offered unlimited opportunities of feeding on the body by the felt cell and wristlet methods in my experiments. Only the longest lives recorded.

	No. of adults	Longevity	Remarks	Authority
corporis	1 ♂ 1 ♀	♂ 28 days, ♀ 29 days ...	on skin of arm ...	Nuttall
capitis	1 ♂ 1 ♀	♂ 23 days, ♀ 22 days ...	in wristlet	,,

[1] Bacot, II. 1917, p. 234. [2] Engelhardt, 1915, p. 165. [3] Fantham, 1912, p. 513. [4] Galli-Valerio, 1913, p. 501. [5] Galli-Valerio, 1916, p. 37. [6] Hase, 1915, p. 67, cited by Müller. [7] Heymann, III. 1915, p. 253. [8] Heymann, 18. VIII. 1915, p. 308. [9] Müller, 1915, p. 74. [10] Noeller, 1915, abstr. [11] Peacock, 1916, pp. 40, 50. [12] Sikora, 1915, pp. 164, 533. [13] Warburton, 1911, pp. 23–27. [14] Wilder, 1911, p. 43. [15] Fiebiger, VIII. 1915, p. 645. [16] Galewsky, III. 1915, p. 286. [17] Sergent and Foley, III. 1914, p. 471. [18] Nocht and Halberkann, 1915, p. 626.

Summary regarding the longevity of Adult Lice when fed.

Corporis. The foregoing records show that a female may live up to 30 days when kept at 28° C. and fed once daily; when fed twice daily and kept at 24° by day and ca. 35° by night, the male may live 35 and the female 45 days; when afforded an opportunity of feeding during 6–7 hours out of the 24 on the person and carried in the pockets during the interim, the maximum age attained by a male was 32 days and by a female 46 days (Bacot's average for 7 females = 34 days). When kept continuously on the body and given unlimited opportunities of feeding, as in nature, the longest lives observed were 28 days for a male and 29 days for a female. Bacot's *corporis* + *capitis* hybrids: a male and female fed for 6–7 hours out of the 24, lived 45 days. *Capitis.* The longest lives recorded for a male and female fed for 6–7 hours out of the 24 were 30 days and 38 days respectively (Bacot's average for 16 females = 27 days). When kept continuously on the body by the wristlet method, the longest life of a male was 23 days, of a female 22 days; the experiment should, however, be repeated in cool weather, for I believe they will live longer.

Therefore the females usually outlive the males. The longest lives observed by me in *corporis* (and *capitis*) are markedly shorter than those recorded by Sikora and Bacot, the age of the females in both cases falling 5 days short of Bacot's average. The reason seems clear when we consider that my females laid more eggs per day, their metabolism being necessarily more active under the more natural conditions in which they were maintained. Under approximately like experimental conditions, *corporis* lives some days longer than *capitis*.

FEEDING HABITS.

The act of sucking blood was first observed microscopically by Robert Hooke (1665, pp. 211–213), who mentions that it is accomplished by a "pump" in the head[1]. Leeuwenhoek (ed. 1807, p. 163) relates that the louse everts a nipple-like protuberance from the front of the head from which the piercing organ issues; the latter being enclosed in a retractile sheath. Leeuwenhoek describes how the louse raises the posterior portion of its body when feeding; in the absence of hairs it clings firmly by its sharp claws to the skin surface; the blood is seen to flow through the oesophagus whilst the intestine shows active peristalsis. The process of feeding was also observed by Swammerdam (ed. 1682, p. 60) who described how he saw the blood flow like waves into the gut, recalling the rush of water through a sluice; the blood entered with such force that the excreta were propelled outward, whilst the gut moved actively.

Various matters relating to the mechanism of feeding will be considered in detail in the section dealing with the mouthparts[2]. Regarding the general behaviour of lice when feeding, little has been added to what was so well observed by the old authors just mentioned. Having anchored itself firmly upon the skin or by clinging to the base of one or more hairs, the louse feels about with its head depressed. The object of depressing the head is to permit the teeth of the haustellum to penetrate the skin. The haustellum, or "nipple-like protuberance" of Leeuwenhoek, is provided with rows of dorsally projecting recurved

[1] Nevertheless Widmann (18. VIII. 1915, p. 290) makes the absurd statement that the blood is sucked up by "gut peristalsis"!

[2] Lice refuse to feed on a drop of blood (Widmann, 28. IX. 1915; Galli-Valerio, 9. V. 1916, p. 37).

chitinous teeth which are inverted when the suctorial apparatus is withdrawn. The hooklets serve to anchor the head of the louse to the skin; they are figured by Swammerdam. Schjödte (1866, pp. 213 et seq.) found that the haustellar teeth offered a slight but appreciable resistance when he attempted, with the aid of forceps, to pull the head of the louse away gently from the skin to which it was anchored.

Many lice, when feeding, tilt the long axis of their bodies almost vertically to the skin surface; this seems to me attributable to the firm grip afforded by the haustellar teeth which permits a relaxation of the efforts of clinging with the legs and of depressing the head; this position, moreover, places the head in the most favourable position for maintaining the grip with the haustellar teeth and using the piercing mouthparts. In other words, the haustellum with its teeth acts in a somewhat similar manner to the mouthparts of a tick in anchoring the parasite to the host, so that little or no effort is required by the legs. Having anchored itself by the haustellum, the louse protrudes the piercing organs and proceeds to pump. It may draw blood at once or repeated efforts may have to be made at different places before blood is successfully drawn.

Assuming that blood is found, the insect proceeds to pump it in by means of its pharyngeal apparatus which can be readily seen with a hand lens or better under a binocular microscope. The pulsations of the pump are so rapid that they can scarcely be counted. Sikora (VIII. 1915, p. 531) states that there may be 150 pulsations a minute, but this seems to me largely guesswork. From the pump, the blood is propelled back through the fine tubular oesophagus into the midgut whose peristaltic movements become extremely active. As the intestine fills, excreta are commonly voided in more or less profusion. The time occupied in feeding, the amount of blood imbibed and of excreta voided, are largely dependent upon the state of hunger.

The frequency with which Lice feed.

The louse larva feeds at once on emerging from the egg as was first noted by Warburton (1911) and has since been confirmed by Fantham (1912) and Swellengrebel (1916); the latter's statement that larvae feed more promptly than adults is contrary to my observations on equally hungry larvae and adults. After helping a larva to emerge, by means of a needle, I have transferred it on the needle-point to the back of my hand and seen it suck blood immediately. Later stage larvae and adults are ready to feed very soon after moulting; thus Sikora saw an adult feed 45 minutes after ecdysis.

Repeated observations of lice under natural conditions has convinced me that they feed much more frequently than is generally supposed. Brumpt (1910, p. 550) states that *corporis* feeds mostly at night. Lelean (1917), no doubt confusing laboratory experiments, possibly those of Bacot, with what takes place in nature, states that lice feed twice in 24 hours. When I have examined lice immediately upon their removal from infested persons, or lice maintained continuously upon the body under experimental conditions, I have been much struck by the fact that they are very rarely found gorged with blood. When they contain an appreciable amount of red blood, it is almost always in moderate quantity and frequently the contents of the very sparsely filled alimentary tract appear black. Again, when I kept lice continuously upon the person, I noticed that they started to bite at all times when I kept quiet. It is doubtless correct to state that lice bite most frequently at night, but it is certain that they bite frequently and at all times during the day, especially when the host comes to rest or there is little movement of the part of the body where the lice happen to be.

The frequency with which lice feed is naturally dependent upon the rate of digestion, which in turn is influenced by temperature. Lice will feed much more frequently at body temperature than when kept cool. Entirely false conceptions may result from ordinary laboratory experience regarding the feeding habits of lice, and it is to correct the tendency to such misconceptions that I lay stress on the subject. The only author who records experiments bearing on the matter is Hase (1915, pp. 72–74, cited by Müller), who maintained 11 lice at 37° C. and saw 7 of them feed again after an hour, whilst of 6 lice placed at 6° C., only 2 fed after an interval of 9 hours. I would remark, however, that at such low temperatures the digestive processes are suspended, and, unless the insects had partaken of but a very modest meal, they would not again bite from hunger.

The gorging of Lice.

When lice become ravenous with hunger, they feed to excess. They fill their midgut to its utmost capacity with blood and the abdomen becomes proportionately swollen (Plate II). Not content, they may expel bright red, undigested blood from the anus. It occasionally happens that a few minutes after gorging, or at times later, that the insect assumes a pink and then a red colour all over owing to the rupture of the intestine and the diffusion of haemoglobin throughout its coelomic cavity; such insects invariably die after a short time. Gorging may be observed in lice kept at 28–37° C. and fed only once or twice a day, or after longer periods of starvation.

Several authors have taken the pains to weigh lice before and after they have gorged in the manner described. Widmann (1915, p. 1336; 18. VIII. 1915, p. 290) states that an adult *corporis* may increase 0·7–1·2 mg. in weight (= 0·6–1 c.m. of blood); Heymann (18. VIII. 1915, p. 307) found that lice imbibed 0·2–0·3 mg. of blood at a meal; Rocha-Lima (I. 1916, pp. 17–31) reports that Sikora and Halberkann found the ♂ imbibed 0·325 and the ♀ 0·89 mg.; finally Galli-Valerio (1916, p. 37) found adult *capitis* capable of imbibing ca. 0·5 mg. of blood. The interest in these weighings may be twofold; they may afford (*a*) a measure of the loss of blood the host may suffer when infested by a given number of adult lice, and (*b*) give an indication of the multiplication of a virus taken into the louse's body with the blood it imbibes, say in the case of typhus. In the latter, for instance, the blood of a typhus patient may be infective by inoculation in doses of 5 c.c., whereas the bodies of 10 crushed lice, hypothetically equal to say 10 c.mm. of blood imbibed, may prove equally infective, and the inference that the virus has multiplied may be correct. As a measure of the loss of blood these weighings are fallacious, for normally the louse only gorges infrequently upon the host and the amount of blood imbibed in many little meals may be greater than when large meals are taken at long intervals although the insect perhaps fills itself to bursting point. Moreover, the loss of blood is not merely due to adults, since the immature stages usually preponderate upon infested persons.

The time occupied in feeding.

When hungry lice are placed upon the skin, they instantly proceed to feed, be they in daylight or darkness, or in the presence or absence of so-called repellants, and, usually in a few moments, the blood may be seen entering the midgut. At times there is some delay before the blood flows, because the insects must first find a blood vessel. A number of authors have timed the process, stating that it may take: 10–15′, at times 25′, in larvae, and 20–30′ in adults (Fantham, 1912, p. 514); 5–10′ (Legroux, 1915, p. 470); 7′ (Musselius, 1915, p. 170, who fed them on himself); 3–5′ (Widmann, 18. VIII. 1915, p. 290); 8–21′, at most 23′, when they have starved (Hase, 1915, p. 85, cited by Müller); larvae fed twice a day took 9–22′, but fed more rapidly when fed thrice a day (Peacock, 1916, p. 39); all stages are satiated in 2–15′

(Swellengrebel, 1916, p. 23). The only observations not agreeing with the foregoing are those of Sikora (VIII. 1915, p. 531), who states that adults take 1–1½, at times 2–3, hours to feed, sucking intermittently. I have only observed such prolonged feeding in enfeebled lice, and agree with others that gorging usually lasts about 3–10′ in hungry insects. When not ravenous they may feed for shorter periods.

DIGESTIVE PROCESSES.

On examining the young unfed larva under a low power, the slight contents of the midgut present a greenish colour. When it gorges, its previously short flat body becomes elongated and swollen. Whilst feeding for the first time, it expels some of the ingested blood by the anus. This expulsion of undigested, bright red blood, takes place in all stages, when they feed to repletion; there is no evidence that it occurs when the insects feed moderately and at frequent intervals as they usually do under natural conditions. The issuing droplets of blood dry rapidly, and cohere to form short chains of irregular or spiral form and dark red colour, subsequently becoming blackish. Whilst the insect feeds, and for a variable period afterwards, the gut shows very active peristalsis.

The rate at which digestion occurs is much influenced by temperature. After 4 days at 12° C., a larva will still appear swollen and red, whereas at 31–37° C. a reduction in volume takes place in a few hours, and the bright red colour soon vanishes, changing from the haemoglobin-red to reddish brown and black as digestion proceeds. Whereas the gorged midgut at first renders most of the internal organs invisible, it gradually contracts and appears as a blackish, median longitudinal line under a hand lens, and finally the excreta accumulate in the posterior reaches of the intestine, the various organs of the insect having become again visible by transparency. In the meantime the insect has voided a large amount of blackish excreta. When lice are kept at 28° C. they do not need to be fed as often as at 35–37° C. because they digest more slowly and lose less water.

All who have studied lice have observed these appearances; Swammerdam (ed. 1682, p. 60) observed the expulsion of blood in the act of feeding; Sikora (VIII. 1915, p. 532) noted that lice kept at 6–8° C. contained unaltered blood after 8–10 hours, whereas at 35° C. digestion was completed in that time; Widmann (18. VIII. 1915, pp. 290–292; 28. IX. 1915, pp. 1337–1338) found that the gut became empty in 10 hours at 28–30° C., in 12 hours at 20° C., and in 16 hours at 15° C.; at

28–30° C. the blood in the gut had become dark or black in 3–4 hours; the red blood corpuscles being destroyed in 5 hours at latest and replaced by detritus consisting of amorphous particles. The empty gut is faintly acid (this spoils Giemsa staining unless neutralized by ammonia vapour), but on feeding, a weak alkaline protease is given off into the gut. Widmann found the gut contents to be sterile in 25 lice examined for aerobic and anaerobic bacteria; from 5 out of 25 lice that had been dead 10–12 hours he isolated a small anaerobic bacillus.

Widmann found the faeces to be faintly acid. When fresh faeces are viewed in salt solution they are seen to consist of fine granular detritus and yellow-brown prismatic crystals, occurring in bundles or rosettes; the crystals are indistinct, insoluble in water, alcohol, ether, chloroform, and the ordinary mineral acids, but they dissolve in dilute alkalies. These crystals, probably haemoglobin or its derivatives, apparently form outside on contact with air as they are not found in the gut. I have occasionally observed excreta having a whitish colour, and doubtless derived from the Malpighian tubes; in an old adult a long mass of this character was found protruding from the anus of the dying insect.

Some further details relating to digestion will be considered in the section on anatomy that will follow.

Some Reactions of *Pediculi*.

REACTIONS TO LIGHT.

Heliotropic reactions. According to Hase (1915, pp. 48–50, cited by Müller), *corporis* shun the light unless they have hungered 12–24 hours, in which case they wander toward a source of light; if, however, they are disturbed, they seek darkness. Galli-Valerio (1916, p. 37) states that *capitis* wander to the light when hungry and to the dark when gorged. Bacot (II. 1917, p. 233) found *corporis* and *capitis* moved toward the shadow of dark objects; when placed upon squares of black or white paper, they mostly wandered to the shady side; he makes no mention of whether the insects he tested were hungry or not.

I have made a few experiments with *corporis* at ca. 15° C. in diffuse daylight about 5 feet away from a window. About 200 hungry insects in all stages of development were placed on a square of dark cloth measuring about 10 × 8 cm., in the centre of a large glass dish. When agitated, on first being placed on the cloth, they repeatedly ran to the upper illuminated surface, when the cloth was reversed at intervals of about two minutes. When left quiet and exposed to the light, they retreated beneath the cloth or along its shady border; they walked away from the light, or, when the cloth was sufficiently near (ca. 3 cm.), toward the light, to gain the shady side of the cloth. Gorged lice exposed to strong light run rapidly to darkness (see p. 100).

Effect of light on development. The following experiments were carried out so as to determine if light exerts any effect on the development of lice (*corporis*).

The insects were fed twice daily upon the arm and, between feeds, they were kept at 31° C. in an electrically heated thermostat with double glazed doors facing a large window through which strong daylight penetrated in summer (July 1917). The lice were confined in glass vessels provided with a white background and each containing a hair-grid upon which eggs were laid and the lice clung. This arrangement prevented the insects from having access to any shade other than the small amount afforded them by each other's bodies when aggregated in masses. After the females had laid the desired number of eggs on the hair, they were removed; the eggs and larvae which issued therefrom were maintained in the light, nights excepted, until they attained maturity. By way of control, other lice, the progeny of the same adults used in the light experiment, were raised in the dark in the same thermostat under otherwise identical conditions.

Exposed to the light:

(*a*) 3 ♂ 5 ♀ laid 103 eggs of which 85 (83%) hatched. From the 85 1st stage larvae were raised 30 adults (35%), the rest failing to reach maturity.

(*b*) 4 ♂ 4 ♀ laid 89 eggs of which 63 (71%) hatched. From the 63 1st stage larvae were raised 24 adults (38%), the rest failing to attain maturity.

Controls kept in the dark:

(*c*) 2 ♂ 5 ♀ laid 107 eggs of which 101 (94%) hatched. From the 101 1st stage larvae were raised 38 adults (37%), the rest failing to reach maturity.

(*d*) 4 ♂ 4 ♀ laid 93 eggs of which 84 (90%) hatched. From the 84 1st stage larvae were raised 29 adults (34%), the rest failing to attain maturity.

The results obtained in the above experiments show that daylight does not apparently exert an inhibitive effect on the development of *corporis*. The number of adults raised from first stage larvae in the light and in the dark was about the ame. Although the percentage of eggs that hatched in the light was somewhat smaller than in the dark, the difference is too slight to possess significance and may be due to experimental error, for of 1158 other eggs raised at 30° C. in the dark (see p. 153) but 69·6% hatched.

REACTIONS TO WARMTH.

Thermotactic reactions. Various authors have tested the thermotactic reactions of *corporis*, some with positive, others with negative results. Wulker (1915, p. 630) found no evidence of a thermotactic sense, and Nocht and Halberkann (1915, p. 626) observed no effect when the insects were brought in proximity to man. Other authors find that lice only react at a short distance from man, at 2 cm. (Hase, 1915, cited by Müller, 1915, p. 66), at most 3 cm. (Sikora, VIII. 1915, p. 533); or that they wander aimlessly unless quite close to man (Swellengrebel, 1916, p. 13). Frickhinger (1916, p. 1254) enclosed lice in a photographic plate-holder, a part of which was warmed to 20–25° C., and states that the insects sought the warmed part of the holder. Sikora (*loc. cit.*) found that lice were not attracted to warm glass, whilst Major F. M. Howlett informs me that in experiments he conducted in India, lice were attracted to a tube containing warm water[1]. Some of these apparent contradictions, as we shall see, are readily explained.

Apparently some of the discordant results above mentioned are due to the experimental conditions, which, however, are not specified. Judging from personal experience, it is essential that the insects should not be torpid, and it is best for them to be hungry if well marked reactions to warmth are to be observed. With these conditions fulfilled, it is easy to observe that lice promptly react to a source of warmth, either the hand, or a tube containing warm water. Thus, having placed some 200 *corporis* on a piece of cloth, in a room at ca. 16° C., in daylight, the insects, after a time, had all retreated away from the light, beneath the cloth, or along its shady side. On holding the hand ca. 2 cm. above the cloth, they promptly swarmed to the upper surface and followed the finger moved about over the cloth very much like iron filings follow a magnet. Breathing on the cloth likewise produced an immediate swarming to its upper surface. I may add that the warm tube, held at a moderate distance from the cloth, attracted the lice, in a similar manner to the finger.

When the hot water tube approached them too closely, they fled,

[1] See this author's paper, p. 186.

the temperature being too high, though the tube was not unpleasantly hot to the hand. This explains a very interesting observation made by Howlett, of which he told me, namely that an ordinary comb, when warmed and passed through *capitis*-infested hair, causes the insects to become very active, they swarm out from near the scalp and are readily combed out. He recommended the method, for practical trial, to his Indian assistants, and they subsequently reported that their female acquaintances were delighted with the practical results they obtained by this simple means[1].

Effects of warmth on activities and metabolism.

Activities. The effect of temperature on the activities of lice is very marked. At 0° C. they are immobilized, at 10° C. they move very slowly, at 20° C. they are fairly active, at 30° C. they are very active, and at 37–40° C. they are extraordinarily active creatures; all grades of activity are observable at intermediate temperatures. If the temperature is raised above 40° C. they become wildly active and soon succumb to exhaustion. They die in a few minutes at 45–50° C.

The climbing records of lice on hair (see p. 101) demonstrate that *capitis* is more active than *corporis* at 17–18° C., and that *corporis* may climb more than twice as fast at 30° C., than it does at 17–18° C. As stated elsewhere, lice have been observed to abandon persons in high fever, and to wander actively from individuals when these are lying close together and warm.

Metabolism. Development and digestion are arrested at low temperatures, thus whilst hatching occurs in 16 days at 25° C., it takes place in 4–7 days at 37° C.; oviposition does not apparently take place at below 20° C., and 37° C. or slightly over is about the upper limit. 37° C. appears already to be too high, for in thermostat experiments, only 54·3 % of the larvae hatched out at that temperature, whereas 70–80 % hatched out at 30° C. Digestion, as gauged by lice that have gorged themselves, does not take place at 12° C., even if the insects survive 4–5 days, whereas at 35–37° C. it is complete in about 5 hours. Lice can be raised at 28–37° C., but the best results are obtained between 30 and 32° C.

[1] See p. 186.

DO LICE POSSESS AN OLFACTORY SENSE?

The evidence so far collected is all negative. Peacock (1916, pp. 42–44) found that *corporis* were not attracted to recently discarded sweat-impregnated clothes. Frickhinger (1916, pp. 1254–1256) has published a long-winded account of experiments which prove nothing, but from "field experience" he concludes that lice do smell certain persons (!). A series of experiments made by me with different essential oils and other substances commonly described as repellants, show that either in dilute or concentrated form they do not repel hungry lice; the insects feed upon man in spite of so-called repellants; the latter are really insecticides, and, as such, will be considered in a later section. According to Hase (XI. 1915, p. 158) some contend that persons having to do with horses are not attacked by lice, but he has not found this to be true[1]. Neither has Hase found that freely perspiring men, and, incidentally, hairy men, are more often attacked than others.

GREGARIOUSNESS.

Lice show a marked tendency to congregate in masses; this is observable in all stages. According to Bacot (II. 1917, p. 232) the tendency is less marked in the larvae of *capitis* than of *corporis*, but I have been unable to detect any difference.

VITAL RESISTANCE

TO IMMERSION IN WATER, COLD, EXPOSURE TO A VACUUM, AND TO MECHANICAL PRESSURE.

IMMERSION IN WATER. Lice are able to resist immersion in water for a considerable time. The authors who have tested this resistance, do not state how they performed their experiments or with what stages they operated; we must presume that some of the insects were adults.

Müller (1915, p. 54) saw lice revive after 22 hours' immersion; he cites Pick (1915) as having observed sham death in lice that had been submerged. Kinloch (1915, p. 1038) found that lice survived immersion in water for 48 hours, and in normal salt solution for 60 hours; he records neither the number of lice tested nor the temperature. Hase

[1] It is stated by Railliet (1895, p. 803) that *fleas* are repelled by the odour of horses; possibly the two insects have been confounded in this regard.

(1915, p. 72) states that lice survive 28 hours' immersion; 10 lice were placed in water at 6° C., and were removed and dried at intervals; seven of the insects survived after 4 successive immersions lasting 14, 22, 5, and 14 hours respectively, whereas all the lice placed in water at 30–37° C. were dead in 14 hours. Finally Galli-Valerio (1916, p. 41) records that lice were dead after immersion periods of 24 hours at 20° C., and of 72–96 hours at – 3 to 1° C.

I would record a few experiments of mine bearing on the problem:

Expt. (*a*) III. 1917. *Corporis larvae*, immediately after hatching, were placed on a piece of cloth in bottles that were completely filled with water and tightly corked, bubbles of air being excluded.

After 19 hours at 9–10° C. of 10 larvae 9 were dead and 1 alive but feeble.

After 18 hours at 9–10° C. of 11 larvae 9 were dead, 1 feeble and 1 lively.

Expt. (*b*) III. 1917. *Corporis eggs* that had been laid on hair or cloth, were similarly immersed in water at ca. 10° C. The eggs tested were at different stages of development, *i.e.* 0–7 days old, having been maintained at 30° C. in the thermostat. After immersion, the eggs were dried and returned to the thermostat at 30° C.

Age of eggs (at 30° C.)	Immersion period	Result		Controls	
under ½ day	48 hrs	9/13		29/48	
"	96 "	2/12		5/8	
3 days	48 "	14/15		7/7	
4 "	24 "	14/16	71·4 % hatched	7/9	61·2 % hatched
6 "	24 "	12/17		13/31	
6 "	48 "	11/18		6/9	
7 "	24 "	18/21		4/4	

The fractions denote the number of eggs from which larvae emerged, thus 9/13 indicates that 9 out of 13 eggs hatched normally.

The result may appear paradoxical in so far as a higher percentage of eggs hatched from among those that were immersed than from among the controls. This is doubtless attributable to the moistening the immersed eggs had received; the controls having been kept continuously in a dry atmosphere. It will be noted that but 2 out of 12 eggs hatched after immersion for 96 hours.

These results have a practical bearing since they demonstrate the futility of attempting to destroy lice in infested garments by soaking them even for 96 hours (at ca. 10° C.), for some eggs may survive the ordeal and subsequently hatch if brought under favourable circumstances. Incidentally the experiments do not lend support to the statement by Nocht and Halberkann (1915, p. 626) that young nits are more resistant than old ones.

COLD. As a matter of practical importance it is well to know that nits are capable of surviving for a considerable time at a low temperature which checks their development. The active stages are less resistant.

Nits. Widmann (18. VIII. 1915) saw nits survive 13 days at 10° C., whilst Heymann (18. VIII. 1915, p. 305) states they survive 2–3 weeks at 9° C., and several days' exposure to frost. Peacock (1916, p. 41) reports that some nits exposed at ca. 0° C. on a shirt for 8 days, subsequently hatched in 4–5 days when carried on the body; after 13 days' exposure they failed to hatch although he kept them under observation for 28 days before he concluded that they were dead. Kisskalt (II. 1915, p. 154) found that nits survived exposure to −5° C. overnight.

Active stages. The authors cited below do not state upon what stages they made their observations; we may assume that some of the lice at any rate were adults.

Time lice survived	Temperature ° C.	Remarks	Authority
24 hrs ...	−0·2° ...	—	Wulker, 1915, p. 630
24 hrs ...	0° ...	on wet cloth that became frozen	Hase, 1915, p. 70
48 hrs ...	−2·3 to 1·1°	revived when warmed	Bacot, II. 1917, p. 235
4 days ...	−2 to 0° ...	on cloth	Hase, *loc. cit.*
5 successive nights	−8° ...	in winter, revived when warmed	Heymann, 18. VIII. 1915, p. 309
7 days ...	−12° ...	in dry snow (N.B.; they must thaw slowly or they die)	Hase, *loc. cit.*

HEAT. The resistance of lice to heat will be dealt with in the next paper in connection with louse destruction.

VACUUM. According to Heymann (18. VIII. 1915, p. 310) lice and nits survive exposure to a vacuum of 770 mm. for 15 minutes, the insects being lively after the ordeal.

MECHANICAL PRESSURE. Galli-Valerio (1916, p. 41) records that a louse subjected to pressure from a weight of 13 g. survived for ca. 24 hours, the insect being confined between a slide and coverglass.

Sham Death, and the Signs of Death in Lice.

Sham death is observable in lice that have been immersed in water for some hours[1], or in insects that have been temporarily narcotized by exposure to the vapours of essential oils, benzine, petrol, ether, etc., for a period insufficiently long to kill them. The insects may sham death for several hours if the exposure has been sufficiently prolonged; this has led to error in judgment as to the efficacy of various remedies.

Certain authors rely upon the stoppage of digestive peristalsis (Widmann, 18. viii. 1915, p. 290), the cessation of the embryo's movements in the egg (Wulker, 1915, p. 628), and the shrinkage of the eggs as signs of death, but such signs may be misleading. I have seen peristalsis recommence, and embryos resume their movements after hours of inactivity, and considerable shrinkage of the eggs may occur without death taking place. A certain amount of shrinkage invariably takes place a couple of days before the larvae emerge. For practical purposes much clearer evidence of death is required than that here mentioned.

A certain sign of the approach of death is afforded by the larvae and adults turning pink and then red in colour owing to the escape of blood or haemoglobin into the coelomic cavity. Under ordinary conditions this appearance is due, in my opinion, to rupture of the intestine from overfeeding; I have so far only observed it in lice which have been fed but twice a day, and have consequently gorged themselves to excess. In the laboratory, we have seen lice turn red within a few minutes of having overfed.

Sikora (viii. 1915, p. 533) remarked that lice which turn red did not feed, and that lice kept at 20° C. often turned red; she cites Halberkann as having frequently observed this condition in lice experimented upon with insecticides, and she believes that it is due either to altered metabolism, the haemoglobin escaping into the coelom, or to the action of a tyrosinase on chromogen. Müller (1915, p. 54) also states that the turning red is due to the effect of poisons. Bacot (ii. 1917) attributed the turning red of a female to the sexual act. I have seen gorged lice kept at 12° C. gradually turn red after a few days whilst they continued living, and in such cases the phenomenon is probably due to the transfusion of haemoglobin through the gut wall of the slowly dying insect, the condition being doubtless comparable to that following the action

[1] Sham death was first observed by Lazia (1915, p. 301, according to Müller, 1915, p. 54).

of poisons. Lice dipped in water at 70° C. are killed and soon turn pink and then red.

Lice may die simply from overfeeding without any rupture taking place. Apparently deaths due to this cause have also been observed by Fantham (1912, p. 513) and Heymann (18. VIII. 1915, p. 307).

In practice it is best to rely on the unequivocal signs of death afforded in (*a*) nits by the complete collapse of the shell, the contraction of the contents into a small space, the change of colour (whitish, when coagulated as by boiling, or brownish, when heated dry) and (*b*) the shrivelling up and growing brittle of larvae and adults, their change of colour (whitish when boiled, brown or blackish when dry).

NATURAL ENEMIES AND PARASITES OF LICE.

(*a*) *Enemies.*

The chief enemy of lice is modern man who is gradually awakening to the full significance of these ancient parasites of the human race. That many primitive peoples are constantly at war with lice is well known; their efforts may be more or less spasmodic but at times they are fairly well organized though simple as depicted in the accompanying illustration (Plate III) showing an active campaign proceeding such as I have beheld in Mexico, Italy, Spain and North Africa, without the descending scale of actors being so perfectly adjusted.

Among the lowest races of man, the monkey-like manner of dealing with lice has persisted. Thus Denny (1842, p. 18) writes "we are told that the Hottentots and other nations in West Africa, as well as American tribes, eat them, they and their wives collect them and have hence been called Phthirophagi." Dr Richardson informed Denny that during the overland expedition under Sir J. Franklin, he "daily observed the Indian women cracking their parasites between their teeth with much apparent enjoyment." Blanchard (1890, p. 439) states that this habit prevails among the Aleutians and Hottentots (*fide* Sparmann) and Australians (*fide* Labillardière) who thus destroy *capitis*.

Baboons as louse catchers were extensively used in Lisbon in the eighteenth century, the animals being hired out for the purpose of catching and eating the redundant *capitis*.

Ants may also claim the distinction of natural enemies of lice. Gaulke (1863) already mentions them as louse exterminators, and Hase (XI. 1915, p. 158), who refers to this author, states that German soldiers, when heavily infested, reduced their louse population by placing their shirts on ant hills. I have seen a similar statement relating to British troops in the Boer war.

(b) *Parasites.*

As far as I am aware, only one species of parasite has so far been found in the louse apart from *Spirochaeta recurrentis* and the undetermined causative agent of typhus fever. Mackie (1907, p. 1706) casually mentions having found "*Crithidia*" in body-lice and this doubtless gave the clue to Fantham (1912, pp. 505–517) who found the parasite he named *Herpetomonas pediculi* in 25 out of 300 lice he examined. The protozoon occurs in the gut and faeces of the insects where it is stated to form cysts, which, escaping with the louse's faeces upon the human skin, serve to infect other lice that feed upon the contaminated spot on the host.

Acknowledgments. I am especially indebted to Mr Charles Harpley, my Laboratory Assistant, for his willing help, given at the cost of much personal discomfort, in connection with these investigations. My thanks are also due to Dr W. H. Hamer, Mr A. Bacot, and to Captain Harold Orr of the Canadian Army Medical Corps, for kindly supplying strains of body-lice and head-lice with which some of the observations here recorded were carried out.

REFERENCES.

See Bibliography, pp. 1 et seq.