THE LOUSE

AN ACCOUNT OF THE LICE WHICH INFEST MAN, THEIR MEDICAL IMPORTANCE AND CONTROL

BY

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is inclined to be impatient and to think that the treatment is too detailed, he is urged to persevere and to endeavour to master the subject as a whole. The book may appear full; the author alone knows how much has been excluded, particularly on the subject of control, about which much very inconclusive work has been published.

In one respect this book includes material that is not generally considered to lie within the limits of medical entomology: I have taken the unusual step of including a brief account of spirochaetes and *Rickettsias* so long as they live in the louse, and of the epidemiology of the diseases which they produce. That appeared to be essential, for if the entomologist is to contribute to our understanding of diseases transmitted by insects, he should consider not only the vector but the history of the parasite so long as it is in the insect. To take an example from the present book: the entomologist can make little contribution to our understanding of relapsing fever unless he makes it clear that the spirochaete is in the body cavity of the louse from which it can only escape if the insect is torn or crushed.

In quoting references an attempt has been made to include major classical papers and also recent work which generally contains references to preceding work on the subject.

The book owes much to my colleague Dr. V. B. Wigglesworth, F.R.S.; also to Dr. C. M. Wenyon, F.R.S., Dr. R. Lewthwaite and Professor R. M. Gordon, who have read and criticized parts of the text. Colonel D. T. Richardson, M.C., A.M.S., was good enough to discuss the section dealing with control, and his suggestions have led to great improvement in it. Without my colleague Dr. C. G. Johnson I could never have ventured to discuss that formidable subject, the growth of populations. The figures have nearly all been redrawn (and many of them much improved) by my friend Mr. H. S. Leeson. The Cambridge University Press has been good enough to allow me to make use of one figure, which originally appeared in the *Journal of Hygiene*. To all of these my thanks are due.

P. A. B.

CONTENTS

CHAPTER 1

THE ANOPLURA OR SUCKING LICE

1. Zoological Position. The word " louse " has been applied to a great variety of insects, and indeed to other small animals, not closely related to one another but similar in being small and wingless. Even now, though the word is used in a much restricted sense, it is applied to two different groups of insects. The first of these are called the Biting Lice or Feather Lice (Mallophaga): these insects live on the skin of birds or mammals and have mouth parts fitted for biting solid substances. They feed on pieces of feather and fragments of scurf, and some of them also nibble the skin and take blood which exudes. We are not further concerned with them in this book. It is the so-called Sucking Lice (Anoplura) which are our subject. The Anoplura are a comprehensive group, in zoological language an Order.[1] In technical terms the Anoplura might be defined as follows:

> Small, wingless insects flattened dorsiventrally. Antennae short, 3–5 jointed. Eyes reduced or absent, and ocelli absent. Mouth parts highly modified for piercing and sucking blood of host; retracted within head when not in use. Palps absent. Thoracic segments fused together, without the least rudiment of wing. Legs short, tarsi with one joint and one claw: leg adapted for clinging to hair of host. Abdomen without cerci.
>
> Without metamorphosis, occurring on surface of host throughout life. Parasites of mammals exclusively.

The sucking lice or Anoplura stand rather by themselves, not closely related to other orders of insects, except perhaps to the Mallophaga (the biting lice, or feather lice), already mentioned. The view was once held that the sucking lice were related to the bugs (Rhynchota), but this is known to be erroneous.

The orders are in turn divided into " families," of which four are generally recognized in the Anoplura. Only one of these families, the Pediculidae, is of interest to ourselves, for it includes the lice which occur on man and monkeys: all members of this family

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[1] One should perhaps explain that insects are classified first into large comprehensive categories (for example, the Coleoptera or beetles, and the Lepidoptera or butterflies and moths): these major categories are called " orders," and the sucking lice, or Anoplura, are one of these.

past, for considerable differences have been evolved between the parasite of man and spider monkey (Ewing, 1938).

The examples quoted above illustrate the general truth that related hosts carry related parasites. There are, however, a few cases in which one must suppose that a species of louse has been transferred successfully and permanently to a completely new mammalian host.

CHAPTER 2

THE ANATOMY OF *PEDICULUS HUMANUS*

EXTERNAL ANATOMY

1. General. The general relation of the parts to one another is shown in figure 1. It will be seen that the head, thorax and abdomen are clearly separated from one another; that the thorax shows little external sign of segmentation; only seven abdominal segments are distinct. The insect is flattened dorsiventrally.

There is one thoracic spiracle, which probably appertains to the prothorax. The leg of *Pediculus*, which is characteristic of that of Anoplura in general, is shown in figure 2; all parts of the leg are short and strong. The tibia is short and bears a blunt " thumb " on the inner side close to the apex; the thumb terminates in spines and hairs. The one-jointed tarsus is short and carries a single large claw, rough along its concavity. Between the thumb and the claw the louse grasps its host's hair or clothing. The three pairs of legs are similar in structure.

Although it appears, at a cursory examination, that the abdomen (figure 1) consists of seven segments, there are slight indications in *Pediculus*, and clearer evidence in certain other Anoplura, that two segments precede the first evident segment, which bears the first pair of abdominal spiracles: this first evident segment, with the first pair of spiracles, is probably the third segment. There are six pairs of abdominal spiracles, carried on segments 3 to 8. All spiracles (including that on the thorax) possess a closing apparatus, which appears to work by compressing or buckling the trachea a short distance below the surface of the body (figure 3). It seems highly probable that the louse uses this in order to reduce the loss of water from within its respiratory system.

For anatomy of egg, see page 24; for larva, page 28. For fuller accounts of both external and internal anatomy, see Hase (1931), Patton and Cragg (1913); many points are figured by Keilin and Nuttall (1930).

2. Sexual Differences. The adult males and females are readily distinguished. The male is generally the smaller, but there is some overlap in the measurements of total length (see page 12). There are dark transverse bands on the dorsum of the abdomen of the male (figure 1), most evident in the highly pigmented specimens. The abdomen of the female is relatively the broader. There are possess eyes, a character which distinguishes them from all other Anoplura.

To carry the matter further, the lice which occur on human beings, with which alone this work is concerned, are classified into two genera (*Pediculus* and *Phthirus*); in each genus there is only one species attacking man, viz. *Pediculus humanus* and *Phthirus pubis*. The first of these exists in two forms, the body louse and head louse; these are best regarded as biological races rather than species, because the anatomical distinctions between them are somewhat indefinite, though there are more pronounced differences in behaviour and biology (page 11). *Phthirus pubis*, or the crab louse, is generally confined to the inguinal region (page 138). These lice (both *Pediculus humanus* and *Phthirus pubis*) occur only on man and not on other hosts.

It is held that the genera *Pediculus* and *Phthirus* are closely related: anatomical points which they have in common are an antenna consisting of five joints, the presence of pigmented eyes, and the fact that the tibia is provided with a process resembling a thumb, between which and the one-jointed tarsus the hair of the host is grasped.

The points of distinction between the two genera of lice occurring on man are briefly as follows:

Pediculus. All legs about equally strong (but anterior legs of male stouter than those of female). Abdomen about twice as long as it is broad. (See figure 1; pages 5 to 23.)

Phthirus. Foreleg slender with long fine claw. Middle and hind legs strong with thick claws. Abdomen broader than long, and compressed so that spiracles of 3rd, 4th and 5th segments lie almost in one transverse line. Abdominal segments with protuberances at the side. (See figure 44; pages 136 to 141.)

2. General Biology. All sucking lice (Anoplura) are obligate parasites, spending their whole life on the skin of a mammal and living exclusively on blood. Some 200 to 220 species of sucking lice are known. Though all the hosts are Mammalia there are certain important groups which have no parasites of this type; for instance, the Carnivora (exclusive of the dog family), and the Marsupials. A general account of the order is given by Ferris (1934).

The Anoplura have, so far as is known, no insects which are parasitic upon them and probably very few enemies, except their hosts. They harbour certain parasitic micro-organisms, some at least of which (*Spirochaeta* and *Rickettsia*) are pathogenic to the mammalian hosts. For this reason human lice (*Pediculus*) have great importance as vectors of relapsing fever (page 90) and typhus (page 76).

The relation of sucking louse to host is often very close, one species of louse living on one host, or on a few which are closely related to one another. In general it seems probable that this specificity is maintained by the parasite's reaction, which prevents it biting hosts other than the normal.

Those who have studied the Anoplura, or lice, have found that those mammals which are closely related to one another tend to have closely related or identical lice. It seems that in the course of evolution the mammals have often come to differ from one another more than the lice, so that occasionally the insect parasite points to relationships between species of mammal which have become rather dissimilar. To take a very simple case, the Ground Squirrels (*Citellus*) of North America and Siberia are related but different, though the lice on them appear to be identical. A more complicated case is presented by the lice found on man and other Primates. The lice on these hosts all belong to one of the families (Pediculidae) into which the Anoplura are divided, and no member of that family occurs on any other host. On a conservative view, the family may be said to consist of three genera, *Pedicinus*, *Pediculus* and *Phthirus*. Of these, the first is found only on the monkeys of the Old World (Cynomorpha). Both *Pediculus* and *Phthirus* occur on man and higher apes, but not on other monkeys; *Pediculus* has species on two of the gibbons and on the chimpanzee (Fahrenholz); there is, however, some doubt as to whether the record from the gibbon is correct (Ewing, 1938). *Phthirus* includes a most imperfectly known species from the gorilla and has recently been recorded from the chimpanzee (Bedford, 1936): the records from gorilla and chimpanzee may be derived from menagerie material, and it is not conclusively known that these animals are natural hosts of the crab louse. The orang appears not to be infested with lice. Presumably, therefore, these two genera (*Pediculus* and *Phthirus*) have been parasites on the human stock, and its ancestors and close relatives, since very remote times. But in addition there are several species of *Pediculus* (sometimes separated and treated as an independent genus, *Parapediculus*) occurring only on monkeys in tropical America, particularly on Spider Monkeys (*Ateles*). The occurrence of these parasites (so close to man's louse) is puzzling, because on general anatomical grounds the American monkeys are far removed from man and his ancestry. It is possible that the lice found on spider monkeys may have been transferred to them from human beings, but if that occurred it was in the remote also considerable differences in the legs (figure 2), the anterior leg of the male being much the stouter, and provided with a larger tibial thumb and tarsal claw; with this the posterior leg of the female is grasped in copulation. The posterior end of the male's abdomen is rounded, the ventral surface curving upwards so as to bring the anus and sexual orifice to the upper surface. In the sexual orifice (*so*) one may sometimes distinguish the dark pointed tip of the dilator (figure 1). In the female the abdomen terminates in two larger posterior lobes, which give it a bi-lobed appearance. In ventral view (figure 4) one observes the pair of gonopods on

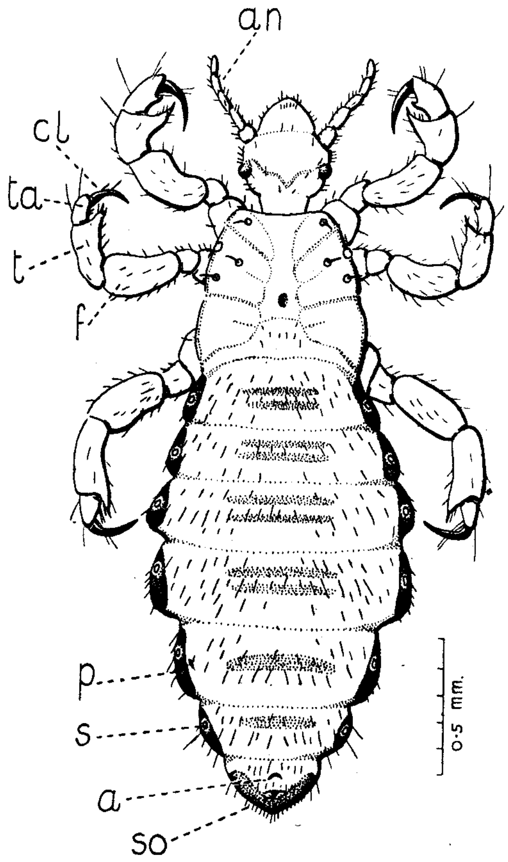

FIG. 1.—*Pediculus humanus corporis*, male, from above.

a, anus; *an*, antenna; *cl*, claw; *f*, femur; *p*, pleural plates; *s*, spiracle; *so*, sexual orifice; *t*, tibia; *ta*, tarsus. (*After Keilin and Nuttall.*)

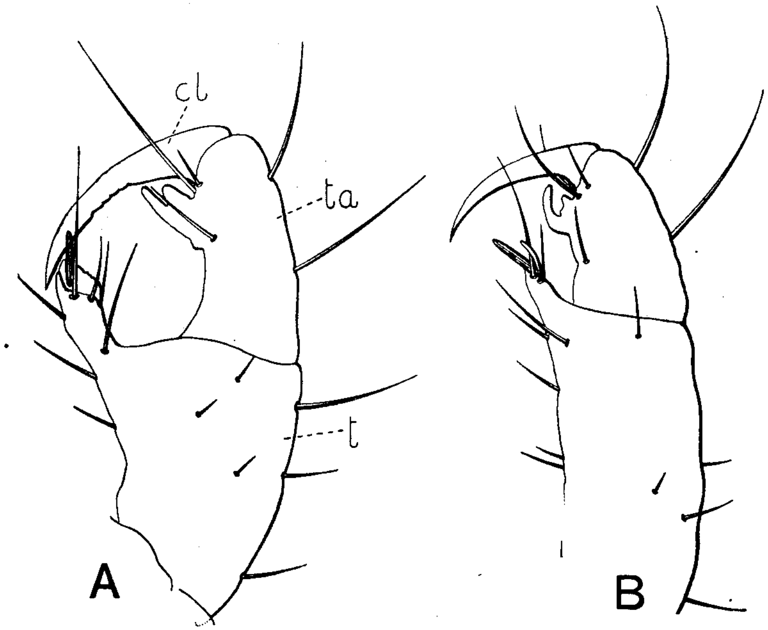

FIG. 2.—*Pediculus humanus.*

A, terminal part of anterior leg of male; *B*, of female; *cl*, claw; *ta*, tarsus; *t*, tibia. (*After Keilin and Nuttall.*)

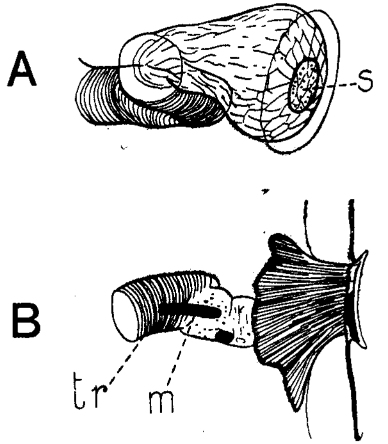

FIG. 3.—*Pediculus humanus capitis.*

A, thoracic and *B*, abdominal spiracles; *m*, muscle, the contraction of which produces a kink in the tracheal trunk (*tr*) and so reduces loss of water from within respiratory system; *s*, spiracle. (× 260.) (*After Hase.*)

either side of the vaginal orifice; also a shield-shaped pigmented area, easily visible to the naked eye.

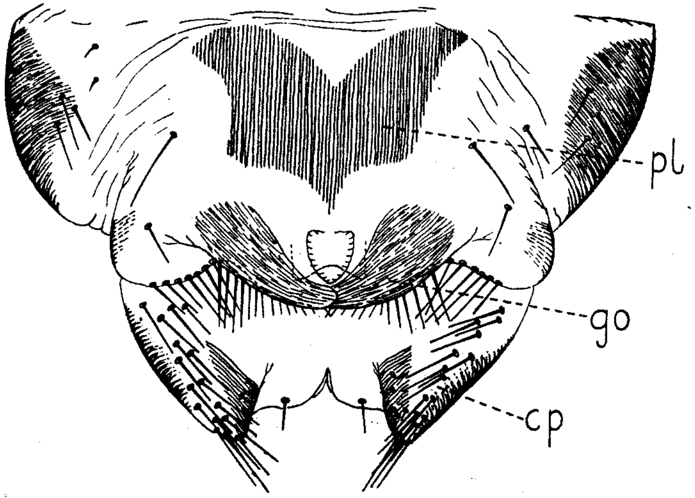

FIG. 4.—*Pediculus humanus corporis*, genital region of female from below.
cp, claspers; *go*, gonopods; *pl*, shield-shaped plate. (*After Ferris.*)

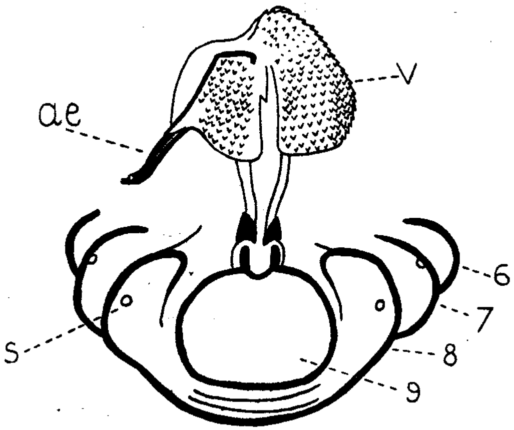

FIG. 5.—*Pediculus humanus*, male forcibly separated from female during copulation promptly killed: the abdomen is viewed from behind.
ae, aedeagus; *s*, spiracle; *v*, vesica; 6–9 abdominal segments. (*After Nuttall.*)

It is only by dissection and observation of specimens in the act of pairing that the very complex copulatory organs of the male may be understood. The male approaches the female from behind, and walks forward beneath her abdomen, seizing the base of her posterior femora with his first legs. The insects then assume a vertical position, head downward, the male being carried completely clear of the surface on which they have been walking. At this moment the male extrudes the dilator, which is hooked into the vagina, into which it penetrates deeply. It is then withdrawn and flexed out of the way, and at this instant the penis or aedeagus is passed into the vagina. A great part of the aedeagus (figure 5) consists of a thin-walled chitinous sac (the vesica), which fills the vagina, teeth on the walls of vagina and vesica anchoring the animals together. It is only after this that the ejaculatory part of the organ performs its function (Nuttall, 1917*a*).

In the study of typhus (page 78) it is frequently necessary to discover the exact position of the anus in order to infect lice by injection. In the male this orifice (*a*) is on the upper surface immediately in front of the transverse sexual orifice: it lies in a minute pit (figure 1). In the female it is at the extreme posterior end of the body, between the posterior lobes and dorsal to the gonopods and vagina (figure 6).

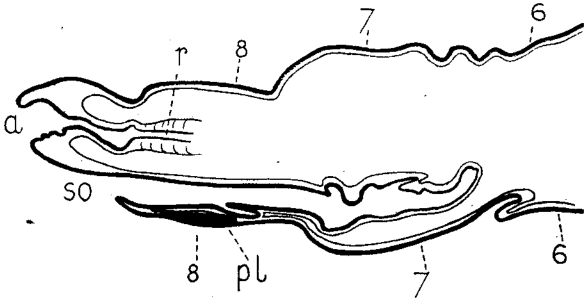

FIG. 6.—*Pediculus humanus*, longitudinal section, almost in median plane, of posterior part of female abdomen.
a, anus; *pl*, shield-shaped plate; *r*, rectum; *so*, sexual orifice; 6–8, abdominal segments. (*After Nuttall.*)

3. Sense Organs. The structure and function (page 38) of the sense organs has been investigated by Wigglesworth (1941). The antenna carries sensillae of three types.

(*a*) *Peg organs.* These are limited to the fifth joint of the antenna, where there are nine or ten. The projecting peg is sharp in some organs, blunt in others; it is thin walled, and the cavity contains a process or filament which can be traced down to a group of sense cells (figure 7, D).

(*b*) *Tuft organs.* These are confined to the fourth and fifth joints of the antenna. Each consists of a minute cone lying in a shallow depression: at the apex of the cone is a tuft of four minute hairs, the base apparently connected by a rod or filament to a group of sense cells (figure 7, C).

(*c*) *Tactile hairs.* These are distributed in small numbers on all parts of the antenna. They are of a type very common in insects, and consist of a slender articulated bristle, connected with a sense cell.

(*d*) *Scolopidial organs.* Inside the second segment of the antenna are certain sense organs which are believed to be proprioceptive, i.e. to record movements and strains, and give the insect information as to the position of the antenna.

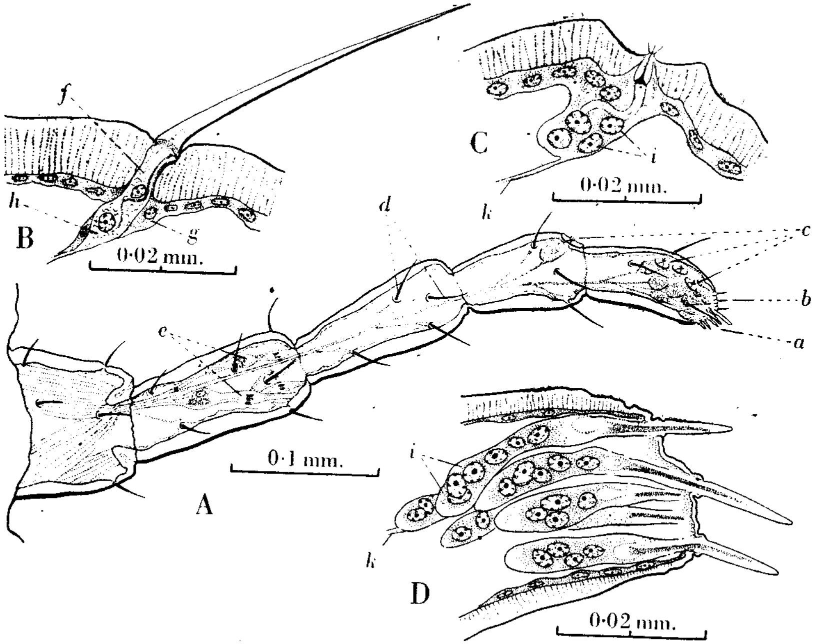

FIG. 7.

A, dorsal view of left antenna. *a*, peg organs with rounded tips; *b*, peg organs with sharp tips; *c*, tuft organs; *d*, tactile hairs; *e*, scolopidial organs. *B*, detail of tactile hair; *f*, trichogen cell; *g*, tormogen cell; *h*, sense cell. *C*, detail of tuft organ. *D*, detail of peg organs. *i*, sense cells; *k*, nerve. (Wigglesworth, 1941.)

No difference has been detected between the antennal sense organs of the male and female louse.

The eye is a single ocellus, on the lateral aspect of the head. The structure is shown in figure 8.

Numerous other sense organs occur, tactile hairs on many parts of the body, and proprioceptive organs of several types which give the insect information as to the position of the successive parts of its limbs.

4. Head and Body Lice. Before leaving the subject of external anatomy it would be well to consider the differences between *Pediculus* from different parts of the human body.

Lice (*Pediculus*) found on the human head usually differ slightly from those found on the body and clothes, and they were regarded as distinct species and named *capitis* and *corporis* by de Geer before the end of the eighteenth century. That view continued to be accepted for more than 100 years, most authors regarding the insects as distinct species, though the points of difference were admittedly difficult to define. But in 1919 Keilin and Nuttall published the results of a careful examination of a large collection of specimens from many parts of the world, and concluded that the head louse and body louse should not be regarded as separate species: subse-

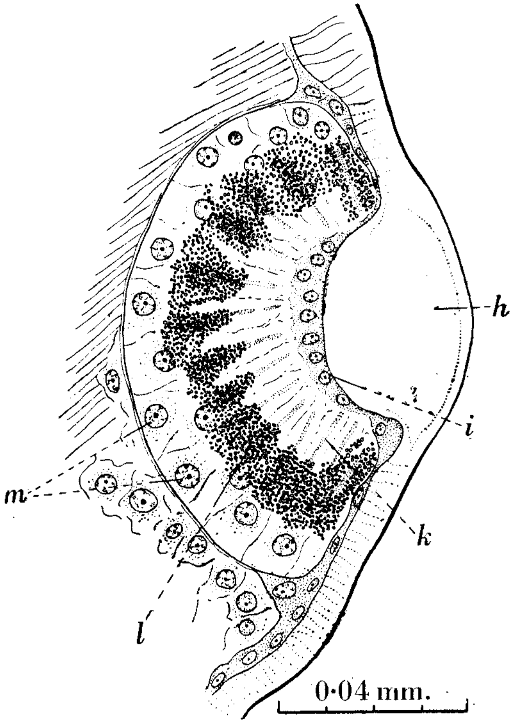

FIG. 8.—Horizontal section through eye.

h, corneal lens; *i*, corneagenous cells; *k*, rhabdoms; *l*, pigment; *m*, nuclei of retinal cells. (Wigglesworth, 1941.)

quent work (Ferris, 1935) supports this view. It therefore seems best to refer to the head and body louse as physiological or biological "races," belonging to one species, *Pediculus humanus* (Linn, 1758); the appropriate Latin names are *P. humanus capitis* (de Geer, 1778) (the head louse) and *P. h. corporis* (de Geer, 1778) (the body louse). The name *vestimenti* (Nitzsch, 1818) for the body louse is a synonym of *corporis* and should not be used.

The best anatomical basis of distinction between these races is provided by the antenna, which is relatively shorter and broader in *capitis*. In particular, the third joint of the antenna is relatively broader in that variety (figure 9), though recent work by Ferris (1935) has shown that the distinction does not invariably hold good: no large body of measurements is available. A number of other points of difference have been shown to be variable and unreliable. It is generally true that head lice are smaller than body lice, as the following approximate figures for mean total length (mm.) show:

	♂	♀
capitis	2·1–2·6	2·4–3·3
corporis	2·3–3·0 (occasionally over 3·0)	2·4–3·6 (occasionally over 4·0)

But the total length of this insect is an unsatisfactory character, for it depends to some extent on whether it has recently fed and on the development of the ovaries in the female; in addition, methods of killing and mounting will affect the measurement.

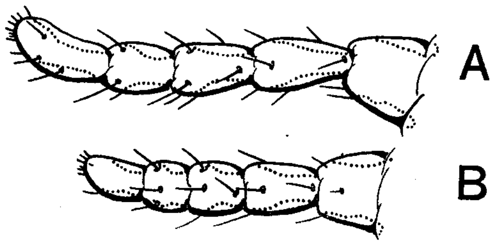

FIG. 9.—*A*, antenna of female *Pediculus humanus corporis*; *B*, of female *Pediculus humanus capitis*; both from England.
(*After Ferris.*)

Head lice are generally more deeply pigmented, but the depth of the colour of *Pediculus* depends on the colour of the background on which it was reared, so that the difference is not constant and probably not inherited; moreover, it frequently happens that different parts of the body of an individual louse are pigmented to different degrees. Head lice may generally be recognized because the indentations between successive abdominal segments are more clearly marked than they are in body lice; this is due to differences in the chitinous pleural plate (*p*), also known as the paratergal plate, or laterosclerite, which covers that part of the segment (figure 1). In general, the legs of *capitis* are said to be relatively shorter than those of *corporis*. Other points of difference have been recorded, but they are inconstant and intermediates are frequently met with, both in wild material and in insects of known history reared in the laboratory. At the same time it must be admitted that there is rarely any difficulty in identifying a head or body louse, on general appearance. In culture the differences do not, in our experience, tend to disappear.

The subject is fully dealt with by Ferris (1935); this author's wide knowledge of the structure and classification of all types of Anoplura gives particular importance to his work. He regards the head and body louse as the extremes of a continuous series, stating that every intergradation exists and even doubting if they are worth recognition as races.

It is not known whether reliance can be placed on differences in size and shape which are stated to be observable in the eggs of head and body lice (see figure 17).

It is a matter of importance that the various points of difference should be examined biometrically, so as to assess the extent to which they vary and overlap, and define the morphological points on which individual lice, or strains, may be identified. At present it is often accepted that lice from the head are "head lice" (and so they are in a certain sense). Biometrical work of this type would permit us to study such things as the migration of head lice to the body, or to other heads; it might be the basis of study on the cytology and genetics of the head and body louse; it would also give precision to our views on the head louse as a vector of typhus.

On the biological side the differences are more easily perceived. In general, lice from the human head attach their eggs to hair (page 24). They are also more active at lower temperatures than lice from the body, perhaps because the temperature at which they normally live on the exposed scalp is lower than that on the clothed parts of the trunk. Lice derived from the clothes or the surface of the body, on the other hand, attach their eggs to the inner side of the clothes. But the distinction between living on the head and the body is not very sharp, and there are records of lice with the anatomical characters of *capitis* establishing themselves on the body and occurring both there and on the head; Keilin and Nuttall (1919) examined several large collections of lice taken from the surface of the body, but appertaining to both races. It seems then that specimens which would be referred to as *capitis* frequently occur on the surface of the body. The occurrence on the head of specimens which appear to be *corporis* is less frequent. We may conclude, then, that the head louse and the body louse may occupy the same territory and that they have every opportunity of interbreeding.

Several authors have reared *capitis* in captivity, in boxes applied to the skin of the body (for method, see page 142), and have recorded that after a number of generations the specimens become intermediate, or assume the anatomical characters (size, length of leg, etc.) of *corporis*. This indicates that the anatomical differences are not constitutional or genetical, but capable of being altered by environmental factors. It should, however, be said that the experience of my colleague, J. R. Busvine, is different: after many generations of being reared under identical conditions the head and body lice remain distinct in general appearance.

In the eight months from September 1940 during which London was bombed, a large part of the population was living crowded in basements, shelters and so forth. During the first part of the period general hygienic conditions were very bad, and people were much crowded, large numbers often sleeping in close contact. Head lice were certainly common throughout the period, at least in the children, but there was no evidence that body lice occurred, except in the destitute, though a careful look-out was kept. The evidence from this large experience does not suggest the transformation of head lice into body lice, but supports the view that the two are biologically distinct.

Hybrids between the head and body louse may readily be raised in the laboratory; these hybrids are fertile, at least to the third generation, beyond which they have not been studied. In some families of hybrids intersexes are produced, that is to say, individuals in which some of the external or internal characters appertain to the one sex and some to the other. The fact that intersexes have also been found in wild populations of lice suggests that hybridization between the races also occurs in nature. The production of intersexes in hybridization shows that there is a considerable genetical difference between the two ancestors; some lack of harmony in the normal division of chromosomes occurs in hybridization, so that the factors which generally determine sex and produce either a male or female occasionally produce an intersex. It would be a valuable contribution to our understanding of the matter if a cytological study could be made of the chromosomes of parent races and hybrid (especially intersex) offspring.

We have very little information on the occurrence of intersexes in the absence of hybridization of the two races. Musgrave (1944) has recently found intersexes in a laboratory strain, which had been derived from garments, and was regarded as *corporis*. Roy and Ghosh (1944*a*) report examining 8,700 adult lice from heads of refugees entering India from Burma; no intersexes were found.

From the facts set out it seems clear that though the head louse and body louse are not identical, they are much more closely related and difficult to distinguish than "species" generally are. Probably, therefore, we should be correct in thinking of them as entities which have not yet evolved very far from one another; indeed, they might be called "species in the making." Inasmuch as the differences between them seem greater in biology than in anatomy they should be referred to as biological or physiological races; this is consistent with general zoological practice.

5. Lice from different Human Races. It has frequently been asserted that lice from different races of man differ from one another in colour, those from dark races tending to blackness, those from pure Nordics tending to be blond. The work of Nuttall (1919) showed that the colour of a louse was greatly modified by that of its surroundings early in life. Differences might therefore arise between individuals of a single family, reared on different men, and it is probable enough that lice from a man with black skin and hair might be darker than those from a fair host. It seems, then, that most of the differences said to occur between the lice of Chinese, Europeans, American Indians and other human races are slight and inconstant, and due to colour and other environmental factors. It has been stated that lice from Africans (heads and bodies) differ from those of other human races in a number of anatomical particulars. Ferris (1935) goes fully into the matter and concludes that the characters are variable, and that they show intergradation with races *capitis* and *corporis*.

No human race (so far as is known) is without lice, or immune to them.

INTERNAL ANATOMY

1. Mouth Parts. The mouth parts are invaginated into the head except when the insect is feeding, and it is only by dissection and the study of serial sections that their relations to one another can be understood. The essential facts are shown in figure 10. In the front of the head is a small tube, the haustellum, which is believed to be formed from the labium; it is soft, eversible and armed with teeth. In figures 10 and 14 it is shown in the retracted position, but in figure 11 the haustellum is everted and the teeth rotated outwards; it will be seen that the opening is terminal and continued as a ventral cleft, the prestomum. That part of the alimentary canal which lies inside the head is separated into four regions (figure 10). The most anterior part is the relatively rigid buccal funnel. Behind are the cibarial pump, and the pharynx, each independently capable of dilation by dorsal muscles arising from the head capsule and divided from one another by a constriction; between them, not shown in figure 10, is the frontal ganglion, an important landmark to the morphologist; the pharynx has strong sphincter muscles. Behind the posterior part of the pharynx comes the commencement of the oesophagus, which is narrow and not muscular.

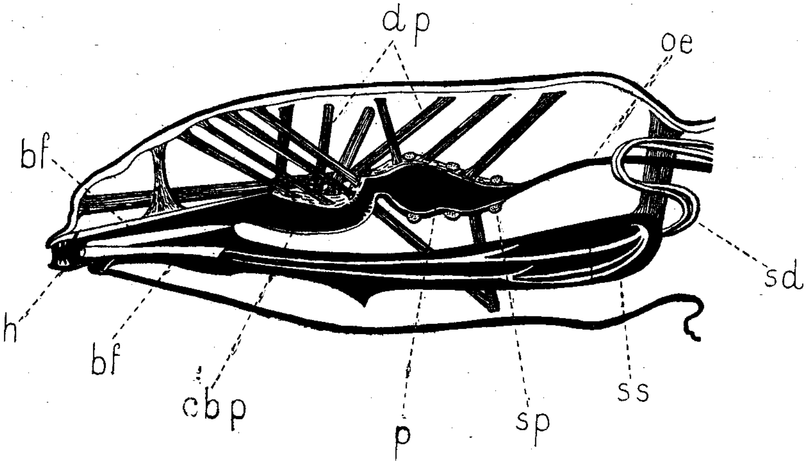

FIG. 10.—*Pediculus humanus*, longitudinal section of head.

bf, buccal funnel; *cbp*, cibarial pump; *dp*, dilator muscles of pharynx; *h*, haustellum; *oe*, oesophagus; *p*, pharynx; *sd*, salivary ducts; *sp*, sphincters; *ss*, stylet sac. (Schematic, modified from Peacock, 1918, and Sikora, 1916; central nervous system omitted.)

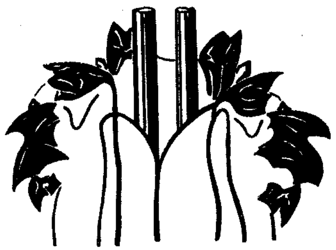

FIG. 11.—*Pediculus humanus*, everted haustellum seen from below, showing teeth, and part of shafts of stylets. (× 1000.)

(*After Sikora.*)

In the floor of the buccal funnel is the opening of the stylet sac, which is blind. Within this sac are three stylets lying one above the other (figure 12). It appears, from the study of the development of the embryo that the dorsal and ventral stylets are formed from a part of the rudiment of the second maxillae, which unite to form the labium in most insects. Early in embryology one may recognize paired mandibles and first maxillae, which disappear later (Schölzel, 1937); other views have been put forward (e.g. Fernando, 1933). The dorsal and ventral stylets are very similar in shape, forked

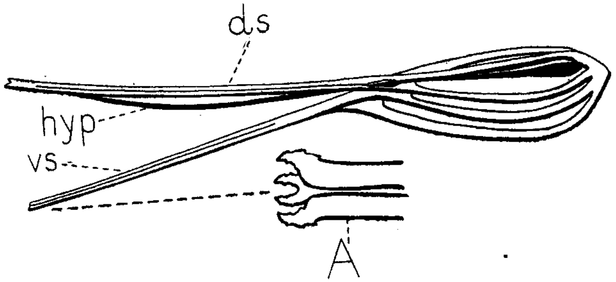

FIG. 12.—*Pediculus humanus*, stylets as seen from left side (the forked structures at the base being those of the left side only).

ds, dorsal stylet; *hyp*, part of hypopharynx; *vs*, ventral stylet; *A*, tip of ventral stylet (× 1250), showing elaborate piercing end and groove in which hypopharynx lies. (*Modified from Peacock and from Vogel.*)

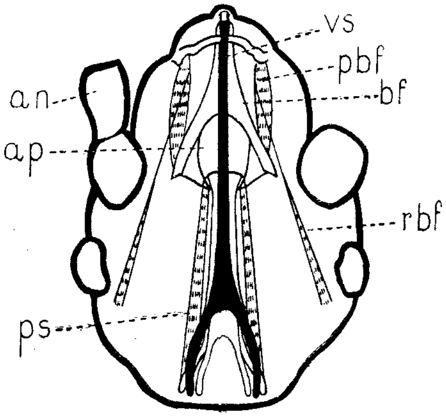

FIG. 13.—*Pediculus humanus*, head from below to show ventral stylet and protractor muscles.

an, antenna; *ap*, anterior part of pharynx; *bf*, buccal funnel; *pbf*, protractor of buccal funnel; *rbf*, retractor of buccal funnel; *ps*, protractor of stylet; *vs*, ventral stylet. (× 195.) (*After Sikora.*)

behind but united in front and sharply toothed at the tip (figure 12, A). Immediately below the upper stylet is a fine tube, formed from a part of the hypopharynx and pierced by the common salivary duct: it is the "intermediate stylet" of Snodgrass (1944). It is continuous with the common salivary duct, and is tubular. There is some doubt as to whether the intermediate stylet is fused at its base with the dorsal stylet. The three stylets (i.e. dorsal, ventral and intermediate, or hypopharynx) are capable of being brought forward through the prestomum by protractor muscles (figure 13). When not in use they lie entirely within the head.

The relationship of the stylets, and something of their function, is made clear in figure 14, which shows them in transverse section. The dorsal stylet, made apparently from two united halves rolled upwards, forms the food canal. Piercing the skin is probably carried out by the relatively robust ventral stylet: it embraces the other stylets and tends to hold them together as a fascicle. The very fine intermediate stylet, or hypopharynx is seen to be penetrated by a canal, which we believe to be continuous with the common salivary duct.

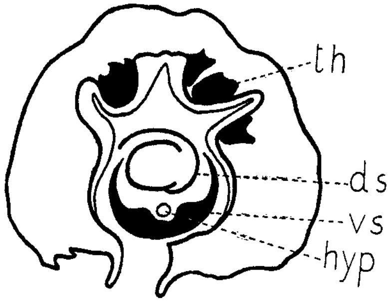

FIG. 14.—*Pediculus humanus*, transverse section of haustellum in the retracted position.

ds, dorsal stylet; *hyp*, hypopharynx; *th*, teeth of eversible part of haustellum; *vs*, ventral stylet. (× about 1000.) (*After Vogel.*)

The description and interpretation of the mouth parts of the louse is a matter on which authorities are not unanimous. The above is derived mainly from Peacock (1918), Sikora (1916) and Vogel (1921). Snodgrass (1944), our principal authority on the comparative anatomy of insects, has recently discussed the matter; the interpretation I have given does not differ from his except in points of nomenclature.

In feeding, the head is depressed and the soft chitinous haustellum thrust out so that the everted teeth anchor the insect's head to the epidermis of its host. The protractor muscles thrust the stylets forward through the opening in the haustellum and move them in and out so that they pierce the skin and lacerate the tissues beneath it; the whole buccal funnel is moved forward at the same time. After the stylets have pierced the skin, saliva is presumably delivered down the hypopharynx by way of the common salivary duct. The mechanism by which blood is taken into the alimentary canal is not certainly known; but it seems probable that the soft eversible haustellum fits closely against the skin and that the capillary blood pressure is sufficient to cause the blood to flow from the capillaries into the mouth along the trough formed by the upper stylet (see unpublished observations of Wigglesworth, page 37). The contraction of the dorsal muscles of the cibarial pump would also give some suction; it seems probable that when the insect is taking blood, the constriction between the cibarial pump and the pharynx acts as a valve and is closed, so as to prevent blood which has already been swallowed from being sucked forward towards the mouth. When the dorsal wall of the pharynx is relaxed the blood would be able to flow to the oesophagus, towards which it might be propelled by the sphincters in the wall of the pharynx. This explanation of the mechanism is supported by observations made on the living insect while in the act of sucking; this may most conveniently be done upon a larval louse, the head of which is much more transparent than that of an adult. It can then be seen that while the louse is sucking blood there is a rhythmical filling and emptying of the cibarial pump several times per second.

2. Alimentary Canal. The general disposition of the alimentary canal, which is about twice the length of the insect, is shown in figure 15. It has already been explained (page 16) that the foregut consists of four parts; the last of these, the oesophagus, which is straight and narrow, enters the midgut in the thorax. The anterior part of the midgut is lobed, forming two gastric caeca; it is large and distensible, and occupies a great part of the abdomen. After a meal it contains much blood, and its active peristaltic movements may be seen through the integument of the living insect. There is no peritrophic membrane, and no crop. The mycetome, a conspicuous round object on the ventral wall of the midgut (*my*, figure 15), is discussed below (page 21). The posterior part of the midgut is narrow and apparently less distensible. At the point of junction of mid- and hindgut the four Malpighian tubules enter the alimentary canal. The hindgut consists of three parts, of which the first and third are narrow with a low epithelium. The second part of the hindgut is short, wide, and almost completely surrounded by six rectal papillae provided with a rich tracheal supply. Each of these is a syncytium, a tissue formed by the fusion of many cells the divisions between which cannot be distinguished; the surface of the syncytium covers a large area of the lumen, and is in direct contact with the contents of the hindgut (Sikora, 1916). Anatomy and structure suggest that these organs are rectal papillae; in insects of many

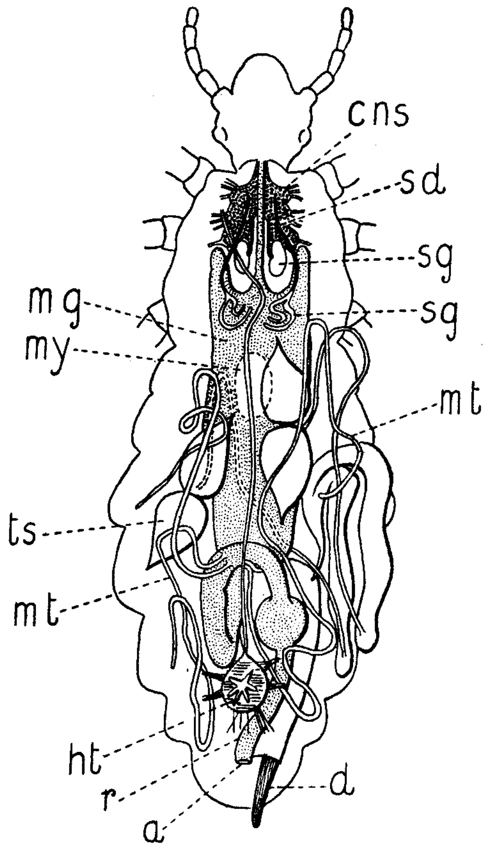

FIG. 15.—*Pediculus humanus*, internal anatomy of male seen from above. *a*, anus; *cns*, ventral part of central nervous system; *d*, dilator; *ht*, heart; *mg*, midgut; *mt*. Malpighian tube; *my*, mycetome; *r*, rectum; *sd* and *sg*, salivary duct and glands; *ts*, testis, (*After Keilin and Nuttall.*)

groups their function is the removal and recirculation of water from the contents of the hindgut. Observations on the living louse confirm this. When the insect begins to feed, a small quantity of blood may be passed quickly from mid- to hindgut, indeed, drops of undigested blood may appear at the anus. But later in digestion the material is kept longer in the hindgut. In the anterior part it is fluid,

but in the second part of the hindgut which is surrounded by the rectal papillae, water is extracted from the faeces, which are passed as dry pellets which frequently adhere to one another in a string. When digestion is completed, the papillae also extract water from the clear excretion of the Malpighian tubules and concentrate it till it is semi-solid (Wigglesworth, 1932).

3. Salivary Apparatus. The salivary apparatus is complex. There are several minute glands in the lower part of the head, the ducts of which open into the sheath of the stylets; though they are generally described as "salivary," their function is not known. There are also two pairs of glands in the dorsal part of the thorax; of these the anterior are reniform, the posterior tubular ("horse-shoe shaped"). Both lie close to the anterior part of the midgut (figure 15). The ducts pass forward into the head and unite inside the stylet sheath to form a median duct, continuous with the intermediate stylet (figures 12 and 14); it is clear from this that these glands are salivary. It has been shown that if the reniform glands are dissected out, emulsified and injected into the human skin, they produce irritation 8–10 hours later, followed by a bluish swelling; the tubular glands produce no such effect (Pavlovskyi and Stein, 1925). It seems, therefore, that the irritation caused by the insect's bite is due to the secretion of the reniform glands alone.

In front of the reniform salivary glands there is a group of large cells, generally binucleate, containing greenish droplets. There are groups of similar cells in several parts of the fat body. These cells have been described as "nephrocytes." It is now held that the function of such cells, which occur in many types of insect is analogous to that of the reticulo-endothelial cells of vertebrates; they are concerned with the "micro-phagocytosis" of colloidal particles (Wigglesworth, 1939, page 238).

4. Mycetome. Reference has already been made to the mycetome or stomach-disc which lies mid-ventrally in the wall of the anterior part of the midgut (figure 15). The organ is rounded, yellowish and readily seen through the ventral integument of the living insect. Towards the end of embryonic life it arises as a pouch in the wall of the midgut, from which it eventually becomes completely separated; its cavity is crossed by radial septa. The cavities between the septa are full of short rods (figure 16, A), which are probably micro-organisms, and which are generally described as "symbionts." A study of the unhatched embryo shows these symbionts lying in a group of cells in the yolk which then fills the lumen of the gut. These cells approach the mycetome at the period when it is a pouch opening into the lumen of the gut, and the symbionts enter it (figure 16, B). There they remain throughout

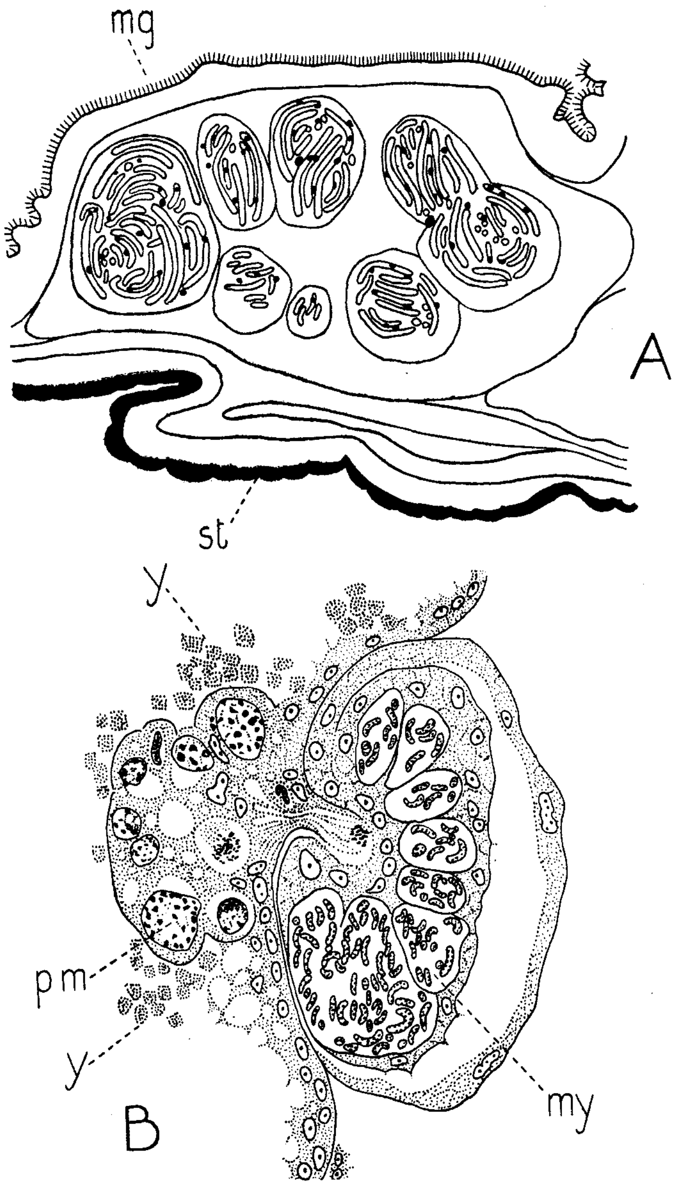

FIG. 16.—*Pediculus humanus*, mycetome in ventral wall of midgut. (× 750.)

A, in larva (male), showing mycetome lying between epithelium of midgut (*mg*) and ventral wall of abdomen (*st*). The symbionts lie in groups, separated by septa.

B, in embryo, showing primary mycetome now degenerating (*pm*) among yolk cells in gut (*y*), and symbionts in position in definitive mycetome (*my*) in gut wall. (*After Ries.*)

the life of larva and male louse. But in the female the majority of them leave the mycetome about the time of the last moult and migrate to the wall of the oviduct; from that position they enter the egg, and so reach the embryo, thus completing their cycle.

In shape the symbionts resemble bacteria; as they retain their characteristic individuality and appearance during this remarkable life-cycle, it is impossible to suppose that they are a part of the louse's tissues, and the view that they are micro-organisms is extremely probable.

Admitting that these rods are micro-organisms, are they parasites or symbionts? The fact of their invariable presence in the louse and of the hereditary transmission suggests that they are symbionts. This is supported by experimental work, for it is possible to remove the whole mycetome by open operation. If this is done on an adult female after the symbionts have migrated to the oviduct, her length of life and powers of laying fertile eggs are little affected; it may therefore be concluded that the mycetome without its contents is not of great value to the insect. But if the mycetome is removed from the female very early in her adult life, while it still contains symbionts, she lives only a few days and lays eggs which are malformed and not viable: removal of organ and symbionts from larvae also causes death. The same result may be obtained by centrifuging the egg and displacing the mycetome. If this is done before the symbionts have entered it, the larva only lives a few days. Clearly, then, the micro-organisms are necessary to the insect's survival and reproduction; i.e. they are beneficial to the insect, and are therefore rightly described as symbionts (Aschner, 1934). It is not known precisely how they are of value to the louse, but work on symbionts of other insects which feed entirely on blood throughout the life cycle suggests that symbionts are micro-organisms which supply vitamins deficient in the blood which forms the louse's sole diet. (For a general account see Wigglesworth, 1939: for recent work with *Rhodnius*, a blood-sucking bug, see Brecher and Wigglesworth, 1944.)

CHAPTER 3

THE BIOLOGY OF *PEDICULUS HUMANUS*

INTRODUCTORY

Pediculus humanus exists in two races not distinguishable with certainty by any anatomical character (page 11), but differing considerably in the position on the body where they occur and in the place at which they attach their eggs. So far as is known, the biology of these races is similar in most respects. The greater part of our knowledge of the biology is based on experimental work with the body louse. Most of our knowledge of the biology of *Pediculus* and *Phthirus* has been obtained by keeping these insects in small containers against the skin, and observing them at intervals. For details, see page 142.

The distinction between the individual and the collective biology of the louse is important. It will eventually be found that collective biology is an important part of medical entomology, for it gives us information as to how many people are infested and in what class of the community; how densely they are infested; the chances of the infestation spreading, or the likelihood that an epidemic of a louse-carried disease may break out.

For further information on biology, see Bacot (1917*a*), Hase (1931), Nuttall (1917*b*).

INDIVIDUAL BIOLOGY

1. The Egg. The egg of *Pediculus* is approximately oval, very large for the size of the louse, about 0·8 mm. long by 0·3 mm. broad (figure 17, A). The colour is yellowish opalescent, and as the chorion or shell is to some extent transparent, the embryo may be distinguished inside it. The shell at the anterior end of the egg forms a cap which has a sharply defined circular edge; along this it ruptures when the egg hatches, the cap coming off unbroken. One side of the cap is unlike the rest of the shell of the egg, for it consists of two layers, enclosing large air cells between them. The layers are pierced by pores so that the atmospheric air reaches the membranes covering the embryo (figure 18). The orientation of the egg and its attachment to hair or fibre by an adhesive secretion which forms an irregular mass round its lower pole is described elsewhere (page 48).

The lethal effect of temperatures above the normal on the eggs of body lice has been investigated in detail (Buxton, 1940). If eggs are under five days old, the lowest fatal temperatures are as follows:

Five minutes	53·5° C.	128·3° F.
Ten ,, ...	52·0	125·6
Thirty ,, ...	50·0	122·0

Eggs of eight or more days old are killed by temperatures several degrees lower than those quoted above: for instance it was found that exposure of about 46 to 47° C. (115 to 117° F.) damages the embryo so that it continues to develop, but fails to escape from the shell.

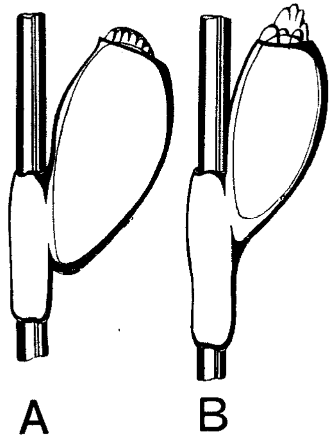

FIG. 17.—*A*, egg of *Pediculus humanus capitis*. *B*, egg of *Phthirus pubis*.
(*After Hase.*)

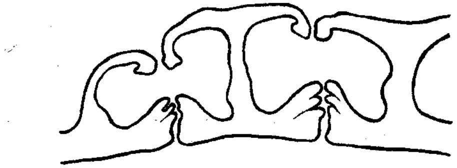

FIG. 18.—*Pediculus humanus*, section through part of cap of egg, showing two layers pierced by pores. (× 535.)
(*After Aschner and Ries.*)

Leeson (1941) has been interested in the range of temperature over which development of the egg is possible. Using eggs derived from cultures of body lice kept in boxes, he finds considerable inconsistency in the percentage which hatch under one particular set of conditions. Most workers with lice have observed an unexplained mortality of 10–30%, even when conditions are thought to be quite favourable: this is not entirely due to infertility, for partial development of the embryo is common. If kept at a constant temperature eggs only hatch between 24 and 37° C. (75·2 and 98·6° F.) and within those limits the relation of temperature to incubation period is shown in figure 19. It is clear that the proportion which hatch is affected by temperature, the range 29 to 32° C. (84·2 to 89·6° F.) being most favourable. Humidity does not affect the incubation period, but high or low humidity tends to increase the mortality: Leeson's figures for eggs incubated at 26° C. (78·8° F.) illustrate this:

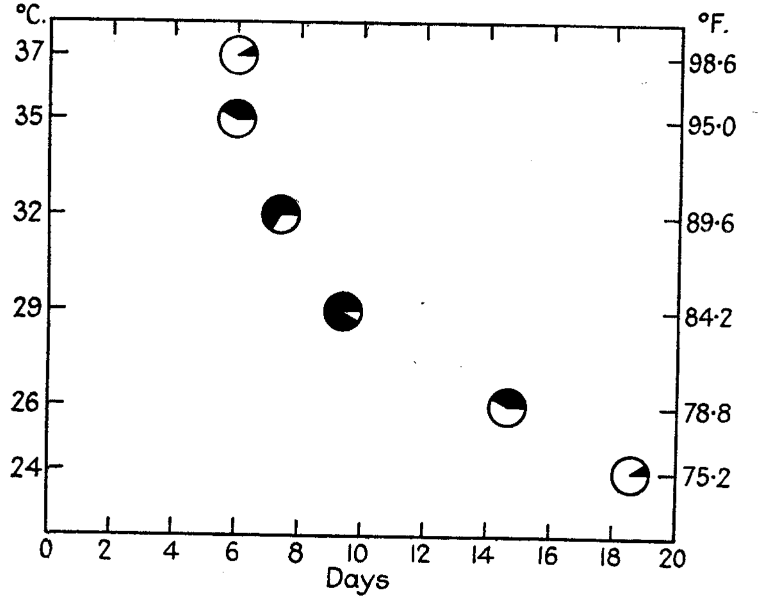

FIG. 19.—Mean incubation period of eggs of body louse at constant temperatures. Black segments of circles represent proportion hatched (Leeson, 1941).

Relative humidity. %	No. of eggs used.	% hatched.	Duration (days).
25	71	41	14–19
50	79	46	14–17
75	80	62	13–15
90	79	30	14–17
95	72	39	14–18

Leeson also experimented with eggs which were transferred to "unfavourable" temperatures, and then brought into the favourable range (24 to 37° C.) at which alone they will hatch. It was found that eggs under twenty-four hours old can survive one day but not two at 39° C. (102·2° F.). Eggs were also kept at 23° C. (73·4° F.): at this temperature some eggs can develop to the point of showing eye spots, but the embryo never succeeds in emerging from the egg. If eggs are kept at 23° C., for periods up to eleven days and then removed to a favourable temperature, a small proportion develop and hatch; an exposure longer than eleven days is always fatal. In a similar manner, exposure to 20° C. (68·0° F.) for ten days or so (but not longer) followed by incubation at a favourable temperature led to some eggs hatching: seven days at 19° C. (66·2° F.) was the limit, or six days at 8° C. (46·4° F.).

Leeson also found that if eggs were kept at a favourable temperature till nearly ready to hatch and then placed at 23° C., some hatched. Even the eggs brought down to 18° C. (64·4° F.) could hatch, and others did so when the eggs were again brought to a higher temperature. At 15° C. (59° F.) none hatched, but if they were kept at this temperature for as long as nine days and then warmed some hatched. Nine days, however, was fatal at 8° C. (46·4° F.).

A study of Leeson's paper justifies one in concluding that there is no combination of temperatures under which eggs could hatch after a month. Storage for that period would ensure the death or hatching of all eggs, under all circumstances. This is consistent with an observation we made in London some years ago. We received an extremely lousy shirt, and removed all adult lice from it. It was kept at room temperature, but warmed up to 27° C. (80° F.) each day: larvae continued to emerge for twenty-four days, but not longer.

Busvine (1944*b*) has defined the fatal period of exposure to low temperatures. Eggs under three days old were slightly more susceptible to cold than older eggs, but the difference was slight, and is neglected in figure 20, which sets out his results very clearly. The line which separates fatal from non-fatal conditions is straight, the time scale being logarithmic.

Leeson's data for duration of egg at constant temperatures have been considered by Davidson (1943): he has calculated the percentage of development per day at the six temperatures at which Leeson worked, and fitted a curve (figure 21). Somewhat similar work (both on eggs and on lice) is published by Alpatov (1942). His paper calls attention to the fact that our knowledge is imperfect from − 10 to 10° C. (14 to 50° F.), and 35 to 42° C. (95 to 108° F.).

2. The Larva.[1] Many of the events which lead up to the larva's emergence from the egg may be seen through the eggshell (chorion). The fullest account of what occurs is that of Sikes and Wigglesworth (1931), who studied the louse of the mouse (*Polyplax*), but observations made by several authors upon *Pediculus* show that the process is essentially similar in the two. The embryos of *Pediculus*, *Phthirus* and other Anoplura have somewhat elaborate hatching devices on a rigid area of embryonic cuticle on the front of the head: the device consists of a pair of upcurved teeth, and several pairs of blades which arise from a depression immediately above the teeth. Towards the end of embryonic life the larva may be seen to swallow amniotic fluid, and at a later stage, air. This causes it to swell and brings it into firm contact with the shell. At the same time the larva moves forward in the egg shell, towards the cap. It seems that the blades of the hatching apparatus probably pierce the vitelline membrane, and that the pair of teeth force up the cap of the egg.

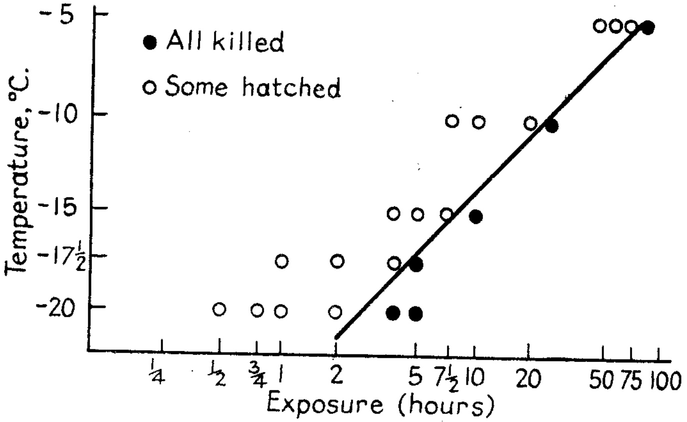

FIG. 20.—Resistance of eggs of body louse to low temperatures (Busvine, 1944).

At this time the larva is enveloped in an embryonic cuticle, which is ruptured and shed as it leaves the egg. In addition to that there are invariably 3 moults and therefore 3 larval instars in *Pediculus*. This was first established by Warburton (1910), who carried body lice through the life cycle. The three larval stages differ little from one another except in size and in the relative length of the abdomen, which increases at each moult. They may most easily be distinguished by the following measurements:

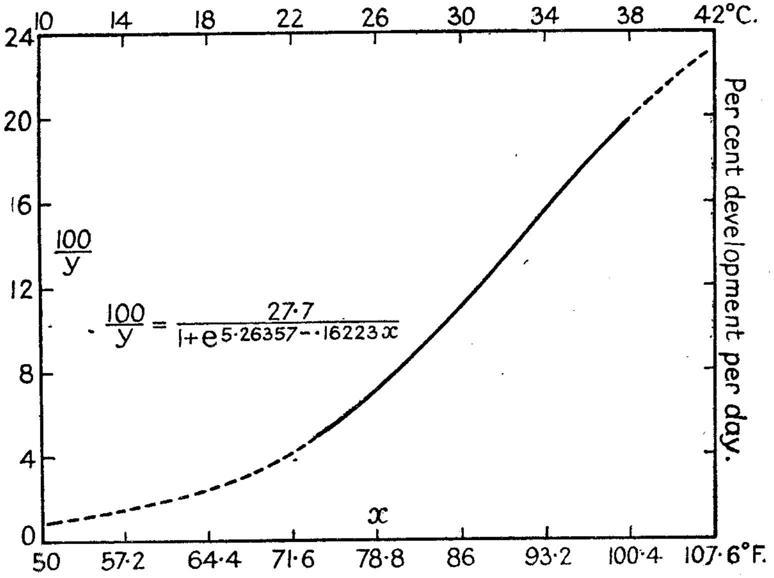

FIG. 21.—Calculated curve showing average speed of development of eggs of body louse at temperatures between 23·5 and 36° C. (Davidson, 1943).

	Mean length 3rd tibia (mm.)	Mean ratio of length of head to length of thorax and abdomen.
1st instar larva	0·197	1 : 2·8
2nd ,, ,,	0·270	1 : 3·5
3rd ,, ,,	0·363	1 : 4·3
Adult male	0·408	1 : 4·2
Adult female	0·377	1 : 4·9

(Buxton, 1938*a*.)

The duration of life from emergence from the egg to the last moult is 8 or 9 days in insects kept continually on the human body: in gauze-bottomed boxes, worn against the skin all day, but taken off during the hours of sleep (conditions which resemble those which

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[1] The reader who is not an entomologist should remember that there are very great differences in the life history of insects. In some orders, e.g. the lice (Anoplura), there is no very great difference between the young insect which comes out of the egg and the adult insect. In others (e.g. moths, flies) the difference is so great that the early active stage, a caterpillar or maggot, in no way resembles its parents. Many entomologists prefer to restrict the word larva to the latter, and would prefer to call the young louse a "nymph." I do not disagree, but regard the point as formal and uninteresting.

a body louse would encounter if it were living among clothes removed at night), the duration of larval life is generally 16 to 19 days, very occasionally 12 to 26 days. The length of time passed in the three instars is approximately equal. The length of life of the larva is not affected by its sex, so that there is no tendency among eggs laid at the same time for adults of one sex to emerge before those of the other (Buxton, 1940*a*).

In most respects the biology of the larva is like that of the adult. Its only food is human blood, and the greater part of its life is spent on the surface of the body or on the clothes. It is not capable of resisting long starvation, and the figures quoted below (page 35) for the adult probably hold equally well for the early stages. Some authors have thought that lice in the first stage are apt to wander farther than they do in later life, but this is not proved. It is, however, known that small lice may be distributed in the open air by wind, and apparently this happens less frequently with larger, heavier individuals. There are several cases on record of small lice being blown on to the outer garments of those engaged in dealing with infested soldiers and prisoners (Schaefer, 1916; Schilling, 1916).

Death of the larva may be due to failure to complete emergence from the eggshell; this is probably an effect of dry air, which reduces the quantity of amniotic fluid and renders emergence mechanically difficult. Death at moulting occurs, but not commonly. Larvae, like adults, frequently rupture the gut and die within a day or two, with haemoglobin from the host's blood dispersed to all parts of the body. In captivity there is a considerable mortality, particularly in the first two days of life; in my own experiments about 38% of larvae died. It is not known whether this occurs in nature or to what extent it should be attributed to difficulty in feeding through bolting silk.

3. Position on Host. It is generally agreed that the head louse, (*P. h. capitis*) is almost confined to the surface of the hairy scalp, and to the hair itself. It is not known to occur on eyebrows or eyelashes (where one may find *Phthirus*). Lice and eggs found inside caps and hats are generally described as head lice, but I am not aware that they have been critically examined, and it may be that some are body lice, and part of a general infestation of the garments. To what extent the head louse wanders to the body or undergarments is difficult to discover, partly because of the difficulty of identifying some specimens.

Within the limits of the scalp and hair arising from it, it is generally stated that lice tend to be more frequent on the nape and in the area behind the ears. No precise information is available, nor do we know whether the adults and larvae tend to occupy different areas.

The distribution of body lice (*P. h. corporis*) on garments has been studied in great detail by MacLeod and Crauford-Benson (1941*b*). They investigated 229 sets of infested undergarments, from a total of 151 men living in common lodging houses in London in 1939–1940. At the first examination 85% of these men had under 100 lice, 15% over that number, and a small number over 1,000. The distribution of the lice was found to be extremely complex, partly because the individual men differed so much in the number of undergarments they wore. There were also very rapid changes from day to day: my own fairly extensive experience with infested men of the same class leads me to think that they have little appreciation of the need for exactitude in scientific research, and that they will roast a garment in front of a fire, or put it off for a day or two, or exchange it with a friend, all of which makes it most difficult to know what conclusion to base on one's observations. MacLeod and Crauford-Benson have established that there is not a great deal of difference in the number of lice on the different seams of a shirt, where two thirds of the lice will be found; that about seven lice out of eight are on the surface next the skin; that the females tend to be found along seams (where oviposition occurs), the males more generally over the surface of the shirt. If a man wears a shirt and one or more vests he does not tend to carry more lice than the man who wears only a shirt: in the layers farther from the skin the proportion of adult lice is higher, because they tend to migrate farther than larvae. For this reason if a man has few lice, say ten or less, the proportion of adults will generally be high, because his lice have been recently acquired. These authors have accumulated a large amount of fact, not easy to summarize. Unfortunately they could get no information as to the number of lice actually on the men's bodies at any particular moment. It is obvious that some lice must be on the body, indeed the presence of nits on trunk and pubic hair shows this to be so, a point to be remembered in disinfestation.

Busvine (1944*a*) has studied the distribution and movements of body lice under garments, by releasing them on clean volunteers. He points out that if one takes a lousy shirt off a man and examines it, the lice are found almost motionless, generally against seams: but it may well be that when the shirt is being worn and they are in the dark they run about. If one releases adult lice at one spot under a woollen vest on a clean volunteer and waits two hours, one finds that on an average they have moved about a foot, measured in a straight line: some will have got outside the vest, or even outside the shirt. This experiment simulates what may happen if a clean person becomes infested. But we know from Wigglesworth (1941; see page 43 below) that lice tend to stop on an area of cloth on which other lice have previously lived, so that one would expect them to tend to collect in certain spots once an infestation has lasted for some time. To study this, Busvine confined sixty lice on a three-inch square inside his vest, letting them feed through bolting-silk. After three days, when the area was heavily contaminated with excrement, he removed silk and lice leaving a dozen on the spot. Two hours later he found that they had travelled as far as those in the first experiments; i.e. they did not tend to be homebound. If lice are liberated on a pleated cotton body-belt they tend to settle down in its folds, and do not move far in two hours, though if the wearer takes exercise and sweats they move further. The adults wander farther than the larvae.

4. Dispersion, Discovery and Choice of Host. Lice normally live on the surface of man's body or garments. To what extent do they occur away from their host, and how do they find their way to another human being? We are here concerned with gross facts as observed in nature. The analytical work described below (page 38) will demonstrate that lice perceive temperature, and tend to move towards the temperature prevailing on the surface of one's body, that they also prefer fabrics which smell of man, or which have been inhabited by other lice and defiled with their excrement, and that they prefer a low illumination and move away from directed light.

It is generally difficult to find lice away from man. For instance, Peacock (1916) examined a certain regiment and found it heavily infested; yet most of the blankets were free of lice, and on others he found very few; the mean number found per man (including clothes) was 31·4, per blanket 0·8. Though nearly all troops in the line were infested, it was not possible to find lice in dug-outs and billets at least during the day: observations made at night on lousy people asleep might be of great interest. Rather similar figures are available from beds in common lodging-houses in London in 1908. It was unusual to find more than one or two lice per sheet, even though the proportion of beds infested ranged from 12% in June to 31% in February (Hamer, 1909). There is recent work by MacLeod and Crauford-Benson (1941*a*), who made observations in April and May 1940 on a community of men living in a hostel, which was rather above the average, in the East End of London. Of sixty-five inmates, only thirteen (i.e. 20%) were free of body lice: about half the remainder had no more than one to ten lice apiece. The sleeping quarters were good, and beds were examined daily and sheets changed if found to be lousy; each sheet was also regularly changed once a fortnight. In spite of this of 200 beds 24% were found infested (32% of beds in regular occupation). It was also shown that if a bed is vacant for a day or two it becomes almost free of lice, though how many lice are dead, and how many have successfully reached another man is not known. An individual bed, slept in every night, may be lousy one week, free of lice the next. The evidence is overwhelming that infestation may commonly be picked up at night, from the bedding.

The converse is, I believe, also true, for one may handle lousy men and garments by day and very seldom acquire an infestation. My own experience in the last few years has been very extensive. I have examined thousands of infested garments (of Egyptian labourers, and London tramps), and counted the lice, but so far as I know, I have never picked up a single louse, though I was not wearing protective clothing. The reason is that in daylight the louse either crouches motionless, or runs off to a fold or seam and stays there.

Busvine (1944*a*) has shown that if one infests a sleeping-bag and then occupies it, one is more likely to pick up lice if one wears woollen than smooth poplin pyjamas. During the night a third or more of the lice escape from the bag, moving six feet or more, point to point. There are other records showing that head lice (*capitis*) may be acquired from the upholstered backs of seats and chairs, and from brushes and combs; also that they travel from hat to hat in schools and other places. It is also probable that hairs with living eggs may become detached and blow about, or be left on the backs of chairs. In a rather similar way the body louse (*corporis*) becomes spread, particularly if people huddle together to keep warm, as may happen to the destitute, and particularly to refugees and to troops on active service. Over short distances it is probable that the dissemination of the insect is rapid; it was observed in France during the war of 1914–1918 that if infested troops were bathed and given clean underclothing, these became infested from the outer garments within half an hour. The distribution of larvae by wind has been referred to above.

It seems probable that lice establish themselves more readily on one man than another, though it would be difficult to prove this. MacLeod and Crauford-Benson (1941*b*) describe the case of a man living among lousy men in a common lodging-house. This man was given a clean shirt, and examined daily, and though two lice were found 24 hours later there was evidence that neither adult lice nor larvae succeeded in establishing themselves for a number of days. Other suggestive cases are described by these authors.

A case is reported in which hungry lice would not feed on a certain volunteer, though they fed at once when transferred to a second man (Moore and Hirschfelder, 1919). The point is important and requires fuller study.

The dispersion of lice is sometimes assisted by human beings, who deliberately remove them from their clothes and drop them about. The author has a vivid recollection of seeing a group of workmen, sitting on the top of a wall in Iran, catching lice and dropping them into the street; typhus and relapsing fever were epidemic at the time. An epidemiologist might make a profitable study of the variety of ways in which different human races dispose of these insects.

It appears certain that lice leave a febrile patient and tend to scatter and find other hosts (a point of epidemiological importance if the patient is suffering from some louse-borne fever). It is for this reason that patients suffering from fever sometimes carry great numbers of eggs but no lice. The experiments described by Lloyd (1919) confirm this. In each experiment he made up a large bed and put two volunteers to sleep in it, releasing 200 lice on one man. Sixteen hours later he searched for the lice, and found that the proportion remaining on the original man was consistently higher if he was healthy than if he was febrile; moreover, the second man complained of lice in an hour or two if his bedfellow had fever, but otherwise made no complaint for 5–6 hours. Busvine's (1944*a*) experiments on himself also demonstrate that if a man takes exercise and sweats lice tend to move away from the surface of the body: it is the adults rather than the larvae which move. (See also Wigglesworth's experiments with temperature, and with moist surfaces, page 42 below.)

Actual observations upon insects released and watched indicate a rate of travel of about 23 cm. (9 inches) per minute at 20° C. (68° F.), and higher rates at higher temperatures. Wigglesworth (1941) makes the interesting observation that, even under uniform conditions (crawling on voile at 30° C.), the rate of progress of individual body lice may range from 6 to 30 cm. per minute. The insect generally meanders about so that the distance covered from point to point is much less than one would expect from the rate of travel, but five feet in an hour, measured on a straight line, has been recorded. The lowest temperature at which the insect can walk is not known.

Owing to the perfection of its sensory mechanisms *Pediculus humanus* is a close and specific parasite of one host, man. There is no evidence that it can establish itself and breed on other hosts. The only possible exception is of certain monkeys, from which lice hardly distinguishable from *P. humanus* have been recovered in zoological gardens; the simple experiment of infecting clean monkeys with human lice and observing the result has not been performed.

5. Biology away from Host. When the louse is not on man it is to some extent abnormal. It cannot feed and it is exposed to whatever climatic conditions may prevail, which affect its length of life and power of wandering. The information available may be summarized as follows:

(*a*) *Upper limits.* In connection with the destruction of lice in garments by short exposures to high temperatures, it is most important to have precise facts on lethal temperatures. At raised temperatures, the lowest which kills all body lice is:

Five minutes . . .	51·5° C.	124·5° F.
Thirty „ . .	49·5° C.	121·1° F.
One hour . . .	46 or 47° C.	115 to 116·6° F.

Sublethal temperatures (e.g. 46° C. for forty minutes) appear to kill the eggs inside the female (Buxton, 1940*a*). On short exposures, up to an hour or perhaps longer, loss of water is not great, and the lethal temperature is the same for dry and moist air. But on long exposures, serious loss of water may occur in drier air, so that the louse cannot survive a twenty-four hour exposure to so high a temperature in dry air as it can in moist, for instance 39° C. (102·2° F.) kills them in moist air and 34° C. (93·3° F.) in dry air in 24 hours. First stage larvae which have fed have the same limits, but unfed larvae die at lower temperatures, owing to exhaustion of their reserves (Mellanby, 1934).

(*b*) *Moderate temperatures.* Just below the lethal temperature the insect's biology appears to be normal; at about 37° C. (98·6° F.) adults will pair and a small proportion of eggs hatch (figure 19, page 34). It is shown elsewhere (page 26) that at a particular temperature the rate of walking is very variable. It would be of interest to obtain figures for rate of walking at temperatures below those prevailing on the surface of the body and to determine the lowest temperature at which the louse can progress.

There is a considerable body of fact on the survival of unfed lice at various temperatures. The insects were kept on rough cloth, in the dark, and were only examined at the end of the experiment, and never disturbed on intermediate days. It was found that either half or all lice (out of 10 or 20) were killed by the following exposures:

		Half dead.	All dead.
35° C.	95° F.	Under 1 day	Two days
30° C.	86° F.	2 days	3 „
24° C.	75° F.	2–3 „	5 „
15° C.	59° F.	5 „	10 „
10° C.	50° F.	4 „	7 „

The period necessary to kill all lice was not different for nymphs and adults; moderate differences in humidity (65 or 90% at 24° C.) made little difference. In considering the above facts it should be emphasized that conditions (e.g. lack of disturbance) favoured survival; the figures for " all dead " give an extreme, not a mean. From the practical point of view they are rather on the safe side (Leeson, 1941).

(*c*) *Lower limits.* Busvine's work on the effect of low temperatures on survival of body lice is summarized in figure 22. In order to avoid sudden changes of temperature, the insects were chilled in two or three stages before exposure to the experimental conditions. It will be observed that lice are much more rapidly killed than eggs (figure 20, page 28) by exposure to temperatures below freezing point (Busvine, 1944*b*). It is recorded by Chung (1937) that if lice are kept at 5–8° C. (41–46° F.) and warmed up and fed daily they survive for weeks.

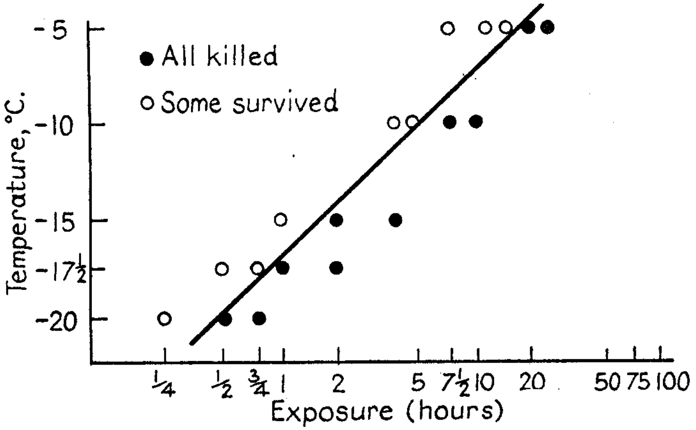

FIG. 22.—Resistance of body louse to low temperatures (Busvine, 1944).

6. Feeding and Nutrition. Normally the louse is on man's surface or on his clothes and is living under closely regulated climatic conditions (page 30). It is not known how much blood lice take at a time or how often they feed, though there is some evidence that this occurs several times a day. From experiments with lice kept in boxes and applied to the skin at intervals it is known that they take a considerable quantity of blood if they have fasted for 6–12 hours. A female louse in that state will take approximately 1·0 mg. of blood, her own weight being about 3 mg. unfed. It is also easy to show that lice lay more eggs, and that the larvae grow more rapidly, if they are held against the skin continuously rather than at intervals, but it is not known whether this is an effect of temperature or of frequent feeding.

The use of the mouth parts and the act of piercing skin and sucking blood are dealt with on page 18.

With regard to digestion nothing is known. The mycetome, an organ in the wall of the midgut which contains essential symbiotic micro-organisms, is described on page 21. The act of defaecation and the important function of the rectal papillae in conserving water are dealt with on page 20.

There are also records of hungry lice (*Pediculus*) being applied to animals, or even birds, and taking blood. There is, for instance, little difficulty in feeding lice repeatedly on monkeys (*Macacus*), in experimental work on typhus; indeed Nicolle (1910) reports that a proportion of body lice were alive after feeding daily for 20 days on this monkey: but it is recorded by Bacot and Ségal (1922) that very few lice fed on *Macacus* lived more than 4 days. Davis and Hansens (1945) have carried body lice through several generations on rabbit. It was necessary to shave the rabbit carefully each day, and to feed the lice twice daily. Even then growth was rather slower than in controls, and mortality high. Work of this type, on rabbit or other animal, might lead to important advances in typhus research, making it possible to maintain and rear *Pediculus* without feeding them on man. There are also a few records of lice being caused to feed on guinea-pigs, mice, fowls, pigeons, etc., but other records of lice failing to feed on these animals: the lice sometimes refuse to feed unless the animal's hair is removed and the skin scrubbed with alcohol. Several records appear to suggest that the blood of some animals (especially of rodents) is harmful to *Pediculus*; no one has performed the simple experiment of comparing the length of life after sucking guinea-pig or rat with that of controls on man, or even of unfed controls. Though *Pediculus* may be fed, under artificial conditions, on various hosts other than man, we have no reason for thinking that this occurs naturally. Man is the only normal host, and control is based on this fact.

It would evidently be of great value if lice could be fed successfully through a membrane, for it might then be safer and easier to infect large numbers with *Rickettsia*, and advances in other directions would probably follow. Dr. V. B. Wigglesworth carried out experiments in 1940 and 1941 and allows me to summarize his unpublished results. He worked first at atmospheric pressure, placing his lice in a shallow box, on a membrane which was floating on blood at 30–35° C. A number of membranes were tried including mouse mesentery, and the horny layer of human skin (the skin removed at operation being digested in pepsin and hydrochloric acid). The lice probed these membranes, and penetrated them, but only a few took up blood, and then in very small quantities. He then carried out a number of experiments in which the blood was at a pressure of about 30 mm. of mercury, about that of the capillary blood. Of the membranes tested, only fresh mouse skin would withstand this pressure, and even it oozed after a time. A considerably higher proportion of lice (about 40% of 60 lice) succeeded in taking blood, and becoming fully gorged. The work was discontinued because results were uncertain and irregular. It seems that Psenichnov (1943) has also discovered the importance of presenting the blood under slight pressure. He finds citrated blood preferable to defibrinated blood, and has reared lice from egg to adult in this way, feeding them through a membrane. The method is promising, but not yet fully worked out.

The method of feeding lice by rectal injections with defibrinated blood is described on page 145.

If rats are kept on diets deficient in certain vitamins they become lousy (see page 71). This is probably *not* due to any effect of vitamin deficiency on the insect.

7. Behaviour : Sensory Physiology. In nature one observes an animal in an environment which is complex. In an experiment one may vary one factor holding the others constant, and in this way analyse (and frequently illuminate) the natural events. The work of Wigglesworth (1941) on the behaviour of the louse under experimental conditions goes some way to give precision to our understanding of its normal life, and brings order to the rather heterogeneous body of observations which have been accumulated.

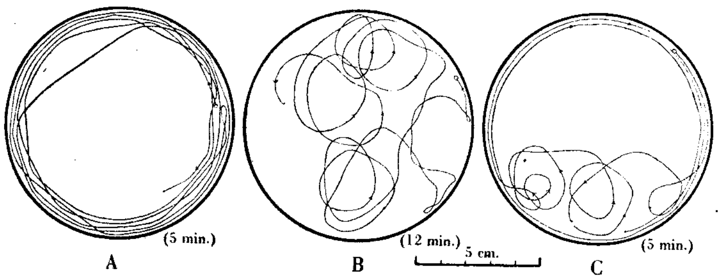

FIG. 23.—Tracks followed by lice in a uniform horizontal arena.

Wigglesworth's general method was to arrange a horizontal circular arena, so contrived that the two halves of it could be made to differ in temperature, humidity, roughness, or some other single factor. The edge of the arena was a glass ring up which lice cannot

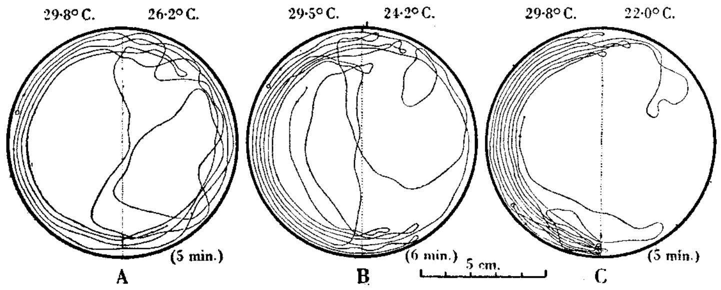

FIG. 24.—Tracks followed by a single louse as the temperature in one-half of the arena was progressively lowered.

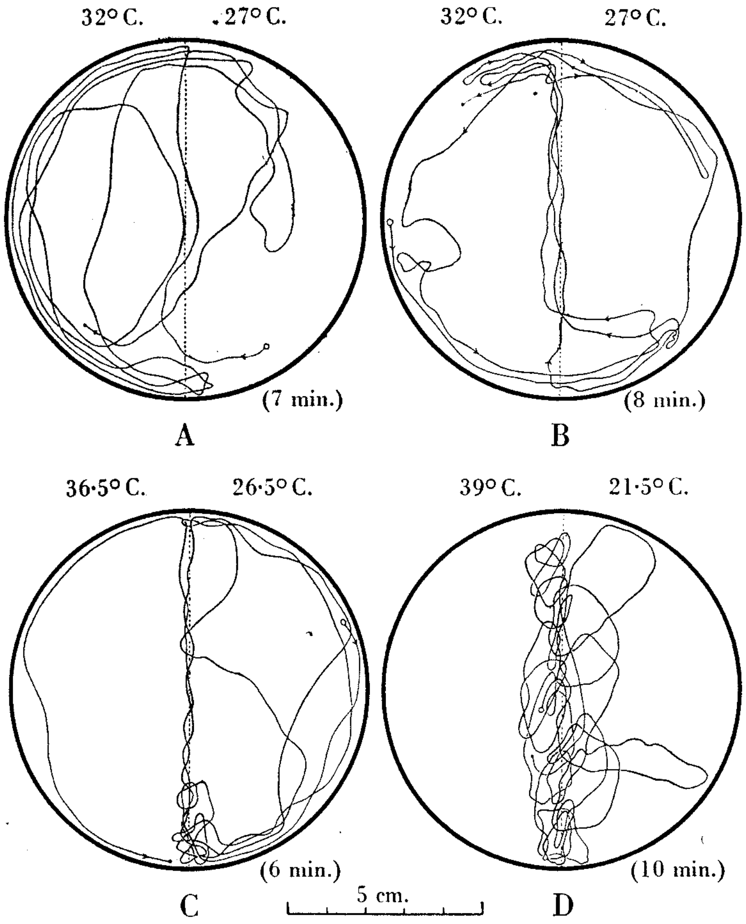

FIG. 25.—Tracks of lice when the temperature was above the optimum in one half of the arena and below the optimum in the other half.

climb. A single louse was liberated and its tracks drawn at short regular intervals. One could then study the point at which it changed direction, the places where it rested, and the amount of time spent on one or other part of the arena.

If conditions are uniform in all parts of the arena and the floor covered with voile a well-nourished louse will walk more or less straight, frequently colliding with the walls, so that it goes round and round uninterruptedly: such a track is shown in figure 23, A (the successive perambulations being shown concentrically in order to distinguish them). Some individuals have a bias, permanent or temporary; for instance figure 23, B shows the track of a louse with a definite bias towards the left. The speed of a louse at 30° C., other things being equal varies to a remarkable extent, from 6 to 30 cm. (say 2¼ to 12 ins.) per minute.

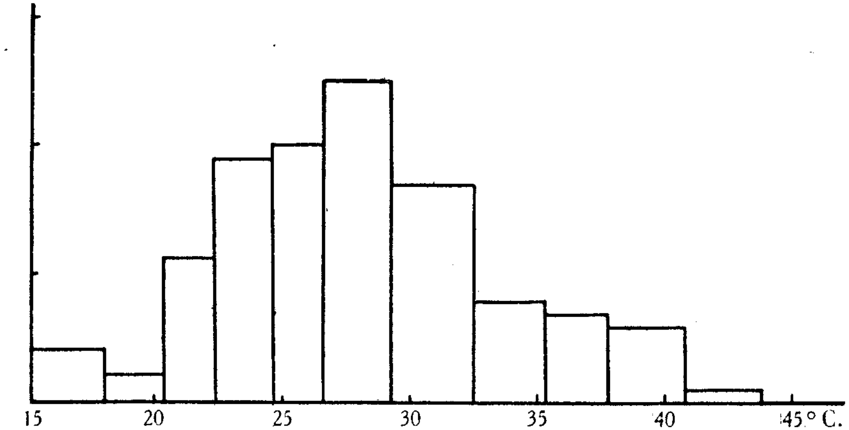

FIG. 26.—Relative numbers of lice collecting within different sections of the temperature gradient.

The apparatus is then set to give two temperatures on the floor of the arena, the intermediate zone being sharp. Tracks such as those shown in figure 24 may be obtained, showing a preference for 29–30° C. (84·2 to 86·0° F.) against lower temperatures. In the same way it can be shown that 29–30° C. is preferred to 32° or higher temperatures. In each case the avoidance becomes increasingly strong, as the alternative rises above 32° (89·6° F.) or falls below 27° (80·6° F.). If one-half of the arena is above, the other below the optimum the louse may discover the zone of intermediate temperature, and walk on it with considerable precision (figure 25). If lice are exposed to a temperature gradient in a long narrow chamber, they show the same tendency and collect at 28–31° (figure 26). It can also be shown that, at least from 20° (68° F.) to 40° (104° F.) the insect's reaction is to air temperature, not to radiant heat coming from the walls of the apparatus.

Wigglesworth has also devised a chamber in which the insect is presented with a choice of humidity (sharply divided) at a uniform temperature (30° C.). The type of response is shown in figure 27, B and C: the insect pursues its normal course at 76% relative humidity, and turns back immediately when it passes into 95%: or it may pursue a convoluted course, and show agitated movements at the high humidity, returning to normal behaviour when it reaches the drier side (figure 27, C). The individual louse's reaction to humidity may be weak or intense, moreover the response is influenced by the conditions under which the insect had previously been kept. There is, however, a general tendency for the insect to prefer a lower or medium humidity, and also to avoid a change after it has spent some time at a given humidity: it is much more sensitive at the high than the low end of the scale, having a strong preference for 92% against 95% but being indifferent between 10 and 60% relative humidity.

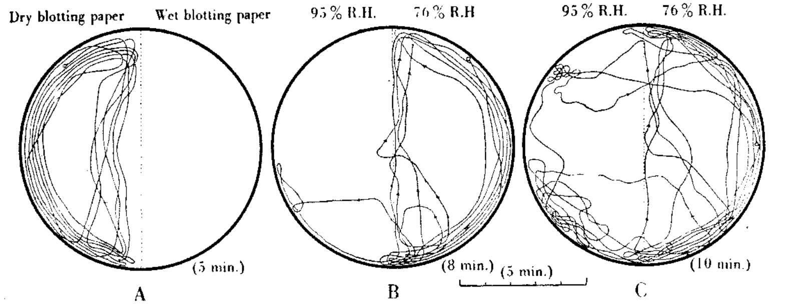

FIG. 27.—*A*, response of louse to a wet surface. *B*, *C*, responses to atmospheric humidity.

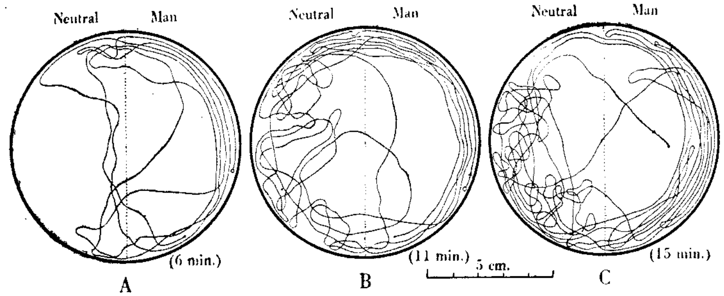

FIG. 28.—Reactions of lice to the smell of man.

If a part of the floor of the arena is dry blotting paper, and the other part wet the louse shows a very strong avoidance of the wet (figure 27, A).

Wigglesworth also investigated the sense of smell, in an apparatus

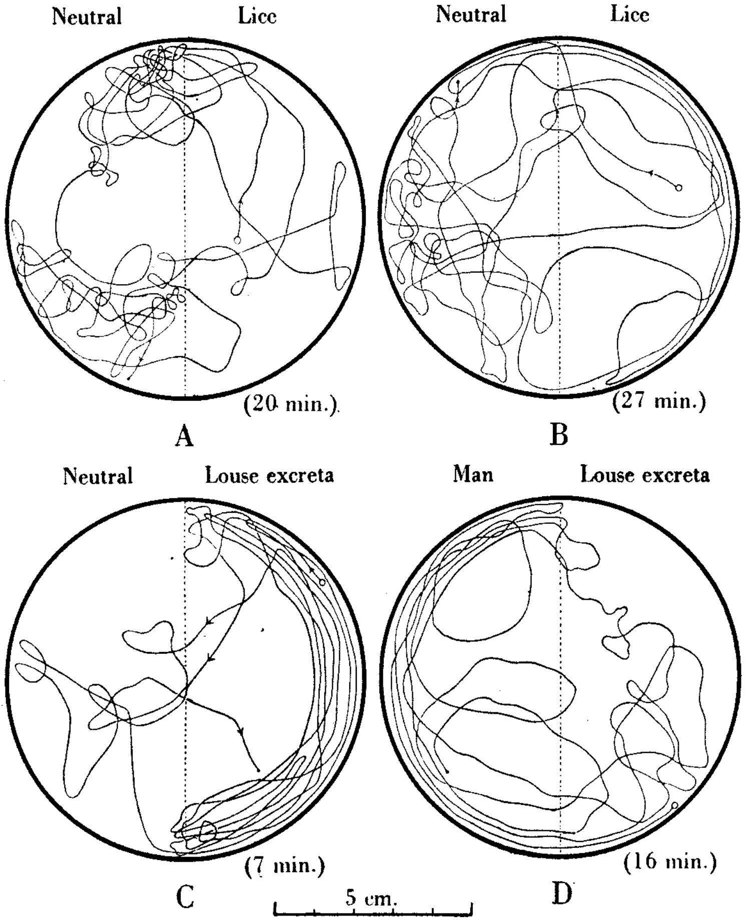

FIG. 29.—*A, B,* tracks of single female lice when half the arena covered a chamber containing other female lice. *C,* reaction to the smell of louse excreta. *D,* reaction to smell of man when the other half of the arena contained louse excreta.

similar to that used for experiments on perception of humidity. Figure 28 shows the paths of lice presented with the choice between cloth which had been worn next the skin, and clean cloth. The normal behaviour on the " man " side, and the sharp turns at the boundary give an interesting contrast with the twisting course over the clean cloth. In a similar experiment lice showed preference for cloth worn by man compared with cloth rubbed on dog, or rabbit. Lice also show a preference for the half arena immediately over other lice, as against the half which is neutral; also for louse excreta (figure 29 C).

The same apparatus can be used to test the repellent effect of mineral oils, etc. Quite sharp reactions may be demonstrated in this type of choice chamber.

A series of experiments were carried out in a chamber of which

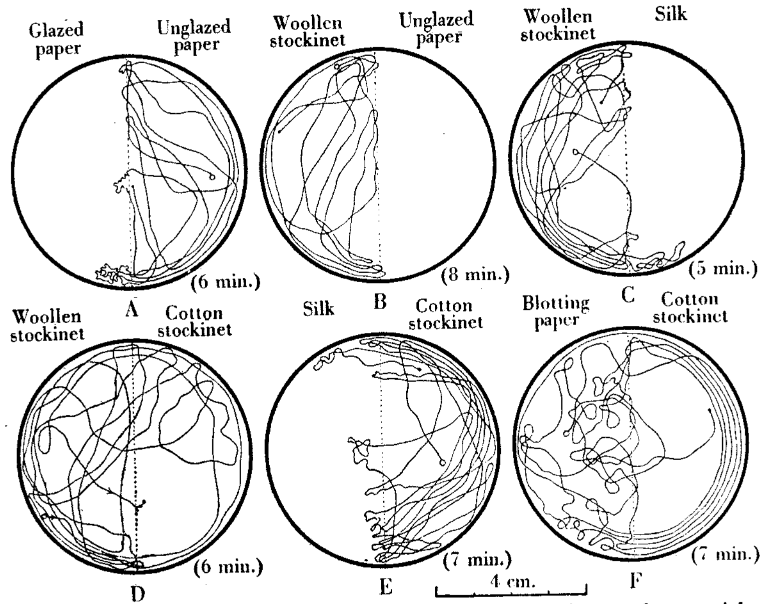

FIG. 30.—Reactions of Lice in contact with rough and smooth materials.

the floor was covered with materials of different degrees of roughness. There is a general tendency for the insect to follow a straight course on the rougher and a convoluted course on the smoother alternative (figure 30). It should, however, be noted that the louse quickly becomes habituated to a smooth surface, and then appears to feel at home on it.

It was also found that air currents have very little effect on the louse's course, unless they are so strong as almost to dislodge it.

All the stimuli which have been considered (temperature, smell, humidity) are diffuse: there may indeed be a gradient but the insect can only detect the region of increased or decreased stimulus by moving about. Light on the other hand may act as a general diffuse factor, but may also be directed. In some of Wigglesworth's experiments lice were kept in the dark for a period, and then exposed in the arena at an extremely low illumination, at which it was just possible to see them. If light is then suddenly increased several thousandfold the insect commonly stops crawling and remains motionless for some minutes. When the louse resumes its walk, particularly if it has been disturbed, it may move slowly and with halts : in other similar experiments the louse's course, when illumination is increased, becomes devious and convoluted, just as it does under other conditions which are slightly adverse. The louse could also be aroused by several alternations of bright and dim light.

The effect of light as a directed stimulus was studied in an arena of which one half had black walls, the other half white walls, both being fully exposed to bright light from above. Under these circumstances the louse tends to swing away from the white wall, and to walk close to the black wall (figure 31, A). If in addition the area with black wall is shaded from above the louse remains entirely in the shaded side, turning away before it enters the light (figure 31, B). In other experiments lice were liberated in an arena diffusely lit from a window : they moved away from the light, but could perceive and move towards a black area on the wall (figure 32, C, D). These movements are clearly determined by light reaching the insect's eye (figure 8) in a horizontal direction.

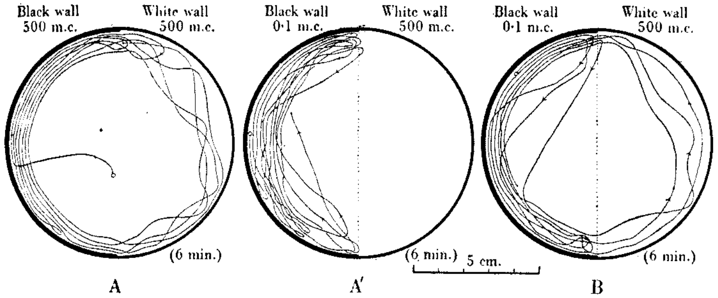

FIG. 31.—Reactions of the louse to light reflected from the walls of the arena. *A*, entire arena light ; *A′*, track of same louse with black-walled half of arena shaded ; *B*, track of another louse under the same conditions.

The matter has been carried a little further, for it is possible to identify some of the sense organs which perceive such stimuli as temperature, smell or humidity. Something of the way in which these stimuli affect the louse may be learnt from watching it in a chamber. As it walks its antennae are continually moved from side

to side. If it comes into a zone of high temperature (40° C.) the vibrations of the antennae become very fast, and the insect turns and moves away. As the insect walks on a rough fabric one can see that antennae and legs are frequently in contact with upstanding fibres, whereas on smooth silk it is the legs only which are touched. If it moves from dry to wet blotting paper the louse stops with antennae alone extended to the moist area. These observations suggest that the antennae are the seat of organs which perceive several different stimuli.

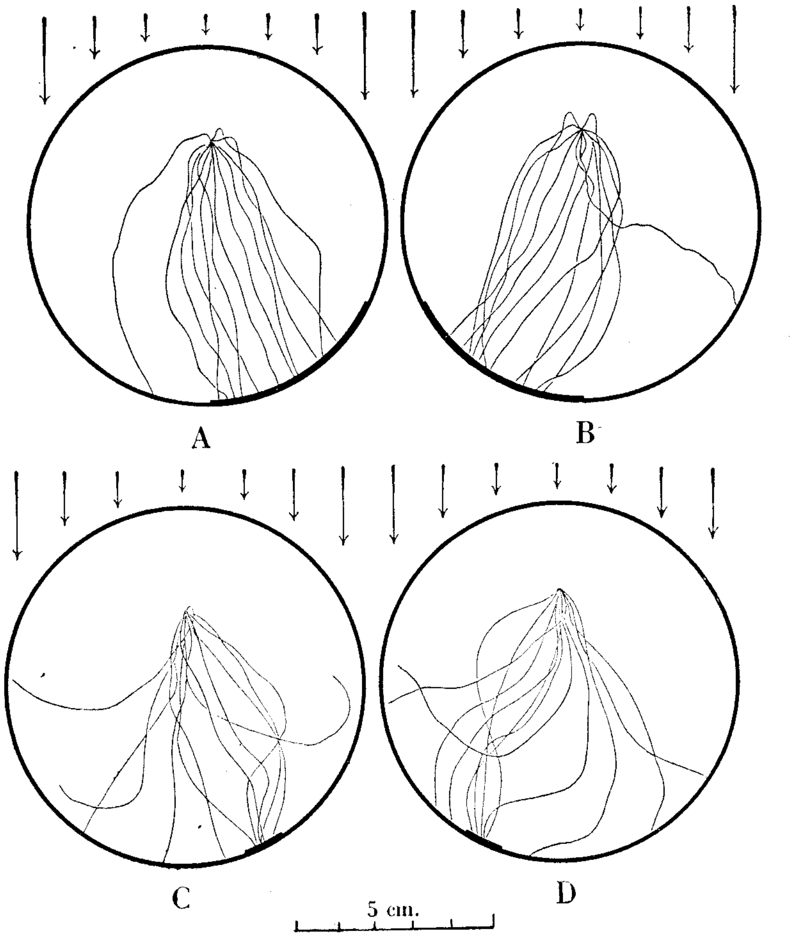

FIG. 32.—Tracks of lice liberated in the middle of an arena with a black segment on the otherwise white walls. The arrows show the direction of the light.

It will be remembered (figure 7) that the peg organs and tuft organs are confined to particular parts of the antenna. Wigglesworth has found it possible to cover either set of organs with paint and then expose the louse to a choice of conditions. Lice deprived of the use of peg organs could not smell odourless distillate but could distinguish degrees of humidity; absence of tuft organs produced the contrary effect (figure 33). The association of the tuft organ with perception of humidity is particularly interesting, for its four minute hairs (figure 7, C) might perhaps be hygroscopic and alter their shape with changes in atmospheric humidity. This, however, could not be demonstrated.

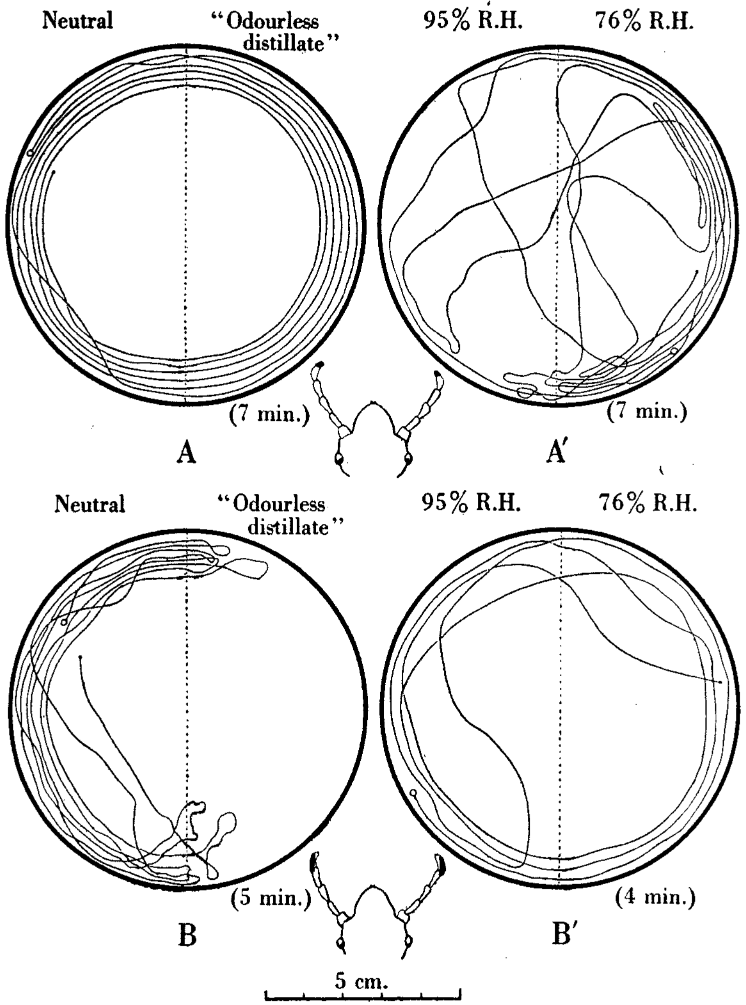

FIG. 33.—*A*, *A′*, reactions of louse, with peg organs alone covered, to smell and humidity. *B*, *B′*, reactions of louse, with the tuft organs alone covered, to smell and humidity.

The perception of temperature is not confined to the antennae, for the louse shows an efficient choice even if both antennae, or antennae and front of head, are completely removed. An insect deprived of both antennae generally continues to prefer a rough to a smooth surface. It will, however, probe a warm smooth surface, whereas the normal louse does not do this unless it receives the additional stimulus of smell.

One might perhaps conclude by pointing out that the experimental method seems to justify itself or "explain" the field observations. For instance it answers the vexed question whether the louse possesses a sense of smell (and indeed goes further, to localize the sense organs): and it takes such a fact as the congregating of lice in one part of a shirt seam, and illuminates it by demonstrating the insects' attraction to the smell of other lice and their excrement. The method reveals an unexpected complexity, showing that the insect's behaviour depends in part on stimuli it is receiving, in part on the conditions to which it has previously been exposed. On the other hand the experimental method might lead one astray, if one followed it without regard to the natural history of the insect. The method has its limitations; for instance in Wigglesworth's experiments the lice were in the light, which is certainly unnatural to them.

8. Reproduction and Egg Laying. Lice may pair during the first 10 hours of adult life (Sikora, 1915): if either partner is under 24 hours old pairing is not invariable, as it is with older lice. A young member of one sex will pair successfully with an old member of the other (Buxton, 1940*a*). Pairing occurs frequently, and at any time in the adult's life. It is possible for one male to fertilize many females; Bacot (1917) put a male with 21 females in succession, each for a single day, and found that 18 of them laid fertile eggs. If the sexes are separated after pairing, the female will lay fertile eggs for a variable period, up to 20 days. The mechanism and act of copulation are dealt with on page 8.

The pre-oviposition period, i.e. the length of time from the last moult to the laying of the first eggs, is about 2 days in lice kept in gauze-bottomed boxes on the body all day but put off at night (Buxton, 1940*a*). In insects kept in a felt cell permanently on the body and with nothing between them and the skin, it is 24–36 hours (Nuttall, 1917*b*). At the end of her life the female often ceases to lay eggs for a period of a day or two before death.

When the female is about to deposit an egg she grasps the hair (or fibre of a garment) between the gonopods (figure 4, page 8). The egg then issues from her body, the pointed end coming first. At this moment there is a flow of cement from glands which open into the side of the common oviduct. This cement covers the pointed end of the egg and the shaft of the hair (figure 17), but ceases to flow before the broad end of the egg with the cap or operculum has left the female's body. The eggs are orientated along the axis of the hair or fibre. *P. h. capitis* attaches its eggs to the hair with their caps facing away from the surface of the scalp. Eggs are generally attached close to the base of the hair, and the part of the scalp most commonly chosen is that behind the ears. According to Mellanby (1942*a*) hair grows at about 0·4 mm. per day, so that one may roughly calculate when an egg was laid from its distance from the scalp. Oviposition inside hats is frequent. The body louse (*P. h. corporis*) most generally lays its eggs on the inner surface of undergarments, but quite commonly on hairs growing on the trunk. It has been shown that if body lice kept in a box are offered both hair and cloth they tend to deposit most eggs on the cloth; with head lice the converse is true. In nature body lice tend to oviposit on rough materials (wool and flannel) rather than on those which are compact or smooth (linen, drill, leather), but there is no absolute avoidance of any type of fabric. The following data, obtained under laboratory conditions, are instructive: 100 female body lice were kept for 24 hours at 37° C. (98·6° F.) with a number of pieces of material; 255 eggs were laid, 76% on woollen stuff, 12% on human hair, 11% on glass, and less than 2% on silk material (Hase, 1915). Bacot (1917*b*) kept groups of female head or body lice in boxes, offering a choice of pieces of flannel, and bundles of hair for oviposition. He records several experiments, such as:

Corporis	359 eggs,	on hair	11%,	flannel	89%
Capitis	274 ,,	,, ,,	95%	,,	5%
,,	340 ,,	,, ,,	98%	,,	2%

But such figures do not justify the belief that one may avoid infestation by wearing silk underwear: where the insect is not offered choice it will infest silk, and Wigglesworth's experiments (page 43) show how soon a louse becomes habituated to some particular material. In nature the eggs of the body louse are often attached to garments at places where the material is folded or pleated; there is a tendency for the females to resort to particular spots and for very large numbers of eggs to accumulate there. If the man is quite nude, the body louse will infest beads and necklaces.

After the egg of head or body louse has hatched the empty shell may remain cemented to the hair for long periods and eventually be carried away from the skin by the growth of the hair. It is important not to accept such empty shells as evidence of present infestation. The cement substance is not softened by soap and hot water, or vinegar, or indeed by any material which could be used (and many have been recommended!) to assist in removing nits. It exhibits negative birefringence which indicates the presence of long orientated molecules (Schmidt, 1939).

Haddow (1941) kept isolated virgin female body lice, in groups of ten, each fed for a different period. The group fed continuously laid a mean of 230 eggs (standard deviation 96·6, max. 329, min. 11). This corresponds to a mean of 7·7 eggs per day (S.D. 2·0). He once had thirteen eggs laid by one female in one day, and it was fairly common for a louse to maintain 10 eggs a day for several days. There was no statistically significant difference between the group fed for all the twenty-four hours, and those fed twenty, sixteen or twelve hours (always in one continuous period); lice fed for shorter periods laid fewer eggs and also lived a shorter period. The work was done entirely on unmated females, but there is no reason for thinking that they differ in output of eggs from mated females.

If a female *Pediculus* is deprived of the opportunity of taking blood very few eggs are laid, and none if she is kept at or below 20° C. (68° F.).

If larvae in the last instar are isolated and monogamous pairs are made up, fertile eggs are always produced. The sex ratio of the offspring of any particular pair is very far from equality; unisexual families have been recorded, but more commonly both sexes occur, the one much more abundantly than the other (figure 34). Actual numbers of males and females reared, and of larval deaths, for the strains Bermondsey I and II are given by myself (Buxton, 1940*b*). Figure 34 shows that in different strains of body louse (we have no reason to doubt that the same thing occurs in head lice) the families differ greatly in sex ratio; some strains produce families in which the sexes are approximately equal in numbers, others are nearly, and others again quite unisexual. The cytology of oogenesis and spermatogenesis has been described (Cannon, 1922; Doncaster and Cannon, 1920; Hindle and Pontecorvo, 1942), but throws little light on sex determination.

Parthenogenesis, the laying of fertile eggs by virgin females, does not occur. Many authors using different strains of lice have isolated large larvae and kept the virgin females till death. My own experiments were based on eggs from 69 virgin females (Buxton, 1940*b*). Many eggs are laid (though the pre-oviposition period tends to exceed the normal), but they are invariably sterile.

The number of eggs which a female will lay depends on conditions. Using boxes with gauze bottoms, worn by day but not generally by night, several authors have obtained figures ranging from 100 to 200 (*P. h. corporis*): the number of eggs laid per day is about 3 to 5: the mean number of eggs per reproductive day, for 34 pairs of body lice reared in this way, was 4·03 (Buxton, 1940*b*). It is probable that in nature, if the garments are worn day and night, the production of eggs is higher. Nuttall (1917*b*) quotes figures obtained in a felt cell worn continuously; for a group of female body lice the production per female per day was 9–10. Perhaps, therefore, one may assume a total production of 270–300 eggs per female body louse in nature. The figures obtained with *capitis* are generally lower, but this may be due to the conditions of rearing being less suited to this insect; Bacot (1917*a*) gives a mean of 88 eggs for a group of females and a mean daily production of 3·7.

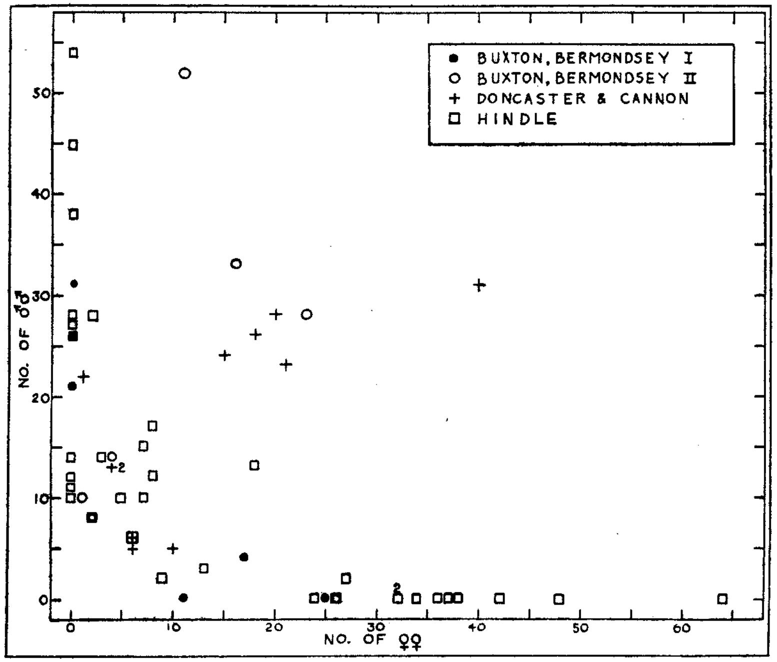

FIG. 34.—Showing the number of males and females in monogamous families of *Pediculus humanus corporis*.

(*Data from Hindle,* 1919; *Doncaster and Cannon,* 1920; *Buxton,* 1940*b*.)

9. Duration of Life on Host. We have no information about length of life of adults under natural conditions; under artificial conditions (feeding through gauze, or for a limited period daily on bare skin) a number of facts have been accumulated, the most useful of which are given in Table 1. Earlier and smaller collections of fact for body lice (Sikora, 1915; Bacot, 1917) are similar. One might perhaps sum the matter up by saying that the adult *corporis* generally lives a little more than a month, two months being the longest adult life recorded. The few observations on *capitis* suggest that its life is shorter than that of *corporis*, but Bacot himself attributed this to *capitis* being less suited to his experimental technique. The difference between Bacot's mean for ♀ *capitis* and mine for ♀ *corporis* is not significant. The difference between my figures for males and females is not significant. Figures on the length of life of larvae are given above (page 30).

Haddow (1941) shows that isolated virgin females live about 30 days if fed continuously day and night by the box method: groups fed 20, 16 or 12 hours daily, in one continuous period, do not show a significantly shorter life. Groups fed only 8 or 4 hours, in one period, only live some 13 days.

TABLE 1

LENGTH OF LIFE OF ADULT *PEDICULUS HUMANUS* REARED UNDER LABORATORY CONDITIONS

Race	Sex	Number	Length of life				Author
			max.	min.	mean	stand. dev.	
Capitis . . .	♂	4	30	7	16	—	Bacot, 1917
,, . . .	♀	16	38	11	27·0	8·33	,, ,,
Corporis * . .	♂	34	52	6	30·56	11·93	Buxton, 1940*b*
,, * . .	♀	34	60	8	28·76	13·40	,, ,,
,, † . .	♀	40	44	5	± 30	—	Haddow, 1941

* From monogamous pairs, made up from isolated larvae.

† Virgin isolated females, fed twelve to twenty-four hours daily.

10. Causes of Death. There are several "natural causes" of death. If lice are observed from day to day it will be found that a female ceases to lay and does not feed; she remains thin, empty, and lethargic for a day or so, and then dies: a similar course of events may precede the death of the male. Such insects die of old age, and in experimental work this is the commonest cause of death. Occasionally the gut ruptures, the whole body and limbs become tinged with red colour derived from the host's blood, and the insect dies within a couple of days; death from this cause may be observed in males, females or larvae. It sometimes happens that a virgin female fails to lay eggs, becomes enormously swollen and dies: this is clearly due to an obstruction, perhaps due to the cement substance which should attach the eggs. If the insect gets away from its host and fails to discover another, it is doomed to die after a period, which is mainly determined by temperature (page 35); we do not know whether this is a common event.

It is often difficult to get newly emerged larvae to feed, even on bare skin. It seems that the young larva feeds more readily on one man than another, but that there is also an inherent mortality in certain batches of larvae (Buxton, 1940*a*).

So far as is known lice suffer very little from predators, though it has been recorded that certain ants will carry them off: indeed, people in many parts of the world have found that a garment may be disinfested by spreading it on an ant's nest (Hase, 1942). No parasitic insects attack any of the Anoplura. *Pediculus* has few internal parasites, and the gut is sterile (at least when tested by ordinary bacteriological methods). Deaths apparently due to bacterial diseases do not seem to occur, even in crowded cultures. One or two infections are on record, for instance, a bacillus which lives in the copulatory organ, a spirochaete pathogenic to man (page 91), a *Herpetomonas* in the gut, and a Microsporidian: moreover, some of the *Rickettsiae* are harmful to the louse (page 78). In cultures we have sometimes seen high and unexplained mortality of larvae: see also Nauck and Weyer (1941*a*). But, broadly speaking, *Pediculus* has few enemies or diseases and might look to living to a ripe age and dying by gradually losing its grip on its surroundings. We have, however, two good reasons for thinking that this does not occur:

1. As the adult's life in captivity is about 30 days, and the larva's 9, we should expect adults to be more abundant than larvae (in a proportion of about 3 to 1) in a stable population, if all lice died of old age. But in natural populations larvae are always more abundant than adults, often by about 1 adult to 5 larvae (page 61).
2. The arithmetical argument (page 55) points to the same conclusion. Even if one makes a most liberal allowance for mortality in early life, a louse community might reach prodigious figures in a few months: this seldom occurs.

On both these grounds we conclude that death from old age is not common: we know that there are few enemies or diseases. To account for the facts we must think that man is responsible for a very large proportion of the deaths: even among people who do not regard lousiness as abnormal, many deaths must be due to human activity (combing, hand picking, washing, laundering, etc.).

COLLECTIVE BIOLOGY

1. Powers of Increase. It is clearly important to gain some idea of the rapidity with which a population of lice might multiply under favourable circumstances. The facts already set out, about the duration of the various stages, normal mortality, number of eggs per female, etc., furnish our basal data; for most of these items we possess mean values based on a number of observations made on body lice kept in boxes against the skin. The basal data are taken to be as follows[1]:

The *female* lives 34 days, laying no eggs on days 1, 2 and 34: she lays 9 eggs a day, a total of 279 (31 × 9): every female is fertile.

The *eggs* have a total mortality of 30% (including those which are infertile, and those in which the embryo dies in the shell): the stage lasts 9 days.

The *larva's* life is 9 days, and the mortality 40%.

In the *adult progeny* it is assumed that males and females are produced in equal numbers, and that they become adult at the same time.

As we are interested in the increase of population, one may limit attention to those eggs and larvae which are destined to grow up and reproduce themselves, and call them "viable." And one may speak of "viable offspring," implying both eggs and larvae, which need not be distinguished. Thus one may say that, with the mortality of eggs and larvae which is quoted above, 100 eggs produce 42 adults, so that the female's viable offspring is 117 (i.e. 42% of 279 eggs): as she lays 9 eggs a day, her daily viable offspring is 3·8, of which 1·9 are females.

What may be expected to happen is set out in an abbreviated form in Table 2, in which successive generations are distinguished as G1, G2, etc. As we are interested in the population of lice which are alive at any time, the table shows not only daily births, but total births to date. If it were continued further, columns would have to be added for daily deaths, and total living population (i.e. total births less total deaths). For simplicity's sake the table deals only with females: if figures for all lice are required it may be sufficiently accurate to double all figures, though it would be more accurate to

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[1] Several of these figures differ a little from those given above in the present edition. The discrepancy is of little significance, for the present section of the text illustrates a general principle. It would entail much unnecessary labour to recalculate Table 2, etc.

use a correction based on sex ratios given in Table 3. In any case the table shows only the "viable" individuals: at any moment there are in addition many eggs and larvae which are not destined to survive and reproduce themselves.

The early part of the table is self-evident. The original female (G1) is born (as an egg) on day 0, becomes adult on day 18, and starts to lay eggs (G2) on day 20. Each day she lays eggs, of which 1·9 are viable and female: she does this from day 20 to day 50, and then dies. At that time many of her daughters are laying eggs, and some of her grand-daughters (G3) are larvae.

Meanwhile the eggs (G2) laid from day 20 onwards produce adults which lay eggs (G3) starting on day 40. The matter is a little complex, for on the 40th day 1·9 females (laid as eggs day 20) are each laying 1·9 eggs, so that the production is 3·61 viable female eggs. But on the next day the females laid on days 20 and 21 are all laying eggs, so that the production of eggs is 1·9 × 2 × 1·9 = 7·22. Daily production of G3 eggs continues to rise to day 70 (on which day it is 1·9 × 31 × 1·9 = 111·91): after that it declines owing to the death of the senior members of G2.

It would be difficult to carry the matter much further, for the complexity increases with each generation. For instance, in G4, the first eggs are laid on day 60, by the 3·61 individuals (G3) which were born on day 40. On day 60 there are therefore 3·61 × 1·9 viable female births: on day 61 the figure is (3·61 + 7·22) × 1·9, and on day 62 (3·61 + 7·22 + 10·83) × 1·9, and so forth. Moreover, from day 52 the population is reduced by death, so that the last column no longer indicates the total number alive.

Fortunately, short methods are available, worked out by Thompson (1931): this author and Soper (who contributed an appendix to Thompson's paper) have provided general formulae which give us daily births and deaths, total number alive, etc., even for insects of which many generations may be alive at the same time. These formulae are the basis of figure 35 in which the curves have been carried to the 80th day. On that day there are very nearly 15,000 viable females alive and nearly 1,700 births, figures which would almost justify the journalese use of the word "astronomical." It will be remembered that the viable females alive may be either eggs, larvae or adult lice, and it might be of considerable importance to know how many fall in each of these groups. This is easily discovered from a table of daily births (similar to the first column in Table 2) which was prepared as a basis for figure 35. As the egg stage lasts for 9 days one can see that on day 80 all births which occurred on days 72–80 inclusive will be eggs: similarly all births which occurred on days 63–71 inclusive will be larvae, i.e. on day 80,

TABLE 2

SHOWING THE EARLY STAGES OF THE INCREASE OF A POPULATION OF *PEDICULUS HUMANUS* LIVING UNDER GOOD ARTIFICIAL CONDITIONS

G1, G2, etc. = first and second generations

Day	Event	Viable female births daily				Viable female births to date			
		G1	G2	G3	Total	G1	G2	G3	Total
0	Parents (♂ ♀) laid as eggs	1	—	—	1	1			1
9	Egg becomes larva	0	—	—	0	1	—	—	1
18	Larva becomes adult ♀ (G1) . . .	0	—	—	0	1	—	—	1
20	Above ♀ lays eggs (G2)	0	1·9	—	1·9	1	1·9	—	2·9
21		0	1·9	—	1·9	1	3·8	—	4·8
22		0	1·9	—	1·9	1	5·7	—	6·7
29	First larvae emerge (G2) . . .	0	1·9	—	1·9	1	19·0	—	20·0
38	First larvae (G2) become adult . .	0	1·9	—	1·9	1	36·1	—	37·1
39		0	1·9	—	1·9	1	38·0	—	39·0
40	Adults (G2) lay eggs (G3) . . .	0	1·9	3·6	5·5	1	39·9	3·6	44·5
41		0	1·9	7·2	9·1	1	41·8	10·8	52·6
42		0	1·9	10·8	12·7	1	43·7	21·7	66·4
43	First G3 eggs become larvae . . .	0	1·9	14·4	16·3	1	45·6	36·1	82·7
49		0	1·9	36·1	38·0	1	57·0	198·5	256·5
50		0	1·9	39·7	41·6	1	58·9	238·3	298·2
51	♀ G1 dies	0	0	43·3	43·3	1	58·9	281·6	341·5

of the 14,987·3 viable females alive, 10,540·9 are eggs, 3,337·8 are larvae, and (by difference) 1,108·6 are adults. Curves shown in figure 35 for eggs and larvae are worked out in this way.

It is perhaps instructive to consider a second case in which conditions are much less favourable to the insect, rather as they might be on an infested person who failed to achieve a radical cure but did what he could by inefficient methods. We will suppose that the mean life of the adult female is reduced to only 20 days: that she only lays 6 eggs per day, of which 80% fail to grow up to maturity: and that the other factors are as before. Such a female only produces 0·6 viable female offspring daily. The growth of the population and the proportion of eggs, larvae and adults in it are shown in figure 36. It will be seen that even under these very severe conditions the population rather soon enters a period of rapid increase.

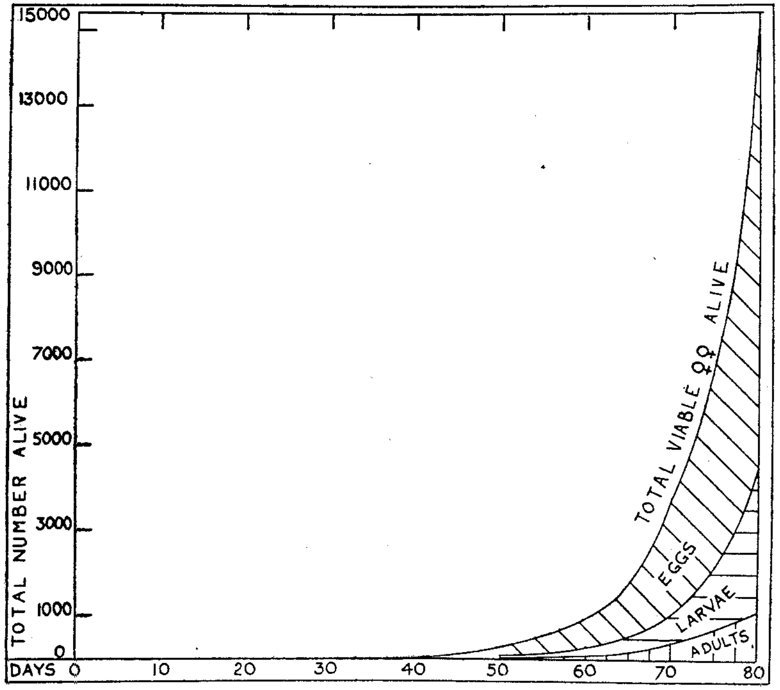

FIG. 35.—Showing potential growth of a population of *Pediculus humanus*, under the rather favourable conditions defined in the text.

The curves show the total number of " viable females," and the number of eggs, larvae and adults which compose that total.

There is no reason to doubt that a population of lice obeys the same general rules as all other populations of plants and animals. It increases at first on an approximately geometrical ratio, but pressure of the environment reduces the rate of increase, and would bring the population to a level at which no further increase occurs. In the case of *Pediculus* we do not know at what point this pressure of the environment (i.e. human effort) begins to be effective, but we think that the point is very different with different men (page 67).

Rather similar calculations, not carried very far, are published by Shukhat and Revich (1939). Their female lays 100 eggs and has 27 adult offspring.

It is reasonable to ask to what extent these calculations and graphs correspond to reality. It is shown elsewhere (page 61) that natural populations of head and body lice commonly consist of about 10 or 20 insects, though hundreds are not very rare, and populations exceeding a thousand have been recorded. (It is to be understood that these figures relate to larvae and adults, whereas the " viable females " discussed above included a large proportion of eggs.) It seems, then, that natural populations do not increase indefinitely, so that one is not justified in extending the curves into regions where the populations become very large: indeed the curves in figure 35 have already been carried too far. But suppose we limit ourselves to the earlier part of the curves in which the total population is not very great, are they then of value? The view is developed elsewhere (page 52) that human interference is the commonest cause

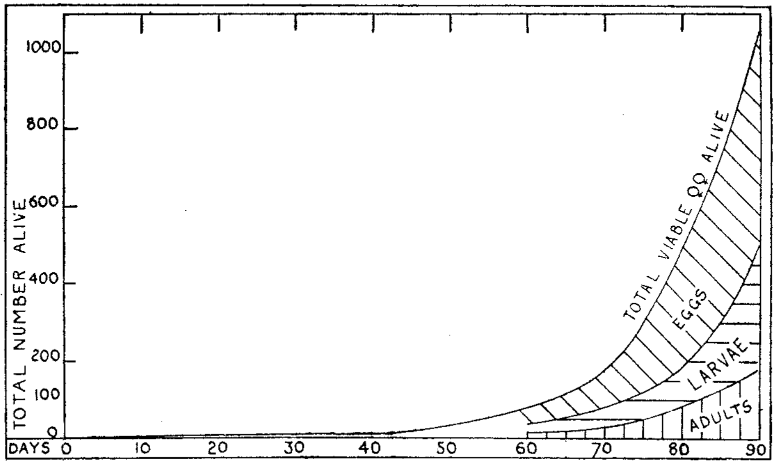

FIG. 36.—Showing potential growth of a population of *Pediculus humanus*, under the unfavourable conditions defined in the text.

of death in these insects, and that death from old age or from parasites and enemies is rare. Human action against the lice has two characteristics:

1. Man does not act regularly, killing a small proportion daily: on the contrary, he selects a particular day for washing his shirt or taking some other sort of drastic action. The mortality that he produces is therefore exceedingly irregular.
2. On the whole, man's activity will be more intense as the population of lice rises, so that the mortality produced will tend to be a function of the density of population.

It seems to follow that with fuller knowledge more elaborate methods of calculating births and deaths will come into use, but even then it will be difficult to take account of catastrophes caused by irregular human action. None the less, the calculations in their present form may be valuable up to the point where the number of larvae and adults reaches a few hundred or perhaps a thousand, for the method at least gives one the maximum figure to which a population might increase under certain defined circumstances.

2. Constitution of a Population of Lice. It is possible to take the crop of hair of a human being (removed from the scalp with a razor), dissolve it in sodium sulphide and an alkali and recover whatever lice it may contain. This method has already given information about the constitution of normal populations of head lice and about the distribution of these parasites among populations of human beings, in several parts of the world (Buxton, 1936, 1938*b*, 1940*b*, 1941*b*). Very often it is impossible to remove the whole crop of hair and dissolve it. Results which are apparently reliable may be obtained by the use of a fine comb, provided it is carefully done (Mellanby, 1942*a*). Roy and Ghosh (1944*a*, *b*) killed lice with pyrethrum extract and then combed them out and counted them.

One of the interesting things discovered by these methods is that the number of male and female *Pediculus humanus capitis* in a single crop of hair is generally very far from equality. This inequality of the sexes in a natural population is not unexpected, for it will be remembered that the family of a monogamous female is often nearly unisexual (page 49), and some of the wild populations may be the descendants of a single pair. The effect of this inequality must often be that the population is in danger of dying out, particularly if the human host succeeds in destroying nearly all his parasites. This has also been observed in experimental work: a particular strain of *corporis* tended to an excess of males and brought itself close to extinction by producing 190 males to 3 females (Buxton MS.).

In a single natural population of head lice, studied by the method described above, either males or females may be in excess. Even

in a group of heads from one place, either sex may preponderate, and the difference from a 50 : 50 ratio may be statistically significant: for instance in groups of heads from six places, the percentage of male head lice ranged from 38·5 to 56·8 (Buxton, 1941*b*). In one particular large collection (from 125 infested heads, from Colombo jail, Ceylon), there was a marked change in sex ratio with increasing numbers of lice. This phenomenon is well shown in Table 3 and

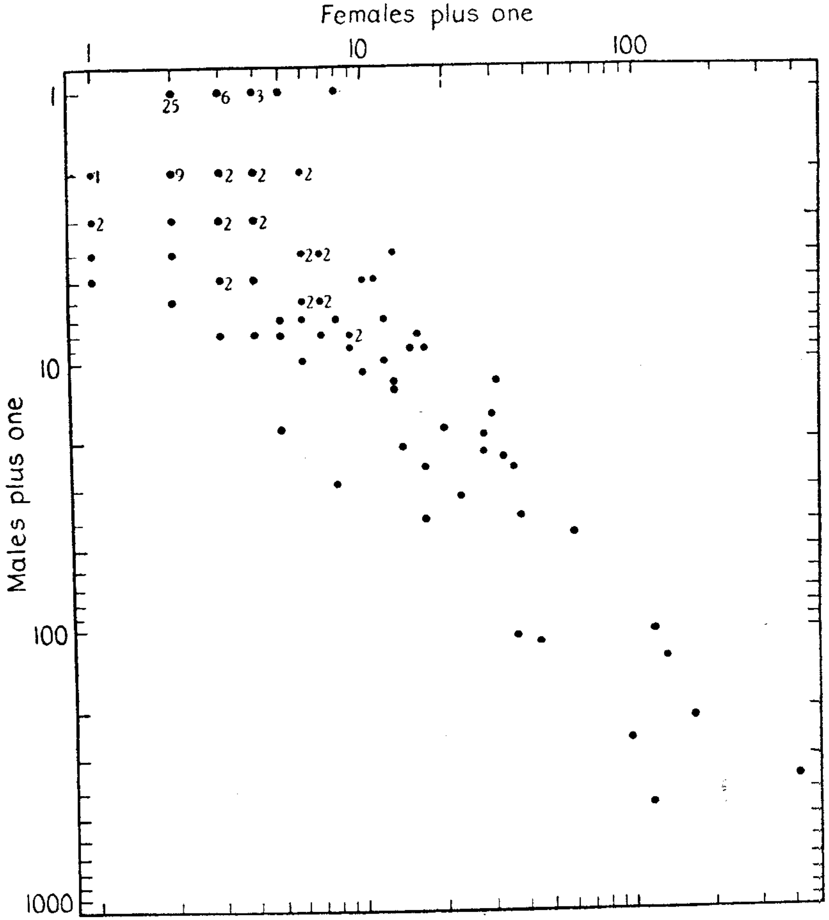

FIG. 37.—Showing the number of male and female lice on heads from Colombo, Ceylon. The scale is doubly logarithmic, for the sake of compactness. It shows the number of males and females *plus one*: this is necessary because there are many heads in which one sex is not represented (e.g. 2 ♂♂, 0 ♀♀), and zero cannot be shown on a logarithmic scale (Buxton, 1941*b*).

figure 37. In the largest populations (with over 100 adult lice) the excess masculinity was consistent and not attributable to chance. (P is less than one in a million.) Unfortunately we have no comparable data from other localities, for high counts (over 100 adult lice per head) are generally very unusual. It is not therefore known whether this change of sex ratio with density of population is of general occurrence. It seems probable that in a dense population any given female pairs at frequent intervals and that this is harmful to her, shortens her life, and thereby reduces the proportion of females in the population. This is supported by experimental work, for if one confines a single young female (*corporis* was used in these experiments) with six or more males in a gauze-bottomed box, she dies in a few days, having laid very few eggs; paired with a single male she would have lived more than a month and laid several eggs a day. The length of life of males is not affected by crowding, nor is it unfavourable to the female unless she is quite young (Buxton, 1940*a*).

TABLE 3

SHOWING THE NUMBER OF MALE AND FEMALE HEAD LICE ON 125 INFESTED HEADS IN COLOMBO JAIL (Buxton, 1937)

Adult lice per head	No. of heads	No. of lice		Males per 100 females
		Male	Female	
1–2	49	20	46	43·5
3–10	32	85	101	84·2
11–25	22	166	198	83·8
26–100	13	307	310	99·0
101 and up	9	1,768	1,179	150·0
Totals	125	2,346	1,834	127·92

One might sum the matter up by saying that if a single pair of lice colonize the head of a complacent host, the insects may die out because the progeny are unisexual or nearly so. If, on the other hand, they establish themselves, they will tend to increase on a ratio approaching the geometrical, until the population becomes dense, when there will be a tendency for the females to die young and lay few eggs. The population would then drop to a level at which this no longer occurs, after which it may continue to fluctuate indefinitely. When the population is dense the males act on the females rather as enemies: their effect is little or none in a sparse population, and proportionately greater as the density increases. It should, however, be stated that there is no evidence that this occurs in body lice in nature. MacLeod and Craufurd-Benson (1941*b*) examined 229 sets of lousy underwear in London, and counted over 16,000 lice. They find no evidence that sex ratio is a function of louse population. If this is confirmed elsewhere the explanation may be that the body louse roams over a larger area than the head louse, so that the young female body louse does not meet a male so frequently as to harm her.

There are very few records of the sex ratio in separate populations of body lice (*corporis*), but they show that either sex may predominate greatly. MacLeod and Craufurd-Benson (1941*b*) examined 1,736 adult body lice, derived from garments of many different men in the East End of London and found 1 male to 1·27 females. As to head lice (*capitis*), Roy and Ghosh (1944*a*) collected 8,700 adults from 67 heads and found only 23·3 % of males, or 3·28 females per male.

It is my belief that the study of the number of larvae per adult, or per female, in natural populations, will eventually yield valuable information about larval mortality: but we are not yet able to use such facts as we possess, so that the subject may be dismissed briefly. A large amount of fact has been analysed by myself (Buxton, 1941*b*). Taking the facts from 733 infested heads from five places, with over 2,000 females and 14,000 larvae, one found that the mean number of larvae per female in different places ranged from 5·4 to 10·9. The differences were statistically significant. No cause to account for them could be discovered. Other ratios for head lice are recorded by Mellanby (1942*a*), Roy and Ghosh (1944*a*); for body lice MacLeod and Craufurd-Benson (1941*b*). We have as yet no knowledge of the cause of these differences, though a number of possible factors have been considered and excluded. In one small part of my material the larvae were tabulated by instars, and it was found that the death rate was much higher in the third instar than in either the first or second.

3. Distribution of Lice in a Human Population. By dissolving the whole crop of hair of the scalp it has been shown that infestations of ten or fewer *capitis* per head are commonest, but counts up to a hundred, a thousand or even higher occur though rarely. Table 4 illustrates the type of distribution that appears to be characteristic (Buxton, 1936, 1938*b*, 1940*b*).

The largest collection was that from Cannanore, 1,437 individual crops of hair of which 543 were positive. A good deal of attention was given to the study of these figures, with rather disappointing results (Buxton, 1940*b*), but it was established that, as in other collections, there is a high positive correlation between weight of hair, and rate of infestation, as Table 6 shows. As the man's age rises there

TABLE 4
Frequency Distribution of Head Lice in Infested Heads

Place	No. of heads	Total infested heads	Percentage of heads			
			Without lice	1–10	11–100	101 lice and up
Sokoto	409	42	89·6	7·6	2·2	0·5
Nairobi	415	37	91·0	5·8	2·9	0·2
Kakamega . . .	359	90	74·9	10·9	11·7	2·5
Colombo * . . .	240	125	47·9	33·8	14·6	3·7
Lagos	102	21	79·4	6·9	8·8	4·9
Cannanore, Malabar Coast	1,437	543	62·2	24·7	12·0	1·0

* Only adult lice are counted; figures from other places include adults and larvae.

is a tendency for infestation to be less frequent, but this is probably to be explained by his having less hair. There are large differences between religious groups (Hindus, Moslems, Christians), in part but not entirely due to differences in weight of hair. It would be a matter of great interest to pursue such studies as these in relation to social, religious and anthropological groupings.

Dr. C. B. Williams (1944) has gone further in the analysis of my figures from Cannanore. Taking Hindus only, for sake of uniformity, he shows that the number of men with 1, 2, 3 . . . lice per head forms a hollow curve (bottom of figure 38). The curve seems to resemble a hyperbola: the formula for that curve would be $n_1, \frac{n_1}{2}, \frac{n_1}{3}$ . . . where n_1 is the number of heads with one louse. On further examination, however, the figures were found to fit much more closely (as figure 38 shows) to a logarithmic series worked out by Fisher and Williams for a different purpose. In this the number of heads with 1, 2, 3 . . . lice is represented by $n_1, \frac{n, x}{2}, \frac{n, x^2}{3}$ . . . where x is a constant for each particular series, always less than unity. The values of x and n, and hence every member of the series, can be readily calculated if the total number of lice and of infested heads is known.

It is interesting to compare my data from places in Africa and Asia (Table 4) with those collected by Mellanby in England (1941) particularly as his technique was entirely different: he had access to the records of 60,000 admissions to fever hospitals in England, where children's heads are carefully combed on admission. His results for the industrial cities (including all those in England with over 400,000 inhabitants) are given in figure 39. The figure shows a much higher rate of infestation than had previously been admitted.

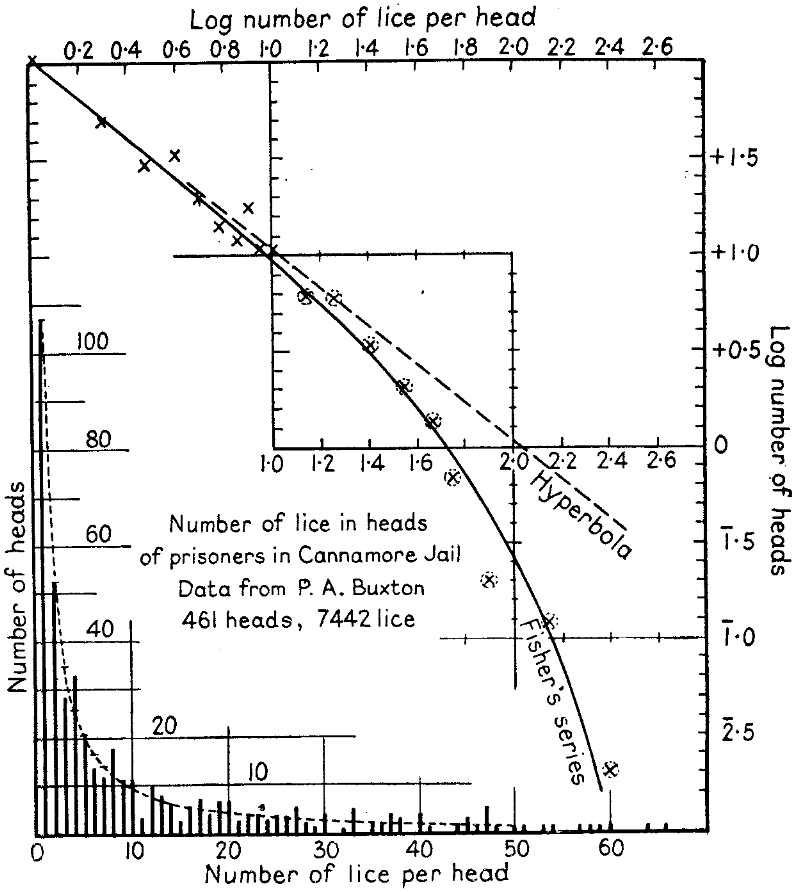

Fig. 38.—Lower part of figure, number of lice per head (Hindu prisoners, Cannanore Jail, India). Upper part of figure, attempt to fit the above, on a doubly logarithmic scale, to a hyperbola, and to Fisher's logarithmic series (Williams, 1944).

Girls are more frequently infested than boys, the difference increasing with age after four years old: the highest rates are in the pre-school groups. He also showed that in rural areas of England the rates of infestation are much lower, less than 5% of children being infested.

In a second paper (Mellanby 1942*a*) attention was concentrated on louse counts from one industrial city in northern England, and 93 infested heads were studied. Two-thirds of the infestations were light (under ten lice): girls were more heavily infested than boys. A point of interest is that though so many infestations were light they had probably been established some time, all stages (eggs, larvae and adults) being found in 79% of heads, and nits being found at some distance from the scalp.

The figures published by Roy and Ghosh (1944*a*) were based on refugees who had undergone very great privation in escaping from Burma into India. The work is of great interest, because no comparable information exists from any other part of the world, relating to really heavy mass infestation. The total number of heads examined was 67, rather a low figure especially in view of the fact that the people were heterogeneous in age, race, sex and so forth. But it is clear that the counts were very high, and that the commonest value was very much above unity: the *average* count was 130 adults and 418 larvae. Another point of interest is that the patients had been "clean" and living normal lives till three months before, so that this very heavy infestation had built itself up within that period.

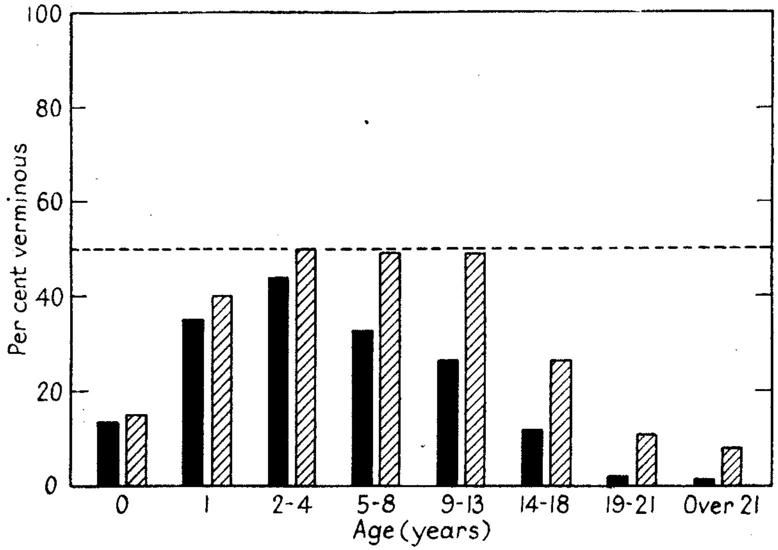

FIG. 39.—Incidence of head lice in industrial England, by persons' age and sex; black, boys and men; striped, girls and women. Data based on over 50,000 examinations, from the large industrial cities (Mellanby, 1941).

Peacock (1916) gives facts on the distribution of body lice among British troops on active service in France. Peacock gives graphs for the number of lice per shirt and per man; in each of them the mode (i.e. the commonest value) is between 1 and 10, and the frequency falls regularly but very gradually, high counts being occasionally found; for instance, among 306 shirts, 14 were found to contain more than 100 lice, the maximum being 700, and among 143 men 8 carried more than 100 lice, the highest figure being 900. MacLeod and Craufurd-Benson (1941*b*) have counted lice in more than 200 sets of infested underclothing in the East End of London. They find that a count of one louse per garment is commonest, but on two occasions they had counts exceeding 1,000.

The biologist is not generally interested in record breaking, but one may want an approximate idea of the number of lice on a very heavily infested person. Nuttall quotes 3,800 body lice as being a very unusual figure, and mentions a paralytic person from whom he recovered 1,004 head lice, of which 208 were adults. Peacock's results have just been quoted. In my own work on head lice I have recovered 1,286 adults and larvae from Lagos, and 774 (adults only) from Colombo. But in my largest collection, from Cannanore, in 543 infested heads the highest count was 385 lice. Roy and Ghosh (1944*a*) dealt with refugees who had undergone great privation. Their highest count was 1,434 adult head lice, on a woman with short hair. In view of the very large number of heads examined one may conclude that figures in excess of 1,000 larvae and adults are very unusual, though they occur.

It has also been shown that those parts of a human population which are most frequently infested are also those in which the number of head lice per host is highest. This has been found in data from several parts of the world, the people being grouped by age. The figures given in Tables 5 and 6 illustrate this.

Statistical tests show that the fall in the percentage infested as age rises (Table 5) cannot reasonably be attributed to chance; inspection of the figures also shows that whereas in the children more than 20% were infested and infestations of more than 11 lice were common, in the last two groups (the adult men) the percentage infested was only three or four, and all the infestations were very light. The same principle obtains in Table 6. Here the men with heavier crops of hair are more frequently lousy: they are also the group in which the higher louse counts are more prevalent. A similar general law holds good if one divides the population in other ways. For instance, women at Lagos, Nigeria, are more commonly and also more heavily infested than men. This general rule is in no way surprising, but it is only recently that it has been demonstrated.

TABLE 5

FREQUENCY DISTRIBUTION OF HEAD LICE, BY AGE OF HUMAN BEING, FOR MALES AT SOKOTO, NIGERIA (Buxton, 1938*b*)

Age. Years	Total heads	Number of heads with			Approx. percentage infested
		No lice	1–10 lice	11 lice and over	
6–10	53	42	5	6	21
11–15	140	124	14	2	11
16–20	87	77	7	3	11
21–30	68	65	3	0	4
31 and up	58	56	2	0	3
Totals	406	364	31	11	10

TABLE 6

FREQUENCY DISTRIBUTION OF HEAD LICE, ACCORDING TO WEIGHT OF CROP OF HAIR ; HINDU PRISONERS, CANNANORE JAIL

Hair grams	Number of heads with			Total heads	% infested
	Nil	1–10	11 lice and up		
Up to 9·9	217	47	9	273	20·5
10 to 19·9	203	112	41	356	43·0
20 and up	192	145	107	444	56·8
All weights . . .	612	304	157	1,073	43·0

As the head and body louse tend to inhabit different parts of the body the same conditions do not always favour their multiplication. Troops on active service in 1914–1918 became much infested with body lice, and it required a considerable organization to deal with the matter. But it seems that comparatively few infestations with head lice were seen, and that no particular effort was required to prevent the spread of this insect. On the other hand the head louse is much more abundant in Britain at present. To take another example, in N. Nigeria, as has already been shown, boys tend to be more infested with head lice than youths, who in turn are more infested than men. But small boys are naked and almost entirely free of body lice, whereas adults, particularly Hausas, are heavily clothed when money permits, and notorious for their populations of body lice. Malaya provides a similar example. Body lice appear to be non-existent, perhaps because Malays are so scrupulous in washing clothes, but head lice are abundant (Gater, 1932).

Many factors influence the distribution of the head louse among a population of human beings. It is known for many parts of the world that children are more infested than adults, and young males more than grown men. In many places also girls and women are more heavily and frequently infested than boys or men. Sobel (1913) pointed out that in New York City the infestation rate in boys' schools ranged from 1·5 to 6%, in girls' schools from 10 to 28% in the period from 1909 to 1912 (see also figure 39, and Mellanby (1941)). But the distinction is not invariable, and there are places in which the sex of the human being appears to make no difference. Race is also a factor, long-haired people tending to be more infested than short-haired Africans ; there is a tendency within one sex, race or age group for the weight of hair to be greater in the infested that in the non-infested. In general, most of these differences may be attributable to local customs and social standards, and to such unmeasured things as the use of cosmetics and soap, or the care that mother gives to child, etc.

As might be deduced from the insect's biology, there is a strong tendency for infestations to spread through small groups of people, so that the members of a family, or men living closely together in a ship or tent may quickly infest one another. It is perhaps partly for this reason that in a certain English population, the head louse is more frequent, both in boys and in girls, the larger the number of children in a family (Mellanby, 1942*b*). The distribution through a human population is very far from random.

Apart altogether from general differences characteristic of particular groups of people, there is a large personal factor. The subject is difficult and much neglected, but it is known that some individuals react much less than others to the bite of *Pediculus*, which may make them careless ; if facilities for washing and changing are not available, these individuals may even be ignorant of the fact that they are infested. In addition, it should be remembered that destitution, disabling illness, feeble-mindedness, etc., will tend to a person becoming or remaining infested, whereas qualities such as self-respect or vanity would perhaps have the opposite effect. The recent work of Rollin (1943) has done a little to add precision to a part of this " social " problem. Recruits for one of the women's services were received at a depot, tested for intelligence and examined for lousiness. The records of some 600 (about half of them lousy) were studied: those with the lowest score in three separate intelligence tests tended to be the most frequently infested.

Mellanby (1941) made an investigation on the incidence of the head louse in England (above, page 62), and repeated the work in the early years of the war in certain areas previously investigated (Mellanby 1943); the second investigation covered the four years 1940–1943. His conclusion is that conditions in the war period had scarcely altered the incidence, which is still determined by such factors as age, sex and place. There is, however, a rise in the rate in women over eighteen years; this one might perhaps associate with living away from home and working in factories, the large number of women in the armed forces being excluded from the examination. It is discouraging to see no improvement in spite of more attention given to the louse, and its successful reduction by the thiocyanate insecticides (page. 109).

The general abundance of the louse (either *capitis* or *corporis*) in human communities no doubt differs enormously in different parts of the world. There is a general tendency for these insects to be most widely distributed among poorer classes and among those whose hygienic standard is lowest.

4. Seasonal Distribution. The cardinal fact is that conditions of temperature and humidity on the surface of the human skin tend to stability; man's internal temperature is constant, and by the use of houses, clothes and artificial heat he can generally produce conditions which are regarded as comfortable. Man's power of controlling both temperature and also humidity, at least on the clothed parts of the body, is well brought out in some data collected at different seasons in S.W. Iran. Readings of temperature and humidity were made beneath the clothes of a sedentary worker in the cool season and in the height of the extremely hot, dry summer. The results are shown in figure 40, those obtained on different days being given separately. It will be seen that though the conditions of temperature and humidity in the room differed very greatly, those beneath the clothes tended to be nearly the same. The following means are derived from the same collection of data:

	Temp. ° C.	Saturation deficiency mm. Hg.
Beneath shirt, February	28·9	16·4
,, ,, Summer	31·0	19·4

The range of conditions in the room was about three to four times as great as it was beneath the clothes; in the open air it would have been greater still (Marsh and Buxton, 1937). A similar result was obtained by a worker who investigated conditions beneath his clothes while sitting in rooms with temperatures from 0–41° C. (32–92° F.) and a wide range of humidity (Mellanby, 1932).

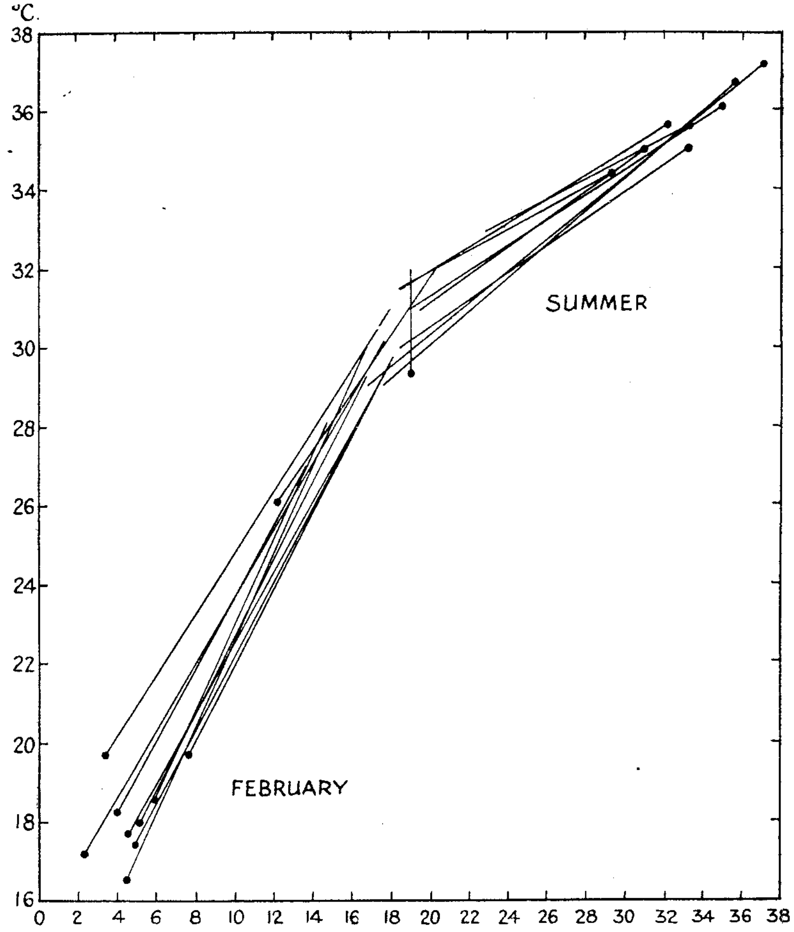

FIG. 40.—Showing conditions of temperature and saturation deficiency, in the laboratory and beneath the clothes of a man doing sedentary work, in S.W. Iran at two seasons of the year.

Each line connects two simultaneous observations, the black circle showing conditions in the laboratory, the other end of the line those beneath the clothes. (*After Marsh and Buxton.*)

From this and similar work it is clear that the environment in which the body louse normally lives is stable; it seems probable that even a specimen of *capitis* on a bare head is not exposed to a great range of temperature, because man's control of his temperature will prevent the surface of the skin reaching very high or low figures. One would therefore anticipate that in many parts of the world there would be no seasonal difference in infestation, and this is found to be true of head lice in the equable climates of Lagos, West Africa and Colombo, Ceylon. But in countries with sharply contrasted seasons, in spite of man's power of stabilizing conditions on the skin, some differences in infestation have been found. Facts have been collected at Agra, India, about the prevalence of body lice on prisoners on admission to jail (Cragg, 1922*a*). It was shown that in February, March and early April most men were infested, and the number of lice was generally high, but in the second part of April and May, that is to say in the extremely hot, dry weather before the monsoon, infestations were both few and light. My figures for head lice from Cannanore on the Malabar Coast do not show any clear seasonal difference, though very carefully examined and tabulated (Buxton, 1940*b*). This is remarkable, for the climate differs greatly from season to season, and the material was collected for twenty-four consecutive months. It has also been found that the body louse is rare in Iran and in Iraq at the height of summer, a season of very high temperatures and low humidity; this relative scarcity of the insect in the rainless summer is believed to occur throughout the Mediterranean region. One may wonder to what extent fluctuations in the louse population are due to the effects of climate on the insect or its egg, and to what extent on human habits, and therefore, indirectly, on the chances of the louse spreading from man to man. Admitting that in the Mediterranean countries and Iran the insect is generally more common and more generally distributed in the cold, rainy winter than the hot, dry summer, may this not be due to people sitting indoors in close contact and wearing many clothes in the winter? It would appear that the insect's seasonal distribution is closely linked to human activities and may well be influenced by recurrent annual events in the social, agricultural or religious life of a people.

Very few facts are available from temperate countries. In the year 1908 a careful examination was made of beds in common lodging-houses in London, of which more than 500 were examined weekly during the year. The percentage in which lice were found was highest (31%) in February, consistently low in the summer months, and lowest (12%) in June (Hamer, 1909). It is difficult to interpret figures such as these and to know whether they give an indication of the insect's abundance or whether rather they reflect its powers of wandering, or of living away from its host, under different temperature conditions at different seasons of the year. MacLeod and Craufurd-Benson (1941*b*) examined more than 200 infested undergarments from men living in common lodging-houses in London, in the period December to April: they could not satisfy themselves that there was a seasonal factor in rate of infestation.

Mellanby (1941) has tabulated results of some 60,000 examinations of heads in English cities. He does not find any clear evidence that the rate of infestation is seasonal.

5. Geographical Distribution. Inasmuch as man stabilizes climatic conditions on his surface, one would expect that *Pediculus humanus* would have a very wide geographical distribution. This is indeed true: Ferris (1935) states broadly that he has collected "innumerable records from every race of man in every part of the world." Going rather more precisely into the matter, one may observe that *Pediculus* is recorded from many temperate lands, in Europe, Asia, America and Australia; also from extremely dry climates in Iraq and the Sahara; also from constant equatorial conditions, such as those prevailing in Ceylon, Assam, the Congo and Tahiti; also from countries with an extreme monsoon type of climate, such as the north of Nigeria, the Sudan and Northern India; also from the Eskimos inhabiting the Arctic. It seems, indeed, that there are no parts of the world from which the insect is naturally absent. Even where it is known that lice are very rare or absent, this may generally be attributed to human habits rather than to the climate; thus it was shown in the examples quoted above (page 66) that there are countries in which conditions are unfavourable to the body louse and not to the head louse, or *vice versa*. One may therefore conclude that the local absence of *P. humanus* (whether *corporis* or *capitis*) is generally due to social or hygienic rather than climatic or geographical causes; we do not know of any part of the world or any type of climate in which head and body lice cannot exist and multiply.

6. Relation to Nutrition of Host. It is an old observation that when domestic animals are in poor health and badly fed, particularly at the end of winter, they tend to be lousy (though this, if true, would not indicate that lousiness is a result of malnutrition, but rather that the two may often follow neglect). This has perhaps been carried a little further by observations on the lice (*Polyplax spinulosa*) of laboratory rats. The first note on this subject (György, 1938) indicated that rats became extremely lousy if they were kept on a diet deficient in riboflavin, and that this did not occur to rats on other deficient diets (including many deficient in vitamin B_6). The author did not regard the infestation as due to diminished vitality, indeed he records with surprise that "the majority of the rats with pediculosis were by no means weakened and inactive." He says that "administration of riboflavin by