LICE

By G. H. E. Hopkins

Lice have been known since time immemorial, particularly as parasites of man. They are mentioned in the Bible as one of the plagues of Egypt (as they still are today) and there is no doubt that they have been attached to man since man himself has existed. Even the fact that other animals possessed lice was known to Aristotle, who lived in the fourth century B.C. But the subject was regarded until comparatively recent times as rather a disgusting one, unworthy the attention of a scientist, so that for many centuries writers confined themselves to repeating fables and fantasies about lice instead of finding out the facts. Some of these fables, derived from Aristotle, held sway for more than two thousand years, among them being his statement that lice were reproduced by spontaneous generation from pustules in the flesh ; they laid eggs but these eggs did not hatch. This story was contradicted, by an Italian physician named Redi, in a book published in 1668, yet it held the field so tenaciously that as late as 1838 an entomological book admitted the possibility that lice might arise from spontaneous generation in certain conditions.

The mediæval churchmen (and some a good deal nearer to our own times) found the existence of lice rather a difficulty, though they managed to extract some good sound morals from the fact. A nineteenth century English clergyman found it incredible that "man in his pristine state of glory, and beauty, and dignity, could be the receptacle and prey of these unclean and disgusting creatures", so he put forward a theory which postponed the creation of lice until after the fall of Adam. The Church seems to have regarded the mythical fate of being devoured by lice as a death so awful that it must be reserved for the worst of criminals, so we find stories crediting with this fate prominent heathens, persecutors of the Church, corrupt bishops, heretics and those who did not believe in miracles. This was, perhaps, a little inconsistent with the belief, also held for many centuries, that an extreme state of filth, often exemplified by lousiness, was a sign of holiness, but the ultra-religious of all ages and creeds have never been remarkable for consistency. Aristotle's statement that the ass (alone among mammals) had no lice also had to be accounted for, and a really pleasing explanation was found : it was a reward for the part played by the ass in Christ's triumphant entry into Jerusalem. One rather wonders what would have happened to the man of mediæval times who was bold enough to examine an ass and see for himself that it does have lice, but no doubt anyone enterprising enough to do this would also have been sensible enough to keep his findings to himself, and (if he did not) why should we worry about the fate of anyone so foolhardy and swollen with pride as to deny the statements of Aristotle ? Other beliefs about lice were that they were created by God to punish man for arrogance and that their bites were the work of the devil – the latter a belief for which one can still feel a certain amount of sympathy. It is, perhaps, necessary to add that the reason why so many of these fables originated with churchmen or have a religious flavour is that in mediæval times all education was concentrated in the hands of the Church ; there is

little doubt that equally ridiculous stories would have been invented by educated laymen had such existed at a time before it was accepted that the best way to find out the facts is to test them for oneself instead of regarding the statements of ancient authors like Aristotle as being incontrovertible.

Redi's book, published in 1668, marks the beginning of the end of the period of fables about lice, and the start of real knowledge. He must have been a remarkable man, for he not only made the observations which enabled him to state that lice, like all other insects, are hatched from eggs, but established the fact that most mammals and birds have lice peculiar to themselves, and gave us a number of drawings of these insects, many of which are quite easily recognisable. After him, however, the disgust with which the subject was regarded again hampered progress, and it was not until one hundred and fifty years later that there was any real advance in our knowledge, and not until 1842 that the first monograph on lice was published by Denny, an English clergyman. Even Denny thought it necessary to find religious reasons for the study of such a disgusting group of insects. This unreasonable attitude persists even today to some extent, and I doubt if there are in the world more than a score or so of serious students of the lice, excluding those who are solely concerned with the handful of species which infest man and his domestic animals. But to the true entomologist no insect is unworthy of study, and to those who love them the lice reveal themselves as among the most interesting of this intensely interesting class of animals.

We have followed lice through fable and fantasy to the beginning of the realm of fact, so now let us see what they are and what they do. The first essential is to rid ourselves of the idea that the lice which infest man are the only ones of any interest or importance. There are two or three thousand known species of chewing lice and two or three hundred known sucking lice, and these must be only a small fraction of the species which exist. To take an example, the chewing lice of African antelopes and carnivora are among the best known of all groups of lice, yet we only know the lice of about fifty of the one hundred and forty or so African species of these groups of mammals. It is in a neglected group like this that one has the best opportunities of adding significantly to the sum of scientific knowledge.

The insects are divided into two main groups, a more primitive group (of which cockroaches, bugs and termites are familiar examples) in which the young resemble the adults in most respects and feed on the same sort of food, and a more specialized group (exemplified by butterflies, bees and flies) in which the young stages are caterpillars or grubs, quite unlike their parents and often feeding on totally different food so that a resting-stage or pupa has to find a place in the life history to allow of the great change-over from one type of food to the other. The lice belong to the more primitive of these two divisions, their young stages living exactly the same sort of life as the adults except that they do not indulge in the pleasures of sex. All lice are wingless, but their winglessness is certainly secondary because they are descended from the same stock as the *Psocoptera* or book-lice (which, in spite of their English name, are not lice), many of which possess wings. The true lice are divided into two main sections, the *Mallophaga* (or chewing lice) and the *Anoplura* (or sucking lice), of which the *Mallophaga* are the more primitive.

The biology of both these groups is similar up to a point: all lice are parasitic on mammals or birds, the female lays a large number of eggs which are glued to the feathers or hair of the host, the life of the insect is rather short (about six weeks), and they never willingly leave the body of the host. But the food is very different in the two main groups – the *Mallophaga* or chewing lice feed (with a few exceptions) on the hair or feathers of their host while the *Anoplura* or sucking lice feed exclusively on blood. Some of the exceptions are of considerable interest: one group of *Mallophaga* lives exclusively inside the pouch of pelicans and related birds, where it presumably must feed on blood or mucus, while some other species bite a hole in the base of a quill-feather and live inside, feeding on the "pith" of the feather. Sexual reproduction is the almost invariable rule in the lice, but it has recently been definitely proved that parthenogenesis (or virgin birth) is normal in at least one species of chewing louse.

The way in which the parasitic habit of lice originated is easy to imagine. The *Psocoptera* or book-lice feed on dead animal or vegetable matter such as bark, dead leaves, books (which are, after all, only dead leaves), hair or feathers; some species are very common on hides and skins, and the step from eating the hair or feathers of a dead animal to eating the hair or feathers of a living host is a very small one. Some ancestral book-louse happened to find itself eating the hair or feathers of a living animal instead of a dead one; deciding (metaphorically speaking) that it was on to a good thing and that there was really no need to leave such a rich source of food and warmth and go out into a cold hard world to forage for itself, it laid its eggs on the hair or feathers of its host and became the ancestor of the *Mallophaga*. Not long afterwards by geological standards (perhaps ten or twenty million years) some enterprising chewing louse whose host had been in a fight started to lick up the blood and found it good; the taste for blood persisted in its descendants, their mouth-parts began to lengthen and became more delicate – less and less useful for chewing feathers or hair, and more and more suitable for piercing skin and sucking blood – and that was the origin of the sucking lice.

Lice may occur in enormous numbers on an individual host. There is a record of over ten thousand of them being found on a single shirt, and it is recorded of Thomas á Beckett that he was so lousy that after his murder his hair-cloth garment "boiled over with them like water in a simmering cauldron" and the onlookers "burst into alternate fits of weeping and laughter, between the sorrow of having lost such a head and the joy of having found such a saint". Lousiness is (I think) no longer regarded as a sign of holiness, but old ideas die hard – not very many years ago a recent immigrant from Europe, knocked senseless in an accident in the streets of New York, taken to hospital and there deprived of his lice before being admitted, later tried to sue the hospital authorities for having destroyed his luck.

The chewing lice normally do little harm to their hosts unless they are present in great numbers, but if this is the case they may cause great irritation by their wanderings about the host's body and may cause serious loss of condition, or even death, among poultry or other domestic stock. Any insect which feeds on blood is liable to carry disease, and the *Anoplura* or sucking lice are deservedly famous in this connection. Leaving aside the diseases they convey to mammals other than man, they carry to man the organisms

of a number of diseases of which typhus is by far the most dreaded, and rightly so, for it is one of the worst scourges with which mankind has ever been afflicted.

Typhus (and therefore the louse which carries it) has many times affected the course of history, for war, pestilence and famine have been grim associates since written history begins, and "pestilence" (in fairly modern times at least) has commonly had typhus as its most important component. In the earlier records of written history the evidence against the louse is not clear ; such world-shaking events as the collapse of Rome, with the consequent centuries of anarchy and the eclipse of learning in Europe, were brought about largely by epidemic diseases, but there is no proof that typhus was among these plagues. The first definite severe outbreak of typhus in Europe was in 1489 (though the disease was probably present much earlier), but from then until the present day typhus has claimed far more victims in Europe than its friendly rival, the sword, and on more than one occasion typhus has snatched the victory from both rival armies. In 1556 a campaign of Maximilian II against the Turks stopped short when his army was dispersed by typhus, and during the thirty years' war in Germany the armies of Gustavus Adolphus and Wallenstein, about to engage in battle for Nuremberg, were both attacked by typhus and were routed by the disease, leaving behind them eighteen thousand of their comrades, slain by the bite of the louse. One of the most striking cases of a victory won mainly by the louse and typhus is the defeat of Napoleon's invasion of Russia in 1812, which was frustrated far more by the ravages of typhus, aided by dysentery, than by the efforts of the Russians, who fought no really decisive battle but retreated and left the issue largely to the louse and the fly. These allies served the Russians well – typhus began to appear at the time that Napoleon's armies crossed the Niemen, at the very outset of the campaign, and by the time of the retreat from Moscow not more than eighty thousand men (out of nearly half-a-million who had crossed the river) remained fit for duty. Then the climate stepped in, effectively seconded by typhus and the Cossacks, and of Napoleon's mighty armies only a miserable remnant, practically every man of which was typhus-stricken, escaped alive out of Russia. In recent history, too, the louse has played no small part : during the Kaiser's war (1914–18) typhus slew one hundred and fifty thousand in less than six months in Serbia, and during the years 1917 to 1923 it is estimated that, in European Russia alone, typhus claimed thirty million victims, of whom three million died. It is too early yet to assess the part played by the louse in Hitler's war, but we know already that typhus slew huge numbers of people in Poland and other parts of eastern Europe. Historians usually lay little stress on this side of war ; they tell us that General This by his skilful strategy defeated General That, but they do not tell us that the real victor was General Louse ; will they fail to record the fact that the victory of the democracies in the war just ended was won very largely (and against the Japanese overwhelmingly) because of the efficiency of our sanitarians, chemists and entomologists ?- Fortunately we can end this section on a cheerful note, for it seems likely that man is now about to achieve final victory in his war against the louse and typhus. A most powerful new weapon (D.D.T.) has been put into our hands, and I believe that the day of the louse as a dangerous enemy of mankind is almost done.

Let us, however, do justice to our enemy, for even the louse of man is not without its uses. In mediæval England, and in some other countries even today, lice were eaten as medicine, particularly against jaundice, and the louse deserves to be the patron saint of wig-makers, because the custom (almost universal among the ruling classes of western Europe in quite recent times) of shaving the head and wearing a wig was almost entirely a means of defence against lice. Another use for lice was discovered by the inhabitants of a certain Swedish town who, in mediæval times, used to elect their Mayor by seating the candidates around a table with their beards resting on its surface, placing a louse in the middle of the table, and declaring elected the candidate in whose beard the louse took refuge. Yet another unusual use for lice is recorded by a traveller in northern Siberia who, on enquiring why young women came into his dwelling and threw lice at him, was told that this was the customary method of making a declaration of love. It seems a pity that picturesque old customs like these should be allowed to fall into disuse.

But a natural interest in the louse of man has rather led us away from our subject, which is lice in general, so let us consider next the enemies of lice. These enemies are rather few. Ants are known to destroy them and the habit of certain birds, which sit with outstretched wings on ant-hills or pick up ants with their beaks and place them among their feathers, is believed by some writers to be an attempt on the part of the birds to use the ants to destroy the lice ; man has certainly employed this method, for in more than one campaign soldiers have spread their shirts out on ant-hills to give the ants a chance to destroy their louse population. Tick-eating birds, such as the ox-pecker, also destroy a certain number of lice. Parasites of lice include a few fungi and the organisms of louse-borne diseases ; the latter are of great importance because typhus (for instance) is even more fatal to the louse than to man. But there is little question that the worst enemy of a louse is its host. Birds take dust-baths largely to rid themselves of lice, and mammals probably rub themselves against trees, take mud baths, or scratch themselves, partly for the same purpose. Man, of course, has devised scores of means of getting rid of his irritating lodgers, from picking them off and cracking them between his teeth to the use of D.D.T., but the only one I propose to mention is used by the peasants of Ruthenia, who put their lousy garments on a horse : the lice are attracted on to the horse by warmth, but are unable to survive on a host so distantly related to their normal source of food.

One of the peculiar points about lice is the degree to which they are specific, that is to say, the way in which each species of louse (in the vast majority of cases) is found on one species of host (sometimes on several very closely related hosts) and not on any others. This narrowness of choice of host is extremely marked : I have collected chewing lice from twenty species of East African antelopes, and in only one case – that of the closely related bush-buck and sitatunga – have I found the same chewing louse on two different species of antelopes. The same principle applies to the sucking lice of mammals and also to the lice of birds, to the extent that one can quite frequently identify a host from its parasites, without ever having seen the host itself. On one occasion I startled a correspondent in the Congo, who had sent me some lice from a "cochon" by telling him that the pig in question

was neither a bush-pig nor a wart-hog, but a domestic pig, and on another occasion I was able to tell another correspondent "On the day you shot the wood sandpiper you also shot a painted snipe and took them home in the same bag" (the reason being, of course, that I had found in the batch of lice from the sandpiper a small number of painted snipe parasites). On both occasions the correctness of my attempts to emulate Sherlock Holmes or Dr. Thorndyke was confirmed by my correspondents.

This close specialization for life on a single host is the most interesting point in the biology of lice, and is in marked contrast with what one finds in other groups of parasites, such as fleas or ticks, in which it is normal for the same species of parasite to infest a wide variety of hosts. Such specialization has considerable advantages for a parasite, and it is of interest to consider why the lice have been able to adopt it, while the fleas and ticks mostly have not. The reason is the difference in habits as regards egg-laying : lice lay comparatively few eggs and glue them to the feathers or hairs of their hosts (which they never willingly leave) so that the young louse has access to food and suitable conditions of life from the moment it hatches from the egg, whereas ticks and fleas drop their very numerous eggs on the ground and the newly-hatched young has to find a host for itself – if its choice of host were very restricted it would hardly ever be able to find one. Because lice never willingly leave their host, and are absolutely dependent on it for food and shelter, the death of the host normally means the death of its entire louse-population; if lice were not confined to a single host it is possible that an occasional individual might manage to transfer from a dead host to a living host of another species, but the extra chance of survival thus gained would be so remote that it would be of no importance to the louse-species.

Since lice spend all their life on the body of the host, how do they get transferred from one host to another ? The best opportunities are during mating or when the female host is caring for her young, and in these the lice merely transfer from one individual to another of the same species. There are other methods of transfer, of which the most interesting is that lice on a dead host may clutch on to other insects, such as parasitic flies, using these other insects like a lifeboat on which to leave the sinking ship. If such lice should be carried to a host of a different species their survival is normally very short, for the blood, hair or feathers of a strange host are generally unsuitable for them and will poison them within a very short time. As Zinsser puts it in his book *Rats, Lice and History*, a louse that has fed on a strange host "suffers from a probably painful and fatal indigestion". There are a few instances in which lice have succeeded in establishing themselves on a strange host, but such cases are exceedingly rare ; I shall return to these exceptions a little later.

I have mentioned that a given species of louse normally occurs only on one species of mammal or bird, sometimes on several closely related species. But we can carry this further, for if we examine the lice of a number of groups of birds (for instance) we find that the more closely related the birds are, the more closely related are their lice, and that geography has little or no influence in the matter. If one is given a collection of bird-lice with no information as to where and on what hosts they were collected, it is quite an easy matter to tell in the majority of cases from what kind of birds they came, but it is impossible to say from what part of the world they came

unless by considering the distribution of the particular group of birds. As an example, on one leave I spent a few days in collecting lice from birds in the Orkney Isles, and on my return to Uganda I compared them with lice I had collected here. I found that the lice off cormorants in the Orkneys were precisely the same as those from the East African form of the same species, while they were totally different from those found on other sea-birds shot in the Orkneys, some of which may well have shared the same ledge of cliff with the cormorants. Furthermore, if we again take our cormorant as an example, we find that his lice are very like those of the shag (belonging to the same genus as the cormorant), rather less like those of pelicans, snake-birds or gannets (all belonging to the same order of birds) and with only a remote resemblance to those found on other orders of birds. The reason for this is that lice have lived on birds for enormously long periods of time and have been passed on almost invariably from one individual to another of the same bird-species. During all this time they have been subject to evolution, but the conditions surrounding them have been so uniform compared with those to which their hosts have been subjected (the temperature, feather-composition, etc., of one species of bird being very like the same conditions in another species) that the evolution of the lice has lagged behind that of their hosts, so that while the birds have altered very greatly the lice have changed comparatively little. Quite similar facts are found in the case of mammals and their lice: the best-known of the sucking lice of man is very closely related to the louse of the chimpanzee, less closely (but very obviously) related to the lice of Old World monkeys, and far more distantly related to the lice found on other groups of mammals. The exceptions to this general rule are so rare that I myself have only met with one instance, this being that precisely the same chewing louse occurs naturally on the white-tailed mongoose and on its rather distant relative the civet. Another well-known instance is of much greater interest, it is the fact that a number of species of South American spider-monkeys are infested with lice that are no more than quite slight modifications of the *Pediculus* found on man, many of the species of spider-monkey having each its own slightly different form. This is so unexpected (for the spider-monkeys are only very distantly related to man) that it is worth examining how it probably came about. The most essential point is that analysis has shown that the blood of spider-monkeys is far more similar to that of man than the degree of relationship would lead one to expect, for it is this perhaps accidental resemblance in the composition of the blood that has made it possible for transfer from one host to the other to take place. The actual transfer was not very difficult: long before Europeans reached South America the Indians used to keep spider-monkeys as pets (as they still do) and the lice could easily pass from man to monkey. No doubt from time to time a captive spider-monkey escaped, rejoined his wild brethren, and passed on to them the undesired gift which man had bestowed on him. Not all the escaped captives would be of the same species and each would rejoin his own kind, so I suggest that the differences between the lice of different species of spider-monkeys are indications of the length of time that has elapsed since an escaped captive of each species succeeded in infesting his wild relatives.

The fact that there are so few exceptions to the general rule that related lice are found on related hosts is very surprising, for opportunities for transfer

of lice between species of different groups are not lacking, but I have never found on a carnivorous mammal any lice derived from its prey, and have only once found a hawk with lice from a bird which it had eaten. The case of the European cuckoo is even more surprising, for one would expect to find young cuckoos infested with lice from the birds in whose nest they were brought up, but actually young cuckoos go on migration without any lice and are found to be infested with characteristic cuckoo-lice when they return as adults in the spring.

The clear implication from the facts I have just mentioned is startling to anybody who has not specialized on the lice, but it is accepted by all those who have gone at all deeply into the subject. If related birds are always found (leaving out the excessively rare exceptions) to have related lice, and the degree of relationship between the lice varies with the relationship between their hosts (as is the case), then relationship between the lice of two birds is evidence of relationship between the birds themselves, and we can use the lice to judge the affinities of a bird which has become so specialized that the ornithologists cannot decide to what group it belongs. Let us take an actual example: the bird books are not in agreement as to the position of the flamingos, some books putting them among the storks, while others place them near the ducks and geese. The flamingos are infested with four different kinds of lice, all of them closely related to the kinds found on ducks and geese, and none of them showing any very near relationship to the kinds found on storks. Now if we remember that there are those rare instances in which a louse has established itself on an abnormal host we might regard one correspondence between the lice of flamingos and those of ducks and geese as accidental and due to the use of that "fly-lifeboat" which I have mentioned, but with two correspondences the odds against such a possibility begin to mount up and with three or four correspondences the odds against it become so astronomical that I regard the four louse-correspondences in this case as completely conclusive evidence that the flamingos are modified ducks or geese.

There is one other direction in which we can use the evidence of lice to make deductions which I, at least, find of absorbing interest. Lice have never been found as fossils, so it is impossible to get direct evidence of the antiquity of the group, as we can do in the case of many other groups of insects. But we know from the evidence of fossils a good deal about the approximate dates at which the various groups of mammals first appeared, and we have a certain amount of similar evidence with regard to the birds. From this, combined with the present distribution of lice on the various groups of hosts, we can deduce the approximate geological period during which a particular group of lice must have started to infest a particular group of hosts. A few examples will, I am sure, make this point a great deal clearer. The fact that, as I have already mentioned, man and the chimpanzee are infested with different species of the same genus of sucking lice (*Pediculus*) means that the common ancestor from whom both man and the chimpanzee are descended was also infested with lice which belonged to this genus; but man diverged from the stock of the great apes in the early Miocene period (about thirty million years ago), so the genus *Pediculus* must have been in existence during that period. Taking the same example a step further, the sucking lice of Old World monkeys are very similar to the genus *Pediculus*, though sufficiently different

to be placed in a different genus ; this means that lice belonging to the group of genera to which *Pediculus* and the lice of Old World monkeys both belong must have infested the common stock from which apes and monkeys are both descended before apes and monkeys diverged, and that takes us back to the Eocene period (about fifty million years ago). I could multiply instances indefinitely, but two more will be sufficient. It has been asserted that the occurrence of sucking lice on dogs must represent a geologically quite recent acquisition from some hoofed animal, because dogs were the only members of the land-carnivora on which sucking lice were known to occur. Later discoveries made this suggestion much less plausible, because similar lice were found to occur on other members of the family to which the dog belongs. Finally my examination of the lice of seals showed that they are fairly close to the lice of the dog-family and must be considered to have descended from the same stock. Now the seals were once land-carnivora but took to the sea (probably in the Eocene period) since when they have not had opportunities of acquiring lice from other mammals. They must therefore, have had sucking lice since before they took to the sea, and at a time when their ancestors were closely related to the ancestors of the land-carnivora, which makes it extremely probable that the land-carnivora also had sucking lice at that time but that they have died out on all the members of the order except the family that includes the dogs. The last example will not detain us long and I include it because it is the clearest example of the survival of a single species of louse over a huge period of time. The elephants are infested with a very strange member of the chewing lice which is peculiar to themselves, and the species found on the Indian and African elephants is precisely the same. The two kinds of elephants diverged before the Pleistocene period, so this piece of evidence makes it nearly certain that one species of louse has persisted unaltered for about a million years.

From this sort of evidence I have tried to deduce the age of the different groups of lice, and I am much strengthened in my belief in the reliability of the method by finding that my results are entirely consistent, that is to say, that the dates I have deduced for the appearance of the more specialized groups are (as they should be) later than the dates for the more primitive groups. I believe that lice first began to live on the bodies of vertebrate animals (mammals and birds or their ancestors) almost certainly as early as the Jurassic period, when the higher mammals did not yet exist and when birds still had teeth, and perhaps even in the late Triassic period, when they may have parasitized either the very earliest mammals and birds or the still more than half-reptilian ancestors of these two groups. This took place roughly one hundred or one hundred and fifty million years ago.

In conclusion, I hope I have shown you that lice (however disgusting they may be when they force themselves on our attention in too intimate and personal a manner) are of absorbing interest, that their influence on our own species has been of no small importance, that they are capable (rightly interpreted) of giving us interesting and important facts about the early history of their hosts, and that their descent is so ancient that (even for this alone) they would be entitled to our respect.