

The Host-associations of the lice of mammals. By G. H. E. HOPKINS,
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[Received June 7, 1948.]

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I. INTRODUCTION.

(1) GENERAL.

The associations of lice with their hosts are of extraordinary interest, but our knowledge of them is rather meagre. The present paper originated as an attempt to deduce the antiquity of the lice as parasites of mammals, but so many interesting and controversial points cropped up that it seemed to me that it would be dishonest to give merely extracts from the evidence (which might be subconsciously selected to suit my beliefs) and that I must give the evidence in full. Hence the host list, for no author since 1880 appears to have attempted the task of compiling a complete host-list of the lice of mammals, though several regional or partial lists have been published. These two sections make up the most important part of the paper, but I have added sufficient on other aspects of the subject to make the whole comprehensible, so I hope, to those readers who have not made a special study of lice, and to indicate some directions in which it seems to me that further research would be particularly fruitful. I have not hesitated to use evidence drawn from bird-lice to exemplify points in the biology or distribution of the lice of mammals.

It was not until I had begun the writing of this paper that I realized how numerous are the permissible meanings of the word "relationship". In this paper the word is consistently used in the sense of kinship; other possible meanings are expressed by the word "associations".

(2) THE CLASSIFICATION OF THE LICE OF MAMMALS.

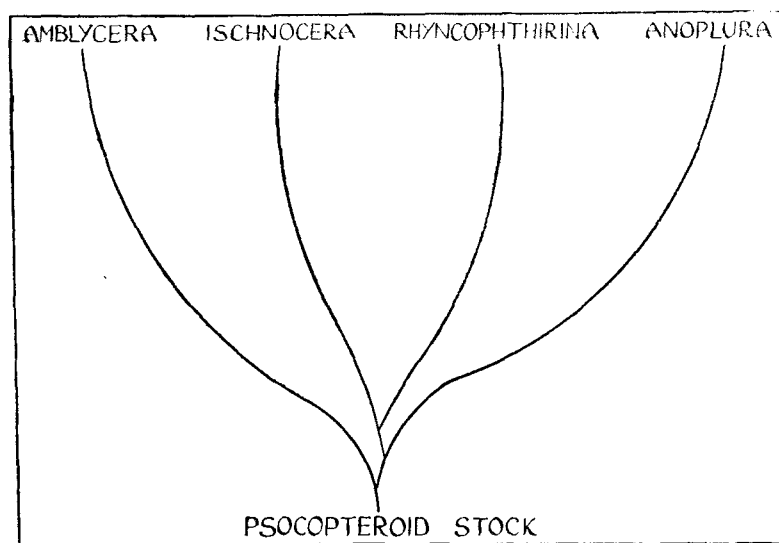
It is generally accepted that lice are descended from Psocid-like ancestors, and they have recently been placed as an order in the superorder Psocoidea, a position which appears to express their relationships with the other insects rather better than any other which has been suggested. They belong to the more primitive hemimetabolous group of insects, in which the newly-hatched insect resembles the adult in most respects. They were formerly divided into two orders, Mallophaga or chewing lice* and Anoplura or sucking lice, but it has now been recognized that the resemblances, between these two groups are of such importance that all the lice may be referred to one order (fig. 1).

The name to be applied to this order is in dispute. Leach (1815) gave the name Anoplura to the whole group and Nitzsch (1818, p. 280) named the chewing lice Mallophaga; the latter name, together with Rhyncophthirina (Ferris, 1931)

* Neither of the usual English names for this group is appropriate: "bird lice" because many species occur on mammals, and "biting lice" because the sucking lice must also bite before they can suck. For this reason I have substituted the less familiar but more accurate term used here.

for the elephant-louse, has never been seriously disputed, but the discovery that the chewing and sucking groups of lice are closely related and should be regarded as suborders has created chaos as to the use of the name Anoplura, a few authors using this name for the whole group (applying the name Siphunculata to the sucking lice), while the great majority continue to use it for the sucking lice alone, as was universal until a few years ago. Weber (1939) included all the lice in the order Phthiraptera of the superorder Psocoidea.* Since ordinal names are apparently not governed by the Rules of Nomenclature, we are free to adopt such names as will be most widely understood and cause the minimum of confusion and misunderstanding; I have therefore continued the use of Anoplura for the sucking lice and have adopted Weber's name Phthiraptera for the whole order.

Figure 122.



A tentative family-tree of the Phthiraptera or lice.

The *Mallophaga* are characterized by the possession of chewing or mandibulate mouth-parts, more or less similar to those of the Orthoptera. They are undoubtedly the more primitive of the two suborders of the Phthiraptera, and are themselves divided into three very distinct superfamilies—the Amblycera, Ischnocera and Rhyncophthirina. The two former groups differ in a number of respects, but principally in the fact that maxillary palpi are present in the Amblycera but absent in the Ischnocera. For this and other reasons it is generally accepted that the Amblycera are more primitive than the Ischnocera, and the resemblances of the former to the Psocoptera are such as to leave little room for doubt that the original Mallophaga were amblycerous.† The

* The suggestion that lice are related to the Psocidae seems to have been first put forward by Packard (1887, pp. 267, 271). Kellogg (1896, pp. 468-471; 1902) came to the same conclusion.

† Bedford (1932*a*, p. 309) differs from the majority of authors in considering the Ischnocera to be the more primitive group, citing as evidence the presence in the Amblycera of a special groove to protect the antenna, and the possession by certain genera of patches of setae or combs of spines on the venter of the legs and abdomen. While agreeing that these are specialized characters, I do not think Bedford right in his main contention, because I consider that the primitive characters of the Amblycera (particularly the presence of maxillary palpi) are more important than their specializations. But this example illustrates well the combination of primitive and specialized characters in the same group (and often in the same insect) which is so common among the Phthiraptera and which constitutes one of the greatest stumbling-blocks in the way of attempts to devise a natural classification of the lice.

Rhyncophthirina are a very curious group with only one known representative, *Haematomyzus elephantis* Piaget, which seems to form to some extent a link between the Mallophaga and the Anoplura: it has chewing mouth-parts, but they are reduced in size, much specialized, and placed at the tip of a long rostrum-like structure: the maxillary palpi are greatly reduced or absent. This species was formerly usually placed among the sucking lice, but Ferris (1931, p. 127), after a detailed study of the insect, placed it in the Mallophaga (not yet combined with the sucking lice) as a third group, Rhyncophthirina, equivalent to the Amblycera and Ischnocera. I consider that Weber (1939) over-emphasizes the differences of *Haematomyzus* from the rest of the chewing lice when he places it in a suborder by itself. Webb (1946) goes to another extreme by placing it provisionally in the family Haematopinidae of the Anoplura because of the close resemblance of the structure of its spiracles to those of *Haematopinus*, but in my opinion these resemblances in a single character, though undoubtedly evidences of relationship between *Haematomyzus* and *Haematopinus*, do not warrant the setting aside of numerous important differences.

The Anoplura are still further specialized: their mouth-parts are modified for sucking and are of a much more complex type than those of *Haematomyzus*; maxillary palpi are absent or unrecognizable.

To summarize: the order Phthiraptera, or lice, is descended from Psocid-like ancestors and is divisible into four very distinct suborders or superfamilies. Arranged in order of primitiveness, these are Amblycera, Ischnocera, Rhyncophthirina and Anoplura, of which the first three are considered as superfamilies of the Mallophaga. The ancestors of the Ischnocera must have been very like some of the less-specialized Amblycera, and the ancestors of the Anoplura must have greatly resembled *Haematomyzus*, though this insect is itself certainly not on the direct line of descent, as is shown by the structure of its mouth-parts. I agree with Harrison (1928 a, p. xxvi) in regarding it as practically certain that the Anoplura branched off from the Ischnocera after the divergence of these latter from the Amblycera. Furthermore, the possession by both the Anoplura and the Trichodectidae (the most widely distributed family of mammal-infesting Ischnocera) of the structures known as gonapophyses (conspicuous hair-fringed lobes in the genital region of the female) suggests very strongly that the Anoplura branched off from the trichodectid stock after the latter had diverged from the main stem of the Ischnocera. These structures are absent in almost all Ischnocera except the Trichodectidae,* but are present in the solitary representative of the Rhyncophthirina.

Families of lice.

Amblycera.—Of the families into which the Amblycera are divided, only two (Boopidae and Gyropidae) occur on mammals, the rest being confined to birds. Until recently the Trimenoponidae were recognized as a third family, but Werneck (1948) considers them inseparable as a family from Boopidae and certain bird-Mallophaga. The Gyropidae seem very distinct, not only from the Boopidae, but also from the various families which are found only on birds. The relationships of these families are further discussed on p. 537.

Ischnocera.—Of the two families of Ischnocera found on mammals, the Philopterae are represented by the single genus *Trichophilopterus*, found on lemurs only, while the Trichodectidae are divisible into a number of genera found on a wide variety of hosts. Kéler (1938 c) erected the superfamily Trichodectoidea for the Trichodectidae, which he divided into three families, Trichodectidae, Bovicolidae and Dasyonigidae, the first-named with three subfamilies, Trichodectinae, Eutrichophilinae and Felicolinae; he left out of account the genus *Geomydoecus*, found on American pocket-gophers, and those species of Trichodectidae which occur on lemurs and monkeys. In my opinion Kéler's

* They are present in *Osculotes*, which also has a very trichodectoid head.

arrangement is a gross exaggeration of the extent to which the Trichodectidae differ from the rest of the Ischnocera. I regard his "families" as being at most subfamilies and his "subfamilies" as at most tribes. The generic arrangement of the Trichodectidae is discussed in a later section of this paper (p. 437), and I need only mention here that the Bovicolinae must be known as Damalininae if my contention that *Bovicola* is not generically separable from *Damalinia* be accepted.

In the Anoplura the super-generic classification is in a still more unsatisfactory state, and it is very regrettable that the final part of Ferris's monograph (Ferris, 1920-1935), in which this matter was to be discussed, has never appeared. Ewing (1929, pp. 131-149) recognizes the families Haematopinidae, Haematopinoididae, Pediculidae, Phthiridae, Echinophthiriidae and Haematomyzidae, the last-named of which was removed by Ferris two years later to constitute the Rhyncophthirina, while Fahrenholz has proposed yet another family, the Neolinognathidae. The family Phthiridae has been rejected by Ferris (1920-1935, p. 603), and the same author (1920-1935, p. 150) regards *Haematopinoides* as being very closely related to *Schizophthirus*, which is a member of the Haematopinidae; I have, therefore, rejected the family Haematopinoididae.* For reasons which are given on p. 546 I have also found it necessary to reject the Echinophthiriidae, which should be degraded to subfamily rank in the Haematopinidae. This leaves only the three families Haematopinidae, Neolinognathidae and Pediculidae, though it must be admitted that the first-named is far more heterogeneous than the others. Webb (1946), in a tentative classification intended to show how a single character can be used, adds three more families, Docophthiridae, Eulinognathidae and Linognathidae, but the first-named includes *Neolinognathus* and is, therefore, the same as Neolinognathidae Fahrenholz, and I do not care to accept the other two families until the spiracle-character has been correlated with other characters, although I consider that Webb has produced a very strong case in favour of this character being an important one. A really satisfactory classification of the Anoplura will not be easy to achieve, and I regret that my only contribution to the task is destructive.

A very interesting character by which most of the lice which infest mammals differ from all those found on birds must be mentioned, if only to point out that it is not evidence of any specially close relationship between these groups to the exclusion of the bird-infesting forms. In all the groups of Mallophaga found on birds the tarsi are two-clawed, as they are also in the Boopidae and Trimenoponidae, but in all the other mammal-infesting groups there is a strong tendency for one of the claws to be lost. The Gyropidae (with the partial exception of *Macrogypopus*, which has two claws on the fore leg), the Trichodectidae, and the Anoplura, all have but one tarsal claw, in *Trichophlopterus* the middle and hind tarsi have two normal claws, but on the front tarsus one claw is vestigial, while in *Haematomyzus* the tarsi are provided with one large claw and a structure of somewhat doubtful nature which is probably best regarded as a very degenerate second claw. That this one-clawed condition is in some way an adaptation to life on mammals is shown by the fact that in the dipterous family Hippoboscidae (quite unrelated to the lice except that both groups are insects) there is a similar tendency for the mammal-infesting groups to have a reduced number of tarsal claws.

(3) WHAT IS A SPECIES ?

Before beginning any discussion of the associations of the lice with their hosts it is necessary to frame some sort of definition of what we mean by

* The only character given by Ewing to separate the Haematopinoididae from the Haematopinidae is that the antennae are three-segmented in the former and five-segmented in the latter. The degree of phylogenetic importance to be attached to the number of antennal segments is shown by the fact that in many Trichodectidae the number differs in the two sexes of the same species.

“species”, for there has been a very strong tendency among a certain school of modern systematists to apply this name to groups of far less phylogenetic significance than has been normal in the recent past.* A common definition (Roberts, 1940, p. xxi, for example) is that “subspecies are those geographical varieties which merge into other geographical varieties of the same species and are not separable on clear-cut characters, whereas species can always be recognized by clear-cut differences in characters”. Roberts also states (*l.c.*) that “genera may be said to comprise those distinct species which could interbreed and produce fertile but hybrid progeny which under the Mendelian Law would eventually, in future generations, revert to the two parent stocks; whereas, were species of two different genera to interbreed the progeny would be infertile and incapable of perpetuating themselves”. The conception of a genus upheld by the school exemplified by Roberts is almost precisely the definition normally given for a species. With regard to the earlier-quoted definition of species and subspecies, its acceptance would necessitate our considering practically all island-forms as full species, no matter how trivial the characters separating them may be, because their geographical isolation normally precludes the existence of intermediates linking them with other forms. If, however, we recognize that forms which are isolated from one another, and between which there are consequently no intermediates, may yet be conspecific in the absence of major differences between them, then the definition becomes more in accordance with my views. My own concept of a species is very similar to those of Ferris (1920–1935, pp. 531–534) and of Huxley (1940, pp. 1–42); I would define a species as “a group of individuals so separated genetically from all other such groups that it would not form with any of them a single permanently interbreeding community if given the opportunity in natural conditions”.

My test as to the specific or subspecific status of two forms may be put in the form of a question: Is there reasonable doubt that if a sufficient number of individuals of each of the two forms were to be placed in a geographically isolated area suitable to their survival they would form a single interbreeding community? If the answer to this question is that there is little doubt that they would form one community, then the forms should be regarded as subspecies; if they would remain two separate communities, then they have acquired the status of species. Obviously the actual test by experiment can seldom be applied where forms are separated on “islands”, whether by water, altitude, desert or other ecologically unsuitable country, but nature has applied it for us on a very large scale where such isolation does not exist. In Uganda there are three common field-rats, *Tatera liodon*, *Lophuromys aquilus* and *Lophuromys sikapusi*. The two forms of *Lophuromys* frequently occur, not only in the same general locality, but on the same ground; they do not interbreed and are, therefore, species. The case of the *Tatera* is completely different; it occurs all over the country, wherever ecological conditions are suitable, and is represented by a number of geographical forms most of which exhibit a zone of intergradation where they meet; but in one area two barely separable forms are isolated from one another by the impassable barrier of the Nile, so that miscegenation is physically impossible, and naturally there can be no zone of intergradation. According to the views of those who insist that all island-forms must be considered as species because of the absence of intergradation, the forms of *Tatera* from the east and west banks of the Nile would have to be called species, yet there can be no reasonable doubt that if a few hundred individuals of the eastern form were to be conveyed to the western bank their descendants would, in a very few generations, be inseparable from the rest of the western population—in fact the two forms are undoubtedly merely subspecies.

Obviously acceptance of this concept of a species must leave some difficult and doubtful cases, but this difficulty is inherent in our acceptance of a belief

* My remarks on this subject apply solely to animals, not to plants.

in evolution, since "species", "genus", "family", and even "phylum", have no meaning except as applied to a particular period of time. If we had a complete series of remains of the Perissodactyla, for example, we would only have to go back a short period, geologically speaking, before we could no longer distinguish between horse, ass and zebra; a little further back we would have difficulty in separating Equidae and Tapiridae; still further and we would be unable to say which of the remains were Perissodactyla and which Artiodactyla. We must therefore adopt such a concept of "species", "genus" and the other divisions as will best fit the facts as they are now; fortunately man's life is so short in relation to evolution that species (thus defined) are likely to remain stable for as long as need concern both ourselves and many generations of our descendants. It is, however, inherent in the idea of evolution that at any given time there must be what might be termed nascent species—forms which are near the borderline between subspecies and species. Such forms are normally separated geographically or ecologically, and so long as they remain on the subspecific side of the borderline are prevented from colonizing each other's range by the fact that venturesome individuals that cross the range-boundary are merged in the population of the other form, but when the two forms have crossed the line between species and subspecies each is able to colonize the territory of the other form without losing its identity. This is beautifully exemplified by the case of the two species of *Lophuromys* mentioned above: *L. aquilus* and *L. sikapusi* show no obvious differences in ecology; the former has an East African range and the latter a West African, but the ranges overlap in the whole of Uganda and the adjoining parts of Kenya, Tanganyika and the Belgian Congo. It seems clear that the two forms developed, first into subspecies and then into species, in East and West Africa respectively; having attained the rank of species, each is now in a position to extend into the territory of the other and is in process of doing so. Uganda is a particularly favourable area for such observations, since it is the meeting-place of many West African and East African forms.

I believe that the concept of a species as a group of individuals capable of forming a single interbreeding community will best interpret the observed facts as they are today. The interbreeding need not necessarily be direct: if we imagine a series of forms A1, A2, A3 . . . A12 extending from New York to Patagonia, experiment might well show that A1 had become incapable of crossing with A12, yet if A1 could still breed successfully with A2, A2 with A3 . . . and A11 with A12, I would still consider A1 and A12 to belong to one species.

Practical application of my definition of "species" (as of any other definition) is beset with difficulties, though the number of doubtful cases is less than might be supposed. I have regarded major differences in structure, particularly (so far as the insects are concerned) differences in the male genitalia, as evidence of specific rank, while recognizing that what constitutes a major difference must often remain a matter of personal opinion and may even be different in different groups.* Since I agree with Huxley in considering that the higher systematic units, such as genera and families, are little more than useful fictions, I have accepted these divisions as employed in the lists of mammals available to me, with very few exceptions, all of which are explained in the host-list. My knowledge of the mammals is not sufficiently great to justify me in making

* These differences in male genitalia would presumably render cross-mating impossible, and their discovery invalidates the conclusions of Kellogg (1913 a), quoted on this point by Chandler (1923, p. 337), as to the variability of a single louse-species on a single bird- (or mammal-) species and the occurrence of the same species on many different hosts. Examination of the genitalia, apparently never performed by Kellogg, usually reveals that the lice from different individuals of the same host vary very little, whereas those from another host-species are so distinct that cross-mating would be difficult. On the other hand, there are many cases, more especially among the Anoplura, to which Chandler's plea for a more extensive use of trinomials is highly applicable.

changes in the accepted specific arrangement except in a very small number of instances, explained in the list, but where Ellerman, for instance, expresses the view that certain forms are probably all conspecific, I have tended to follow this lead.

(4) THE EXTENT OF OUR KNOWLEDGE.

The number of known species of mammals is stated to have been about 3750 in 1928; taking into account new discoveries and those forms which were then considered as species and have now been reduced to subspecific status, the number is probably a little smaller today. From this figure must be subtracted the species belonging to groups not infested with lice (whales, bats and, perhaps, some small groups), leaving a round figure of, perhaps, 3000 species. We know, to some extent, the lice of about 600 of these species, but this figure in no way represents a true picture of the facts because the geographical distribution of our knowledge is so uneven. We have a rather good knowledge of the lice of South America, the Ethiopian Region and Europe, and a fairly good knowledge of those of Australia and North America, but (except that Ferris obtained numerous sucking lice from museum-skins from this region) our knowledge of the forms in the Oriental Region is almost nil. Probably this can best be illustrated by the example of the Trichodectidae of two groups of hosts common to the two regions: omitting domestic animals, we know more than 50 species of Ethiopian Trichodectidae from the land Carnivora and the Pecora; from the Oriental Region, equally rich in these groups of hosts, we know only ten species of Trichodectidae, which merely means that the Oriental hosts have hardly been examined. Even for the Ethiopian Region our knowledge is very far from complete; at a conservative estimate the number of known wild species of true Carnivora and Pecora in the region is about 140, and we know the Trichodectidae of about 50 of them. If it be remembered that the Trichodectidae of the Ethiopian Carnivora and Pecora are among the best-known of all groups of lice, it will be obvious how small our knowledge really is. Perhaps the most striking examples of our ignorance are provided by two domestic animals. The louse of the camel was known to Redi in 1668, but was not rediscovered until 1934, and then only because my friend Dr. Werneck asked a correspondent in Algeria for a special search to be made on camels. In the interval of nearly 300 years the louse had been assumed by some authors to be a fantasy, although Redi's figure of it is surprisingly good considering its date, and the louse appears to be quite a common species. The genus *Katemia* was described in 1911 without any host-record; it was not until 1942 that it was found to be a parasite of so abundant and accessible an animal as the domestic ass.

It is very unfortunate, in this connection, that some workers on lice do not take full advantage of their opportunities to increase our knowledge by giving fuller particulars of the source of their material. Many do not record whether the source of their specimens was a wild host, a captive, or a skin in a museum, though it is obvious that finding a louse on a wild host has much more significance than finding it on a captive or a skin. Others do not record, even approximately, from how many specimens they are describing a new louse, though this is a most important fact, not only in respect of the probability of supposed differences proving to be constant but also with regard to the likelihood of the reported host being the true one. The fact that Ferris (1920-1935, p. 139) obtained numerous specimens of *Hoplopleura emarginata*, for example, establishes a strong probability that the louse was on its true host, even though that host was a museum skin. Single specimens from museum skins, on the other hand, are generally contaminations and should not be described: Piaget's *Trichodectes penicillatus*, supposedly from a kangaroo, and Mjöberg's *Trichodectes madagascariensis*, alleged to be from a mongoose, are both synonyms of well known goat-parasites, while Ewing's *Trichodectes abnormis*, supposed to be from a Madagascan lemur, is now known to be a parasite of a fox, so that both the

faunal region and the host reported for this species are entirely misleading. Similarly, records of single specimens from even wild hosts are liable to be due to straggling, if not to some other form of error, and such specimens should not be described. The difficulty of evaluating records is increased when the author fails to check the host-names he gives. Fahrenholz, for instance, who never published the number of his specimens, described (1938, p. 270) *Polyplax auricularis californiae* from "*Perodipus streatori*" (a synonym of *Dipodomys heermanni*), but apparently did not appreciate that *Dipodomys* is a most improbable host for a form of *Polyplax auricularis* since it is a member of the Geomyoidea, whereas *P. auricularis* occurs on hosts belonging to the Muroidea. On the other hand, there is a *Peromyscus streatori* (a subspecies of *P. maniculatus*), and this is a very likely host for a form of *Polyplax auricularis*, which was described from material obtained from another form of the same species of host. If Fahrenholz had not failed to record the number of specimens of the louse we would be in a much better position to decide whether *P. a. californiae* should be regarded as a straggler or contamination of *Dipodomys* (and quite possibly a good subspecies) or as a genuine parasite of *Peromyscus maniculatus streatori* (and almost certainly a synonym of *Polyplax a. auricularis*). That the mistake I have suggested in this instance is possible is demonstrated by the fact that in the same paper (Fahrenholz, 1938, p. 265) *Polyplax eminentus* is described from material stated to originate from "*Paderoryctes gadut*" in East Africa, because the only African mammal with a remotely similar name is *Tachyoryctes audax*. It seems a pity to vitiate painstaking systematic work by such carelessness with regard to the evidence as to the identity of the host and authenticity of the record.

Another most unhelpful procedure is the description of new lice from hosts which have not been identified at least to the species. An exception may reasonably be made in the case of material obtained from museum skins which are likely to be determined at some future date, but in this case the museum number of the skin should always be recorded.

The errors caused by the wrong ways of procedure to which I have drawn attention are often serious: Not only do we get lice recorded from host-groups on which they do not occur in nature, and from faunal regions in which they are absent, but unsound theories may be based on such supposed facts. The solitary record of *Trichodectes melis* from a hedgehog, for instance, has been used as support for a theory (Eichler, 1936, p. 474) that absence of Mallophaga from certain groups of hosts may be due to the fact that these hosts hibernate, but is not evidence in this (or any other) connection because it is almost certainly a case of mislabelling. Similarly, much criticism of phylogenetic deductions from louse-distribution has been based on records which are completely unreliable. We shall not make much progress with our knowledge of the distribution of lice until collectors and authors learn to be more careful with regard to the collection and presentation of the evidence than is too often the case today. At present we often know only that a certain louse has been taken from a certain animal or its skin, whereas the only information of real value is that the louse occurs on the host in natural conditions or is capable of establishing a permanent infestation of the host.

(5) METHODS OF COLLECTING LICE FROM MAMMALS.

The lice of mammals are frequently so small, and they often cling so tightly to the hairs of the host, even after death, that to obtain them by searching is like seeking for needles in a haystack. In these circumstances a note as to the methods I employ may be of value to others, even though these methods have no claim to be considered original. I use two methods, which might be called "the brushing technique" and "the dissolving technique", the choice between them being dictated by whether it is necessary to keep the skin of the

host undamaged; a third method, "searching", is so laborious and so unprofitable that it should only be used when neither of the other methods can be employed. Both the normal methods are based on the fact that only a small proportion of the parasites leave the host after the death of the latter, the great majority of them remaining affixed to the hair or skin and dying in this position.

The first essential, in dealing with freshly-collected hosts, is to ensure that lice have no opportunity of transferring from one species of host to another, because artificial approximation, after death, of hosts of different species (in a game-bag, for example) is one of the most frequent causes of erroneous records. To guard against this, each individual animal, as soon as it is obtained, should be put in a louse-proof bag of calico or other suitable material and the mouth of the bag should be tied tightly; the animal remains in the bag until examined. Failing bags, a handkerchief, or even newspaper, can be used in an emergency. This method cannot of course be used for very large hosts, but these are not usually collected in numbers. The precaution is of less importance if only one species of animal is being collected, and is useless in the case of dry skins, when any transfer of lice is likely to have already taken place. Another extremely important precaution, neglect of which caused me to be responsible for several erroneous records when I first began to collect lice, is to make certain that the bench is thoroughly cleaned after the examination of each host and before beginning work on the next.

The dissolving technique for examination of hosts is by far the most effective and involves the minimum of work on the part of the original collector (a very important point when he has no personal interest in the parasites), but it involves the complete destruction of the skin, so cannot be applied to valuable or incompletely-determined specimens. The animal is skinned (no matter how roughly) and the skin is sun-dried as rapidly as possible, it being a matter of complete indifference if the hair subsequently "slips". After drying, the skin can be kept, if precautions are taken to prevent it becoming beetle-infested, until it is convenient to examine it, and it can be sent to the specialist without further treatment. On receipt of such a skin my first procedure is to cut it into pieces of a convenient size and to soak the pieces in a 5% solution of sodium hydroxide in water until the hair becomes soft enough to be easily scraped off the skin with a blunt knife. This process usually takes about a quarter of an hour or a little longer, and it is most important not to prolong it unduly, because if the soaking has been too prolonged the skin also dissolves into a jelly-like mass from which it is impossible to separate the partially dissolved hair. In my first experiments with the method I heated the depilatory solution, but this was found to make the process too difficult to time. It is often found that one portion of a piece of skin has the hair sufficiently dissolved, whereas in another part of the same piece the hair has been shielded from the action of the solution (by air caught among the hairs, for instance) and is not ready; in such instances the softened part of the hair is scraped off and the piece of skin is returned to the solution. The partly-dissolved hair is next placed in a glass beaker, about a quarter of its bulk of the 5% solution of sodium hydroxide is added, and the beaker is placed in a saucepan of water and boiled until the hair is completely dissolved, which takes roughly half an hour. The contents of the beaker are then filtered through very fine-mesh stainless steel wire gauze, the solid residue on the gauze is gently washed with a thin jet of water to remove the smallest particles, and the remainder is washed into a petri-dish of water and examined under a mounted lens, the parasites being picked out and transferred to 90% alcohol until it is desired to examine them. It is essential to carry out the filtration while the liquid is still hot, or soap formed by the action of the alkali on fat in the skin will block the holes of the gauze.

The chief disadvantage of this method is that it cannot be applied to valuable specimens. The chief advantages are that all the original collector has to do is to remove and dry the skin, that practically the whole of the lice on the animal are obtained, and that the proportion of damaged specimens is very low. It might be supposed that a process which entirely dissolves hair would also destroy the chitin of which an insect's skeleton is composed, but unless the boiling is prolonged out of all reason the specimens are completely undamaged. A very striking case of the efficacy of this method is provided by *Damalinia victoriarum* Hopkins; the three skins from which the type-series of this species was obtained were first carefully searched and beaten, a total of 20 adults and 11 nymphs being obtained, but subsequent dissolving of the hair produced a further 456 adults and 752 nymphs.

The brushing technique is applicable to dried skins or recently killed animals, the latter being preferable because all the parasites are likely to be still present. In this case, however, the parasites are likely to be still alive and must be killed by placing the animals in a more or less airtight box with a small quantity of chloroform, ether, carbon bisulphide, carbon tetrachloride, petrol or cyanogas, none of which should be allowed to come into direct contact with the specimen. The animal, or its skin, is now vigorously beaten and rubbed with the hand (a brush most not be used as lice become lost among the bristles and may cause errors by being found again when another host-species is being examined) over a large sheet of white paper or a white-painted board; a grating of wire netting on a wooden frame is sometimes useful when inconveniently heavy specimens are being brushed. If it is the skin which is being examined it should be allowed to become thoroughly dry before treatment, but in the case of all recently killed hosts or their skins an attempt should be made to obtain at least a few undried specimens of the lice, because these show certain characters far better than dried specimens. The debris which falls on to the paper, consisting of loose hairs, dirt and (with luck) parasites, is carefully collected and the process repeated many times until no more debris is obtained. The subsequent procedure depends on the amount of debris and on whether it is desired to examine it immediately: if the amount is small and the collector wishes to examine it at once, the debris is placed in a petri-dish of 70% alcohol and examined under a mounted lens, the parasites being sorted out and placed in a tube of 90% alcohol; if the amount is large, or if there is no hurry about examining the catch, the whole of the debris is placed in a tube (dry for material from dry skins and containing 90% alcohol in the case of fresh material), and is subsequently treated in the same way as the part-dissolved hair in the dissolving technique.

This method has the great advantage of being applicable to valuable museum-specimens and to hosts belonging to groups (the hyraxes, for example) in which amateur identifications of the host are particularly unreliable. The disadvantages are that only a proportion (large or small according to the thoroughness with which the process is carried out) of the total number of parasites present can be obtained, and that a proportion of the specimens obtained (especially high in the case of very elongated species) will be found to be damaged.

A modification of the brushing technique, permitting it to be used for living animals, has been described by Dunn (1932). He secures the legs and tail of the animal and places it in a glass jar, then wraps one edge of a towel tightly round the neck of the animal (this edge is held so as to keep the animal upright) and fastens the other edge to the top of the jar by means of an elastic band. Chloroform is then sprinkled on the towel in such a way that it does not touch the animal's skin, but the heavy vapour passes through the towel into the jar. After about four minutes the animal is removed from the jar and rubbed or combed to obtain the parasites; other parasites are collected from the inside of the jar. I have not had occasion to use this method, but it might be of great value for the examination of rare animals which it is desired to keep alive.

Another method which has been found useful with tame animals is to rub pyrethrum powder well into the hair and then comb out the powder and the lice. Few of the lice are killed by this treatment, but they are rendered helpless and are easily removed.

The searching technique needs no description. It appears to have been universal in the past and is still much used, but is not to be recommended except for very scantily-haired creatures. A modification described by Waterston (1912*b*) for collecting *Haemodipsus ventricosus* might be of more general value in cases in which a louse is of infrequent occurrence on the host-individual and it is desired to retain the skin of the host. He suggests skinning the host and searching for the discoloured patches produced on the inside of the skin by the bites of the louse. The method would, of course, only be applicable to Anoplura. Another method suggested by Waterston (1913*c*) is inferior to the brushing technique.

It is very desirable that authors who publish records of examinations of mammals for lice with negative results should specify the technique employed. I have experienced so many instances in which a skin has appeared to be louse-free after careful searching and brushing, but has proved to be infested when the dissolving technique was employed, that I no longer accept negative records in which the latter technique was not used (except from very scantily-haired hosts) as meaning much more than that the specimens examined were probably not heavily infested. Even this latter assumption is not always warranted: I once brushed the dry skin of a young giraffe very assiduously without result, but by the dissolving technique the same skin proved to be very heavily infested with *Linognathus brevicornis*.

(6) METHODS OF PRESERVATION AND EXAMINATION OF LICE.

The subject discussed in this section may appear somewhat remote from my main theme, but I include it because I am convinced that the proper preparation and examination of specimens has a very strong bearing on the accuracy of our knowledge of host-distribution. A considerable number of the mounted specimens which I have received from various sources have been mounted in such an unsatisfactory manner that small differences between species could not possibly be observed, or have even been so badly distorted that they appeared entirely different from properly prepared material of the same species. Werneck (1938*a*) has shown how these factors may result in the description of supposed new species which do not in reality exist, and I am convinced that large numbers of misidentifications of lice are attributable to the specimens being mounted in such a way that the finer specific characters could not be observed. Other misidentifications are, of course, due to the material used for comparison not being from the type host and not being conspecific with the type-material of the species.

Fresh material is best preserved in 90% alcohol, since weaker alcohol has a tendency to cause maceration to take place, the integument becoming fragile and losing much of its capacity to absorb stains. Methods of restoring specimens which have deteriorated in alcohol are described by Kéler (1939), who worked with material in the Halle collection, some of which had been in alcohol for 120 years. He used 20% caustic potash solution in which the specimens were left for at least 12 hours, since he found that weaker solutions did not dissolve the contents of these very old specimens satisfactorily. The exoskeleton of most specimens had retained its original coloration well, but others had become much faded by maceration. For these latter specimens his procedure was to wash the emptied exoskeletons at least one hour in distilled water, followed by a quarter of an hour in tap-water, and then leave them in $\frac{1}{2}$ % haematoxylin solution until the staining was sufficiently intense. They were then retransferred to tap-water (in which the red coloration becomes blackened), followed

by oil of cloves, cedarwood oil, and thence into balsam. By this means specimens which had faded until the sclerotized plates had become quite invisible were restored to more or less their original colour. Specimens over-stained by this method are placed in distilled water instead of tap-water, which removes some of the staining, and then can go direct into alcohol from the water; alternatively (or if this treatment still leaves the specimens over-stained) they are placed in 1% iron alum solution and the removal of the stain controlled by observing it under a microscope.

Storage of the alcoholic part of a collection presents certain difficulties. For this purpose corked tubes are unsatisfactory except for short periods, because evaporation takes place through the cork and the proportion of water in the alcohol gradually becomes greater until the liquid finally dries up. Even sealing the cork with paraffin wax does not wholly solve this problem, because the seal is often not quite perfect. Dr. Werneck preserves his alcoholic specimens in small tubes sealed with a blowlamp, the tubes being cut open with a glass-file when it is desired to examine the specimens. Another method was described by Waterston (1914 *b*, p. 150): he placed the lice in small tubes ($1\frac{1}{4}$ inches by $\frac{3}{16}$ or $\frac{3}{4}$ inch) plugged with cotton wool; these in turn in larger tubes ($1\frac{7}{8}$ inch by $\frac{7}{8}$), and the latter in glass-stoppered jars measuring $3\frac{3}{4}$ by $3\frac{1}{8}$ inches. Whatever system is adopted, it is essential that the specimens be provided with adequate data, which should include the locality if only because of its bearing on the subspecies of the host. The alternatives are to put full data in the tube containing the lice, or to label each tube with a number and enter full details under the same number in a catalogue: the latter is in some ways the more convenient method, but has the grave disadvantage that loss of the catalogue would render the whole collection practically valueless.

The fact that many mammals have multiple infestations with closely related species of lice renders it imperative that every specimen obtained should be thoroughly examined, not merely a small proportion of them as has been usual in the past if the specimens were numerous. This is easiest done by placing each specimen in liquid phenol (phenol crystals to which a drop or two of absolute alcohol have been added) on a microscope slide and protected by a cover-slip. When the specimens have become cleared (24 to 48 hours) they are easily sorted and counted, some being set aside for making into permanent mounts, while others are stored away in alcohol. Examination of specimens in phenol is also sometimes a useful check on supposed differences which may be artefacts caused by distortion during dehydration or by different degrees of pressure of the cover-glass on specimens deprived of their soft contents. Whole specimens made transparent by phenol show the normal appearance of the male genitalia and female gonapophyses in a manner which specimens emptied of their soft tissues are incapable of doing.

Making satisfactory mounts of lice in Canada balsam is a very simple process, though it is certainly more tedious than making useless ones. The lice to be mounted are placed in a 10% solution of caustic potash (potassium hydroxide) in a solid watchglass, and then either a very fine needle is used to make an incision in the abdominal margin or the same needle is thrust into the dorsal or ventral intersegmental membrane; as it is very desirable that the gut, if filled with food, should be pierced, I prefer the latter method, directing the needle so that it pierces the integument and gut in one operation. The incision, however made, is essential because without it there is much deformation of the specimen during the process of dehydration, and it must not be deferred to a later stage because the integument (no longer supported by the soft parts) will then give before the needle and be most difficult to pierce. The specimens are then left in the solution of caustic potash until the soft body-contents are completely liquefied by the action of the solution. This process may be hastened by boiling the solution in a water-bath, but I prefer to carry it out in

the cold because it is then easier to time ; in the latter case the lice are usually ready in about twenty-four hours. The next stage is the removal of the liquefied contents of the abdomen, which is done by gentle pressure with a very blunt needle under a dissecting microscope ; if the contents do not leave the abdomen readily the specimens must be returned to the potash, as the use of force will result in serious damage, but their stay in the solution must not be too prolonged as over-long treatment with potash results in the chitin also being dissolved. Bedford (1931 *b*, p. 226) recommends carrying out the expulsion of the body-contents in water, but I have found doing it in potash much more satisfactory. The process described above is that used for fresh or alcoholic specimens ; dried specimens are treated in exactly the same way except that the making of the incision should be deferred until they have acquired the appearance and consistency of fresh specimens, and that they may require a longer period ; they can be made into very satisfactory mounts. After the body-contents have been removed, the specimens are dehydrated by passage through different concentrations of alcohol (70%, 90% and absolute alcohol are sufficient) into xylol or oil of cloves, and are then mounted in balsam in the ordinary way. In all these manipulations of lice I find a needle-scalpel with the point broken off an invaluable aid, with which the specimens can be transferred from one solution to another without the slightest damage ; the needle is first placed under the louse and then jerked sharply upwards, which causes the louse to rise in the liquid (than which its specific gravity is very little more), when the needle is rapidly inserted under the louse and lifted out of the liquid. The lice have, however, a specific gravity considerably greater than that of xylol, and it is partly for this reason that I prefer oil of cloves. The actual mounting should be done in rather thin balsam, and in this case no trouble with air-bubbles is likely to arise. Because economy of space is essential in my case, and also because comparison of specimens is thus much facilitated, I often mount many specimens from the same host-individual on one slide (but never more than one male and one female in the case of types) ; I place a drop of very thin balsam on the slide and arrange the specimens neatly in it with a fine needle applied gently to their sides, then allow the balsam to dry until it becomes viscous, remove the thickened rim of partly-dried balsam with a pledget of cotton wool wrapped tightly round the tip of a dissecting needle and dipped in xylol, add another very small drop of very thin balsam, and apply the coverslip (without any pressure). A method for arranging the legs and antennae is described by Bedford (1931 *b*, p. 226), but if the specimens have been properly emptied and cleared this is an unnecessary refinement, and in less skilled hands than his it may lead to damage to the specimens.

Many other substances have been used to make mounts of lice, but most of them are extremely unsatisfactory ; many specimens in the exceedingly important Piaget and Kellogg collections have suffered damage through the specimens being mounted in media which proved not to be permanent. One which I have not yet tested, and which is stated to give good results, is Faure's gum (or gum-chloral mountant) ; the fresh or alcoholic specimens are put into a mixture of equal volumes of chloral hydrate and lacto-phenol, and are mounted direct from this into the gum. Most of the gum-mounts of lice which I have seen are not a good advertisement for this mountant, being much distorted, but this was probably because the essential incision in the abdomen was not made, because I have also seen some most satisfactory specimens mounted in gum. Kéler (1939) used this mountant for part of the Halle collection, but later abandoned it in favour of Canada balsam. It dries up to a very troublesome degree, necessitating the addition of gum to the slides over periods which may amount to months, and it is doubtful if gum-mounts are sufficiently permanent, so that it cannot be recommended except for special purposes. Recently I have tried mounting lice in polyvinyl alcohol lactophenol (see Downs, 1943),

and it seems likely that this may prove to be a very satisfactory mounting medium, but I have not yet been able to test it thoroughly.

Identification of lice can usually be done quite satisfactorily without staining the material, and all of Bedford's excellent systematic work was done with unstained specimens, but many delicate differences between closely-related forms are invisible in unstained material, and staining often makes even large characters more easily perceptible. For this purpose the specimens are emptied of their solid contents as described above and placed in the stain (carbol fuchsin) on a microscope slide which is then warmed gently ; the excess stain is cleaned off the slide with a rag, the specimen being moved to one end of the slide during this process. A drop of phenol is then added to the specimen, which is now over-stained. To reduce the staining to the right intensity and make a balsam mount it is necessary to pass the specimen through three mixtures of liquid phenol with xylol, of which the first is 75% phenol by volume, the second 50% and the third 25%. This process takes place under the microscope so that the intensity of the staining may be controlled, and is performed by removing the excess liquid with a rag or a slip of blotting-paper and adding a drop of the next liquid to be used. Before the insect leaves the second solution light pressure on its surface to drive out the contained liquid is permissible, but after this point pressure is not needed, owing to the greater penetrative power of the third solution, and is liable to cause injury to the integument, which loses its elasticity in solutions rich in xylol. The specimen is then passed through xylol into Canada balsam in the normal manner. The xylol and balsam used should be absolutely neutral and stained specimens should not be stored exposed to light ; subject to these conditions the stain retains its intensity for long periods.

Dr. Werneck utilizes a special technique for the particularly difficult case of the genitalia of certain Boopidae, which must be studied with the minimum of disturbance, but which (when so studied) show small but sharp and constant specific differences. He detaches the abdomen from the rest of the body and slits the sides longitudinally, then placing the abdomen in caustic potash solution until the soft parts are dissolved. The dorsal and ventral integument of the abdomen can then easily be lifted away, leaving the genitalia separate and almost untouched, particularly if a micro-manipulator is employed. Subsequent distortions due to dehydration, etc., are avoided by mounting the genitalia direct into gum-chloral mountant to which acid fuchsin stain has been added. It was by the employment of this method (which is described by his kind permission) that he was able to distinguish between *Heterodoxus longitarsus* (Piaget) and *H. spiniger* (Enderlein), long thought to be synonymous.

It is often necessary to re-mount badly-prepared specimens if they are to serve any useful purpose. This is very easily done : in the case of specimens mounted in Canada balsam the labels are soaked off (for subsequent replacement), the slide is dried and placed in a petri-dish of xylene in which it is left for a sufficient time to allow the balsam to dissolve completely, so that the cover-slip comes off without any force being used (premature attempts to remove the cover-slip will result in serious damage to the specimens). The period necessary to dissolve the balsam varies greatly with the age of the preparation, old preparations taking much longer than new ones. The specimens are then passed back through absolute and 90% alcohol into 70% alcohol, from which point their treatment is the same as for newly collected specimens. Material in a gum-mountant is treated in the same way except that the solvent is water and they can go direct from this into 70% alcohol.

(7) ACKNOWLEDGMENTS.

It is my pleasant duty to thank a large number of people who have helped me with material, records, or criticism.

The late Dr. John Eric Hill, of the American Museum of Natural History,

and the late Dr. Austin Roberts, of the Transvaal Museum, most kindly arranged to have many mammal-skins in their charge examined for me, and the Trustees of the Coryndon Memorial Museum, Nairobi, permitted me to examine a large number of skins there. To friends in East Africa who have collected mammals specially for me I owe profound gratitude; they include particularly my friend and former assistant Mr. T. W. Chorley, Mr. T. R. F. Cox of the Uganda Administration, Dr. W. J. Eggeling and Mr. Maurice Kanya of the Uganda Forestry Department, Captain C. R. S. Pitman, Game Warden of Uganda, Mr. J. M. Watson of the Uganda Department of Agriculture, Dr. A. J. Haddow of the Rockefeller Yellow Fever Research Institute, Mr. G. R. Cunningham van Someren of the Nairobi Municipality, Messrs W. V. Harris and D. Thornton of the Tanganyika Department of Agriculture, Dr. C. H. N. Jackson and Messrs. W. E. F. Thomson and F. L. Vanderplank of the Tanganyika Department of Tsetse Research, Mr. F. L. Hendrickx, Mycologist in the Belgian Congo, and Dr. H. J. Brédo of the International Locust Control Organization. Dr. B. De Meillon, of the South African Institute for Medical Research, and Mr. D. H. Davis, Government Ecologist, Union of South Africa, have provided a quantity of South African material, and the latter has also permitted me to include the unpublished records of his louse-collections from Sierra Leone. Further valuable records were obtained from material sent to me by the South African Zoological Survey. Messrs W. L. Jellison and C. R. Twinn have contributed a number of hitherto unpublished records from the United States and Canada respectively.

Dr. F. L. Werneck has freely placed his unrivalled knowledge of the lice of South American mammals at my disposal and my technique has largely been learnt from him. I am particularly indebted to him for permission to quote records from the unpublished part of his monograph of the Mallophaga of mammals.

Dr. R. Broom, of the Transvaal Museum, has given me much help with regard to the origins of the groups of mammals. Dr. Remington Kellogg, of the United States National Museum, kindly obtained for me identifications of a number of skins in that museum from which Ferris (1920-1935) obtained lice and which were incompletely determined when Ferris wrote, and Messrs. T. C. S. Morrison-Scott and R. W. Hayman of the British Museum and the late Dr. John Eric Hill of the American Museum of Natural History have given me much help with regard to the nomenclature of the mammals.

I cannot mention individually those friends, scientific or otherwise, who have read and criticized portions of my manuscript, because their name is legion. Many of their suggestions have been rejected, but those which I have adopted have considerably improved the paper.

Dedications are out of fashion, but in spite of this I dedicate this paper to the memory of Launcelot Harrison. He was one of the first to see the importance of lice in relation to the phylogeny of their hosts, and was the first to perceive the possibility of deducing the antiquity of the parasitic habit in the Mallophaga from their present host-distribution; the tentative conclusions at which he arrived, and which he put forward with much diffidence, have triumphantly survived my more detailed examination of the evidence.

II. BIOLOGY OF LICE.

(1) GENERAL.

Our knowledge of the biology of lice of mammals is very uneven. We know a great deal about the biology of *Pediculus humanus*, thanks to the labours of very many workers of whom Nuttall and Buxton (and his colleagues) are perhaps the most prominent. We know a little about the biology of *Phthirus pubis*, of some half-dozen sucking lice of domestic mammals, and a few Trichodectidae (Mallophaga) of these latter, supplemented by some knowledge of the

bionomics of the Mallophaga of birds. Our knowledge of the biology of *Haematomyzus* is confined to its oviposition and hatching, and the fact that there are three nymphal stages (Weber, 1939). Furthermore, some of the observations which have been made were on lice kept in very unnatural conditions, and may have very little relevance to the natural biology of these insects. The life-histories which we know are all very similar in most respects, and a very rough outline will serve my present purpose; only those aspects of the biology of lice that have an obvious bearing on their distribution on host-species are discussed.

All the Phthiraptera are obligatory external parasites of mammals or birds. The eggs are fastened to hairs or feathers and it has been shown in some instances that they will not hatch if kept at a temperature much below the normal body-temperature of the host. In both Anoplura and Mallophaga there are three nymphal stages, and the nymphs resemble the adults in habits and in general appearance. The duration of the egg-stage and pre-adult life is only known for a very few species and doubtless varies with the normal temperature of the host as well as with the species of louse: the egg-stage may be put at about one to nearly three weeks and the nymphal life at about a week to a fortnight. The pre-oviposition period is from one to three days. The average period from egg to egg is perhaps about three weeks or a month, which would permit of about 12-14 generations per year.

There is also extremely little information about the longevity of the adult, but what evidence is available suggests that it is usually by no means great. Watts (1918) gives the duration of life of the pig-*Haematopinus* as 30-40 days, of which about half represents the adult stage. In the case of *Haematopinus eurysternus* the maximum longevity of adults in somewhat unnatural conditions on the host was sixteen days for the female and ten days for the male (Crauford-Benson, 1941, pp. 336, 337), but it is possible that these figures are unduly low owing to the rather unnatural conditions; in *Pediculus humanus* and *Phthirus pubis* the average life of the adult under an approach to natural conditions is about a month, and in the *Pediculus* the difference between the sexes in this respect is small (Bacot, 1917, p. 257; Buxton, 1939, pp. 37, 95). Matthyse (1944) found the maximum life of the female of *Damalinia bovis* to be forty-two days. It is probable that the fact that the average life of the male may be much shorter than that of the female accounts for many of the frequent instances in which males are much rarer than females, but in some instances the discrepancy in numbers is so great that some other factor must be involved (see p. 413).

The number of eggs laid by *Pediculus humanus* may reach 300; for other species the number known to be laid is very much smaller, but this may mean merely that our observations are inadequate. Lamson (1917) states that *Haematopinus eurysternus* lays from 35 to 50 eggs, and Nuttall records a single instance of *Phthirus pubis* laying 26. Unfertilized eggs of most species are not known to hatch, but Matthyse (1944) found parthenogenesis to be normal in *Damalinia bovis*, and its discovery in some other species in which there is a huge excess of females would not be surprising.

From the above facts it is clear that, in theory, a single fertilized female louse could give rise to an enormous infestation within a very short period, and Eichler (1940 a, p. 35, 1940 c, p. 260) records the rise of an artificial infestation from 200 to 14,000 in 80 days, but in practice biological checks normally limit infestations to far below the theoretical figures. We know very little of the nature of these biological checks, but Buxton (1939, pp. 45-46) has shown that one of them, in the case of *Pediculus humanus*, is the injury inflicted by males on females when opportunities to attempt pairing are too numerous.

(2) Food.

The food varies considerable with the group. The Mallophaga have long been known to feed on hair or feathers (including the "pith" of large quills),

but it is now known that keratin is by no means always their sole diet. Ewing (1942 c, pp. 3-4) could find no evidence that *Gyropus ovalis* and *Gliricola porcelli* (belonging to the amblycerous family Gyropidae) fed on the hair of their host, and noted that heavy infestations of the latter species appear to cause the hair to become brittle. He considered that the main food of these species might be serum and the secretions of the sebaceous glands, and it is likely that his observations would apply to all the Gyropidae. Blood, also, is sometimes an item in the diet of the biting lice. No one who has examined the Mallophaga on freshly shot birds can have failed to find many (perhaps especially members of the Ischnocera) which have obviously ingested blood from the wounds, but Wilson (1933, p. 490) has shown that blood may be ingested by *Menacanthus stramineus* (Nitzsch), a member of the Amblycera, from wounds made by the louse itself in the quills of young feathers "from which the dermal papilla, bearing blood vessels, had not yet withdrawn", and according to Eichler (1936, p. 493) this species is in a definite transitional stage from a normal diet of feather-substance to one of blood. Dutton (1905, p. 140) found another member of the Amblycera, evidently *Dennyus minor*, feeding on blood and lymph as well as feathers. In the case of another genus of the Amblycera, *Piagetiella* (formerly *Tetrophthalmus*), a similar diet has clearly become normal, for this genus lives exclusively in the interior of the pouches of pelicans and certain cormorants, where the lice attach themselves so firmly by their mandibles to the mucous membrane lining the pouch that they are difficult to detach; removal of the parasite discloses a small swollen area bearing at its apex the two small red wounds made by the mandibles. In such a situation the lice obviously cannot feed on feathers, and it seems certain that blood or mucus must be their normal diet. Eichler (1937a, pp. 92-93) and Colas-Belcour and Nicolle (1938, p. 638) quote many other examples of the ingestion of blood by Mallophaga, but in most cases the circumstances are not recorded, and it seems probable that many of them are instances of the ingestion of blood from wounds not made by the lice themselves. *Trimenopon hispidum*, an amblycerous parasite of the guinea-pig, evidently feeds on blood to a significant degree, and probably obtains it from wounds produced by the host in scratching itself.

No observations seem to have been made with regard to the food of *Haematomyzus elephantis*, but as the species occurs nearly hidden in small folds of the skin it seems likely that it feeds on skin-debris and possibly sebaceous matter. The Anoplura feed solely on blood.

(3) REACTIONS TO TEMPERATURE.

For the few species of lice in which the factor has been studied, the optimum temperature appears, as might be expected, to be approximately that of the surface of the body of their normal host; the plumage or fur of the host is an effective safeguard against large fluctuations of temperature, so that normally their environment is very constant in this respect. Lyonet, who died in 1789, used the positive tropism of lice to temperatures approximating that of the host as a means of collecting them (Lyonet, p. 261).

Exposure to temperature only four or five degrees centigrade above the host's normal body temperature may result in death within a few hours, and in *Pediculus humanus* temperatures less than 20° C. above the normal temperature of the host will cause death of the lice within an hour (Buxton, 1940 a, p. 373); if kept at such temperatures, eggs of lice fail to hatch. Furthermore, it is probable that lice which have been exposed to high temperatures and have survived the experience may be too much affected to be able to breed, as Buxton (1940 b) has shown to be the case in *Pediculus humanus*. Great caution is always necessary in drawing parallels between different groups of animals, but the fact that in a few observations on such a distantly related arthropod as a tick (*Ornithodoros moubata*) I found that eggs laid by females which had

survived high temperatures invariably failed to hatch suggests that Buxton's observation may apply to all lice. Buxton (1939) points out that in the tropics and subtropics the temperature of the surface of bare earth is often above the thermal death-point of lice. He also notes (1920, p. 174) that in the dry hot summers of the Persian plateau lice "appear to survive with difficulty and to breed very slowly". Matthysse (1944) found that the normal skin-temperatures of cattle during the summer in the United States are too high to permit of the maintenance of a population of *Damalinia bovis*, and in direct sunlight may even reach a point lethal to the lice. In these conditions the louse-populations drop to a minimum and perhaps survive by migrating to the more sheltered situations on the host, as Brinck (1948 *b*, pp. 142, 143) finds to be the case with horse-lice in Sweden.

Temperatures below the optimum are less quickly lethal, and lice are able to survive long periods at temperatures considerably below that of the host if they are "warmed up and fed daily" (Buxton, 1939, p. 34). Crauford-Benson (1941, pp. 338-339) kept unfed specimens of *Haematopinus eurysternus* at 20° C. and 70% relative humidity, and found that about one-third of them were able to resume normal life after forty-eight hours, that no adults and only a very few nymphs could do so after seventy-two hours, and that none of the lice tested for ninety-six hours were able to resume life on the host. He also found (*l.c.*, p. 341) that eggs of all the cattle-lice are unable to hatch at temperatures much below that of the host, and that exposure to the temperature of a cow-stall for twenty-one days was fatal to all eggs, even when subsequently placed in favourable conditions. He obtained indications that at temperatures lower than 20° C. the period necessary to ensure death of the lice is shorter, and cold has been used for destroying *Pediculus humanus*. Leeson (1941, p. 49) found that there is no marked difference between the survival periods of unfed nymphs and those of unfed adults of *Pediculus h. humanus* when exposed to the same temperatures.

It was formerly thought impossible to keep lice alive for more than a few days off the host, but attention to the temperature-factor has shown that this view is erroneous. Oudemans (1912 *a*, p. 219) and Barber (1921) kept several species of Mallophaga alive for weeks in artificial conditions, and Wilson (1934) and Matthysse (1944) reared other species from egg to adult and obtained a second generation; suitable food was provided. Sucking lice can also be kept alive for long periods at suitable temperatures if they are given frequent opportunities of obtaining the blood of their host.

Slight changes in temperature, such as are produced by pyrexia in the host or by the first stages of the gradual cooling of the host's body after (or just before) death, are apt to produce "a certain liveliness" among the louse-population, the lice obviously becoming uncomfortable and tending to wander about as if to escape the discomfort. Eichler, for instance (1940 *d*), records that just before the death of a dog great numbers of *Trichodectes canis* appeared on the tips of its hairs, causing it to appear as if sprinkled with lice. Further cooling results in a state of akinesis, in which the louse will remain motionless until death if its instinctive responses are satisfied by it being able to cling to the skin, hair or feathers of its normal host (Buxton, 1939, p. 30, and innumerable observations on bird-lice).

Eichler (1936, p. 474) and Wilson (1937) have put forward the interesting suggestion that absence of lice on bats may be connected with the lowering of their body-temperature during hibernation, and Wilson distinguishes between true hibernation, accompanied by a definite drop in the temperature of the animal, and mere "denning-up" for the winter with no drop in temperature. But he gives the woodchucks (genus *Marmota*) as a definite example of true hibernation "with greatly lowered body temperature", and bases his suggestion largely on the supposed fact that "no lice, sucking or biting, have ever been

reported from a woodchuck". Not only are lice known from woodchucks, but the occurrence of some of them on these hosts in natural conditions is fully confirmed (see p. 461). Moreover, bats in the tropics, which do not undergo hibernation, are as free from lice as are the bats of temperate regions. It may well be that the drop in temperature accompanying true hibernation has been one of the factors which have resulted in certain groups of mammals being free from lice, but it certainly will not account for more than a few of the instances of this phenomenon.

(4) ECOLOGICAL NICHES.

In the case of the bird-infesting Mallophaga the fact that different groups of these lice occupy different ecological niches on the host is a matter of everyday observation, certain genera occurring mainly or exclusively on the head, on the wings, or on the body. In the case of the mammal-Mallophaga we have no direct evidence of such a differentiation, and the occurrence of more than one species of chewing lice on the same mammalian host-species is very rare in most groups of hosts, though multiple infestations with Mallophaga are normal among the hyraxes and certain groups of rodents, and not infrequent in the Viverridae, while there are a very few instances of this phenomenon in the Mustelidae, Cervidae and Bovidae. There is no evidence that the numerous genera and species to be found on the hyraxes show any preference for different parts of the body, though it seems reasonable to assume this as a probability. Eichler (1939 c, p. 210) produces evidence that *Trimenopon* and *Glinicola* on the guinea-pig utilize different areas of the host's body for oviposition.

In the Anoplura the best-authenticated instance of preference for certain ecological niches is furnished by the lice of man: *Phthirus pubis* is rarely found on the head, *Pediculus humanus humanus* is very largely confined to the parts covered by clothing (and is uncommon among people who do not wear clothes), while *P. h. capitis* is largely confined to the head; these conclusions are not affected by the disputed status of the two forms of *P. humanus*, because at the very least they must be regarded as incipient subspecies. Another definite instance of this phenomenon is that of *Linognathus ovillus* and *L. pedalis* on the sheep (see p. 534). In most other instances there is no direct evidence on the point, but it seems to me to be very suggestive that, in the great majority of cases in which two or more species of one genus occur on a single host, one of the principal differences between the species is the degree of elongation of the head, since this suggests a difference in feeding-habits. The differentiation in head-shape is very clearly shown among the lice of antelopes, on which it is normal for two species of *Linognathus* to occur, one belonging to the long-headed *tibialis*-group and the other to the short-headed *pithodes*-group. Similarly, hyraxes normally possess a long-headed and a short-headed species of *Prolinognathus*, and the same phenomenon is exhibited by the three species of *Microthoracius* found on South American Camelidae. The short type of head is normally accompanied by a short body, as in the case of *Phthirus pubis*, which shows this condition in an extreme form. It can hardly be doubted that this difference in head-shape has followed some change in ecology, of which it is presumably the result.

A curious extension of the principle of the occupation of ecological niches is that in certain lice it would appear that different areas of the host's body are sometimes used for different purposes. Crauford-Benson (1941, pp. 346-350) showed that populations of both *Haematopinus eurysternus* (Anoplura) and *Damalinia (Bovicola) bovis* (Ischnocera) are differentiated into breeding colonies and nymphal clusters; these show a considerable degree of localization to different areas of the body, which are not the same at different seasons. The differentiation is more complete in the *Haematopinus* than in the *Damalinia*, in which the nymphal clusters are accompanied by many adults. His observations suggest that in the *Damalinia* there is a higher proportion of males in new breeding-areas than in old ones and a still smaller proportion in nymphal areas, but

he was working with a species in which males are very rare, so that it is probable that the casual error is very large.

Some very inadequate observations of my own strongly support Crauford-Benson's suggestion that sex-ratios vary in different areas of the body. A skin of *Alcelaphus buselaphus roosevelti* was being examined by the dissolving technique, the procedure being for an African to cut pieces of convenient size from the skin, remove the hair, and pass the latter to me for boiling and examination. Successive lots of hair (not all of the same size) produced the following counts of adult *Damalinia chorleyi*: 10 males 71 females; 51 males 23 females; 0 males 11 females; 21 males 5 females; 24 males 32 females. In this observation the areas of the body from which the different lots of hair were taken were not noted, but a second skin was available, and this was examined by areas of very roughly equal size (the head and neck somewhat smaller than the rest). The counts from this second skin are given in Table I. Time would not allow the very numerous nymphs to be counted in either of the observations.

TABLE I.—Proportions of males and females of *Damalinia chorleyi* obtained by dissolving the hair of different areas of a skin of *Alcelaphus buselaphus roosevelti*.

Area.	Males.	Females.	Total.	Male percentage.
Front legs	23	65	88	26
Hind legs	52	124	176	30
Head and neck	144	74	218	67
Shoulders and fore-body ..	242	297	539	45
Mid-body	29	21	50	58
Rump and hind-body .. .	44	46	90	49
Total.	534	627	1161	45

In the first observation an apparent correlation was noted between percentage of males and size of nymphs, the nymphs in the two lots of hair with exceptionally low male percentage being all small, whereas in the remaining lots the nymphs were of all sizes and included many in the last stage. In the second observation this correlation did not appear, all the lots including large nymphs as well as small ones, but there were no lots with such low male percentages as in the first and third lots in the first observation, the reason probably being that my areas were too large, so that each of them included several colonies of lice. The apparent relative absence of males where all the nymphs are small needs confirmation, but suggests the possibility that fertilized females are not attractive to males and that these latter congregate in areas where last-stage nymphs are giving rise to adults and virgin females are therefore available. Be that as it may, the fact that the sex-ratios are very different in different parts of the host's body emerges very clearly from the two observations and has an important bearing on collecting technique, for it demonstrates that figures intended to show the proportions of the sexes of a louse may be completely misleading unless the whole body of the host has been examined. Another point which stands out clearly is the great concentration of population of *D. chorleyi* in the shoulder-area, while (in view of the smaller area involved) the head and neck must also be considered a concentration-area. In view of Crauford-Benson's observations of seasonal changes, it may be as well to record that the two specimens of *Alcelaphus* were shot (in Uganda) in September, though it is not very probable that any marked seasonal differences in the areas of louse-concentration occur in Uganda, where differences between the seasons are relatively small. Spencer (1939) states that in wild deer the back is the principal site for parasites (though there is some variation according to the time of year) and that it is on the back that lice lay their eggs.

(5) LOUSE-POPULATIONS OF HOST-INDIVIDUALS.

Lice may occur in enormous numbers on a host-individual, though this is not the rule. Buxton and his collaborators have published many observations on the populations of *Pediculus humanus* to be found on man, and he records (1939, p. 47) one case of the occurrence of more than 3800 lice on a single host-individual, while Nuttall (1917 c, p. 86) quotes a record of 10428 lice on a single shirt, and Eichler (1940 d, p. 215) one of 16822 on a shirt and an estimated 25 to 30000 on the man's whole clothing. There are old records of what may have been even heavier infestations of man: Denny (1842, p. 17) mentions a friend of his on whom lice swarmed to such a degree that "you might have actually scooped them out with a teaspoon", and MacArthur (1927, p. 488) records of Thomas à Becket that "the innumerable vermin which had infested the dead prelate were stimulated to such activity by the cold, that his hair-cloth garment, in the words of a chronicler, "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". Taking into consideration the relative size of the hosts and the parasites, Eichler's record (1940 d, p. 216) of about 6000 specimens of *Polyplax* on a rat is equally noteworthy.

Turning to the ischnocercous Mallophaga, I have myself obtained 1514 specimens of *Felicola subrostratus* from a mongoose and 4070 individuals of the same species from a civet, in both cases by the brushing technique (Hopkins, 1941 b, p. 38). I have also collected 1758 adults of *Damalinea adenota* from an individual *Adenota kob* by the dissolving technique, and consider that a count of the nymphs would have brought this figure up to at least 5000. Eichler (1936, p. 479) found about 2500 specimens of *Trichodectes melis* on a badger. The same author (1940 a, p. 35; 1940 c, p. 260) records more than 14000 specimens of *Trichodectes canis* from a sick fox that had been artificially infested, and states that this population had bred up from an original 200 in 80 days; he also (1940 d) observed a dog with an estimated population of 20000 of the same species of louse.

For the Amblycera there are practically no records, but Werneck (1942 d, p. 298) mentions that guinea-pigs are often infested by two or three thousand individuals of *Gliricola porcelli*. It has been shown in the case of *Pediculus* on man that, as might be expected, those populations in which the heaviest louse-infestations of individuals occur are also those in which the highest proportions of individuals are infested (Buxton, 1939, p. 47).

Leaving out occasional counts of the lice obtained by searching and brushing (which are only a small fraction of the total population unless the work has been done with unusual thoroughness), there are hardly any published records of the numbers of lice found on individual specimens of wild hosts. In these circumstances I would have liked to have published a table showing all counts done by myself of the louse-populations of individual wild mammals, but unfortunately this table proved to be much too large for publication, so I have had to be content with publishing a small portion of it (Table II); the full records are available to any serious student of the lice. My counts are almost certainly too low, because it is likely that a certain number of lice leave the skin before it reaches my hands, and that a few more are lost during the preparation of the hair for examination and the filtering out of the lice. Furthermore, a certain number of the lice eventually obtained doubtless escape notice among the debris, especially when this is large in quantity. Among this mass of debris*, which may

* This debris consists largely of vegetable matter (including fragments of leaves, small burrs and other seeds), sand, fly-eggs and young maggots if the skin has been allowed to get fly-blown, and (if the skin has been stored for long) often dermestid beetle larvae and the cast skins and setae of these latter. Fragments of true hair do not occur if the material has been boiled for a sufficient time.

TABLE II.—Counts of populations of adult lice obtained from individual skins by use of the dissolving technique.

PRIMATES.				
<i>Cercopithecus nictitans mpangae.</i>				
Locality.	Date.	Age.	Mallophaga.	Anoplura.
Bwamba, Uganda.	July 1943	—	0	1
" "	" "	—	0	6
" "	" "	—	0	2
" "	" "	—	0	3
" "	" "	—	0	2
" "	" "	—	0	3
" "	" "	—	Seven skins without lice.	
<i>Colobus polykomos uellensis.</i>				
" "	July 1943	Young	0	4
" "	" "	Young	0	5
" "	" "	Young	0	2
" "	" "	Young	0	0
				(nymphs present)
" "	March 1944	Young	0	2
" "	" "	Young	0	21
" "	" "	Young	0	9
" "	" "	Young	0	16
" "	" "	Adult	0	8
" "	" "	Adult	0	4
" "	" "	Adult	0	15
" "	" "	Adult	Four skins without lice.	
" "	October 1944	Young	0	5
" "	" "	Young	0	3
" "	" "	Young	0	16
" "	" "	Young	0	5
" "	" "	Adult	0	5
" "	" "	Adult	0	34
" "	" "	Adult	0	8
" "	" "	Adult	Two skins without lice.	
CARNIVORA.				
<i>Felis lybica rubida.</i>				
Kivu dist., Belgian Congo.	Aug. 1943	Adult	3	0
" "	" "	Adult	8	0
" "	" "	Adult	Many thousands	0
ARTIODACTYLA.				
<i>Adenota kob thomsi.</i>				
Lango dist., Uganda	March 1942	Adult	93	1
" "	" "	Adult	3	3
" "	" "	Adult	7	0
" "	" "	Adult	1758	2
" "	" "	Adult	0	0
<i>Raphicerus campestris neumanni.</i>				
Sultan Hamud, Kenya.	Oct. 1943.	Adult	44	8
Shinyanga, Tanganyika.	July 1943	Adult	0	0
" "	Sept. 1943	Adult	34	29
<i>Raphicerus s. sharpei.</i>				
Near Abercorn, N. Rhodesia.	Aug. 1943	Adult	189	0
<i>Sylvicapra grimmii nyansae.</i>				
Lango dist., Uganda.	March 1942	—	14	166
" "	" "	—	0	261
" "	" "	—	0	53
" "	" "	—	0	19
" "	" "	—	4	45
" "	" "	—	0	26
" "	" "	—	0	17
" "	" "	—	0	5
" "	" "	—	0	3
" "	" "	—	0	3
" "	" "	—	0	14
" "	" "	—	0	0

be almost completely absent in favourable cases, it is easy to overlook very small lice and especially the earlier nymphal stages. But I believe that the error introduced into the counts of adult lice by these factors is quite small (probably under 10%) and that the counts represent close approximations to the total adult louse-populations of the living hosts.

Less than 200 skins, belonging to a large number of species, have been examined by the dissolving technique, so that the number of skins of each species which has been dissolved is always small. Few general deductions can safely be drawn from such a small number of counts, but I wish to draw attention to the enormous variations in louse-population found within a single host-species, even when the skins were all collected in the same district and at the same time of year. This is very well shown by several of the species included in Table II. Another point which seems worthy of mention is the lightness of the infestations of wild cercopithecoïd monkeys, which is confirmed by examination of smaller numbers of two other species. This is in striking contrast with the fact that captive monkeys of this group are often heavily infested, but agrees perfectly with the observations made by Dunn (Ferris, 1920-1935, p. 598) on ceboid monkeys and with Werneck's note that his single record of many lice on a wild member of this latter group was very exceptional (Werneck, 1937 *d*, p. 162). Evidently captivity favours the occurrence of sucking lice on monkeys, and a possible reason for this phenomenon is mentioned on p. 430.

Although I have dissolved less than 200 skins, I have examined at least 2000 wild African mammals by this and other methods, so certain generalizations are probably permissible in spite of the fact that most of the specimens were examined by brushing. The Rodentia normally have rather light infestations, both as regards number of louse individuals and the proportion of hosts infested; an infestation of about twenty adult lice is heavy for most rodents. Among the Carnivora I have examined very few Canidae, and these were mostly louse-free, though heavy infestations may occur. The Viverridae are commonly heavily infested, the heaviest infestations occurring in those species which have long and somewhat coarse coats. The rather few Mustelidae I have examined almost all belong to the Mustelinae; *Pocilogale* and *Ictonyx* are almost invariably infested, but the infestations are not very heavy, while the few *Mellivora* examined were mostly louse-free; only one otter-skin has been dissolved, and otters possess coats of such a nature that searching or brushing are particularly unproductive methods. Among the Felidae, *Felis lybica* is generally infested, and there is enormous variation in the heaviness of the infestations; the larger Felidae (of which only half a dozen have been dissolved) have always proved to be without lice. In the Ungulata, too, there is an apparent correlation between size of host (or some factor associated with size) and louse-infestations. In my experience small ungulates are usually heavily infested, whereas the large species are often either louse-free or only lightly infested, though there is much variation which appears to be partly specific. The suggestion that size is important finds some support in the fact that the hyraxes, which are the smallest ungulates I have examined, are among the lousiest of mammals, louse-free individuals being very uncommon and considerable numbers of lice being obtainable by brushing from almost every individual. In other groups I have examined too few individuals to be able to generalize except in the case of the monkeys, whose light infestations have already been mentioned.

On the question whether young mammals are more susceptible to louse-infestations than are adults of the same species there is little definite evidence, and this is not wholly conclusive. Of eight skins of young individuals of *Tragelaphus scriptus bor* which I examined by the dissolving technique, four were not infested with Ischnocera (*Damalinea annectens*) and the rest bore an average of twelve specimens, while of eight adult skins four were not infested and the average population of the rest was ninety-five lice. But this apparent difference is almost certainly not significant, because it is almost wholly accounted

for by one exceptionally heavily infested skin, the average population on the rest of the adult skins being only five lice. Crauford-Benson (1941, p. 354) considers that calves are probably more susceptible than older cattle to three of the cattle lice (*Damalinea bovis*, *Linognathus rituli* and *Solenopotes capillatus*), but less so to *Haematopinus eurysternus*; he is inclined to attribute the high infestations of calves to the fact that they are normally kept indoors. Mitzmain (1912) observes that old individuals of the Indian buffalo are largely hairless and have few lice (*Haematopinus tuberculatus*); he considers, probably correctly, that these two observations are cause and effect. In view of the paucity of observations on wild Artiodactyla I can only record a general impression that young animals appear to be more heavily infested than adults: the point obviously requires further investigation. In the case of certain Primates, however, there seems to be good evidence that young individuals are more susceptible to infestations of Anoplura than are adults. Buxton (1941 a, p. 194) finds evidence to support a suggestion that man's resistance to infestation with the head-lice increases as the host grows older, and I have similar evidence with regard to a catarrhine monkey: twenty-five skins of *Colobus polykomos uellensis*, all from the Bwamba portion of the Semliki Forest in Uganda, were roughly sorted into "apparently adult" and "obviously young", and then examined by the dissolving technique (Table II); the thirteen young skins (five obtained in July 1943, four in March 1944, and four in October 1944) were all infested with *Pedicinus pictus*, whereas of the twelve classed as adults (seven March 1944 and five October 1944) only six were infested. This relative immunity to louse-infestations on the part of adult animals is probably a very general phenomenon, for I have often observed young but fully fledged birds to be much more heavily infested with Mallophaga than fully adult specimens of the same species obtained at the same time and place.

Crauford-Benson (1941, pp. 350-358) examines a number of other factors which might influence the size of populations of cattle-lice, and shows that the density of the host's coat (perhaps as influencing temperature or light-intensity) is of importance. Some of the other factors which he considers are shown to have no obvious influence, and others are unlikely to affect lice on wild hosts, but he states (p. 257) that "animals in poor health, usually as a result of feeding on poor quality food, are more susceptible to lice infestations than animals in good health". This agrees with the observations of many other writers, who state that sick animals are commonly much more heavily infested with both Mallophaga and Anoplura than are those in good health. Spencer (1936 a, p. 356) notes that in British Columbia stunted island-forms of deer, and sickly individuals from other areas, are apparently more heavily infested with parasites than large and healthy individuals, but his remarks do not apply solely to lice: he considers that parasites are more abundant on mammals in early spring than at other times, and attributes this to weakening of the host by severe winter conditions. Eichler (1942 a) records many instances of sick mammals and birds with abnormally heavy louse-infestations, and considers that the lowered resistance of the host is the usual cause of this phenomenon. And Thompson (1936 a, p. 36) also draws attention to the fact that Mallophaga may be more abundant on sickly birds than on healthy members of the same species. In the case of birds it has been suggested that the reason is the inability of a sick bird to take the usual measures to rid itself of parasites, but the phenomenon is too general for this suggestion to be a complete explanation, and I agree with Eichler in considering lowered resistance to be the principal factor. Wild mammals in obviously poor health are very rarely seen except during epizootics of such diseases as rinderpest, but it would be of much interest to compare the louse-populations of sick and healthy animals and also to compare the louse-infestations of tropical species during the wet season with those at the end of the dry season, when the grass in some areas is very dry and probably very lacking in nutritive qualities.

(6) COMPOSITION OF LOUSE-POPULATIONS.

Since a fertilized female louse arriving on a new host-individual obviously has a better chance of starting a new colony than any other sort of louse, the composition of natural populations of lice has some relevance to my subject, but I must admit that I deal with it largely because I have a considerable body of new facts to bring forward (Table III).

TABLE III.—Sex-ratios in natural populations of mammal-lice. Only species for which records of at least 50 specimens are available are included.

Species.	ANOPLURA.			Male Total. percentage.
	Males.	Females.	Total.	
<i>Haematopinus eurysternus</i> , a ..	—	—	—	20
<i>Haematopinus suis</i> , b ..	—	—	—	20
<i>Linognathus brevicornis</i> ..	36	118	154	23
<i>Linognathus fahrenheitii</i> ..	29	38	67	23
<i>Linognathus</i> sp. (from <i>Gazella thomsonii</i>). ..	26	48	74	34
<i>Pedicinus pictus</i> ..	84	78	162	50
<i>Pediculus h. humanus</i> , c ..	177	199	376	47
<i>Pediculus h. capitis</i> , c ..	4316	4116	8432	50
<i>Phthirus pubis</i> , d ..	88	144	232	38
AMBLYCERA.				
<i>Heterodoxus spiniger</i> , e ..	114	151	265	43
ISCHNOCERA.				
<i>Damalinea adenota</i> ..	749	1048	1797	42
<i>Damalinea americana</i> , f ..	0	150	150	0
<i>Damalinea annectens</i> ..	57	63	120	48
<i>Damalinea bovis</i> , a ..	—	—	—	4
<i>Damalinea chorleyi</i> ..	640	769	1409	45
<i>Damalinea conectens</i> ..	53	64	117	45
<i>Damalinea equi</i> , g ..	4	>1000	—	<0.4
<i>Damalinea lineata</i> ..	126	141	267	47
<i>Damalinea longicornis</i> , h ..	0	452	452	0
<i>Damalinea ocellata</i> ..	25	62	87	29
<i>Damalinea</i> , sp. nov. near <i>ocellata</i>	43	56	99	43
<i>Damalinea ourebiae</i> ..	166	219	385	42
<i>Damalinea parkeri</i> ..	39	43	82	48
<i>Damalinea reduncae</i> ..	57	57	114	50
<i>Damalinea spinifer</i> ..	138	214	352	39
<i>Damalinea victoriae</i> ..	212	381	593	36
<i>Dasyonyx hopkinsi</i> ..	33	37	70	47
<i>Dasyonyx transvaalensis</i> ..	27	50	77	35
<i>Dasyonyx validus ugandensis</i> ..	29	33	62	47
<i>Felicola acutirostris</i> ..	34	35	69	49
<i>Felicola rostratus</i> ..	1261	1568	2829	45
<i>Procavicola bedfordi dissimilis</i> ..	169	169	338	50
<i>Procavicola lindfeldi</i> ..	41	52	93	44
<i>Procavicola thurtoni</i> ..	24	46	70	34
<i>Procaviphilus serraticus</i> ..	58	106	164	35
<i>Trichodectes ovalis</i> ..	47	46	93	50

a. Craufurd-Benson, 1941. He records that bred specimens of *H. eurysternus* comprised 26 males and 35 females (male percentage 43).

b. Alessandrini, 1919.

c. Buxton, 1941 b.

d. Nuttall, 1918.

e. Includes Plomley, 1940.

f. Jellison, 1935.

g. Werneck, 1914 b and *in litt.*; Dr. C. F. W. Muesebeck of the U.S. Bureau of Entomology, *in litt.* This male percentage is probably much too high.

As mentioned before (p. 407), the compositions of different colonies of lice on a single host-individual may vary very greatly, and for this reason I have rejected from the table all records (including many of my own) which probably do not represent a fair sample of the louse-population. I have made exceptions

in favour of Buxton's records of *Pediculus humanus* and Nuttall's records of *Phthirus pubis* because these forms are sufficiently localized for mere examination to produce fair samples of them (though we do not know if one sex is more given to wandering than the other) and in favour of records of *Damalinia americana*, *D. longicornis*, *D. bovis* and *D. equi* because these illustrate a very interesting point which is not shown to the same degree by any other available figures. Unless stated otherwise, all the records shown in the table are my own. Unfortunately I had to refrain from making counts of some very heavy infestations for lack of time.

The general rule in all groups of lice for which figures are available is that females slightly or considerably exceed males in number in natural populations. This applies to many genera of the Amblycera (for which I have hardly any accurate figures), to *Haematomyzus elephantis*, and to many genera of Anoplura and Ischnocera additional to those represented in the table. I do not know of any instance of a considerable normal excess of males,* and (since the presence of too many males is inimical to the females) it is improbable that such cases will occur in adequate samples, but the female excess may be enormous. The extreme known instances of this phenomenon are *Damalinia americana*, *D. longicornis*, *Geomydoecus scleritus* and *Damalinia equi*, in the first three of which the male is unknown, while in *D. equi*, although the louse is a common parasite of the horse, the male was only discovered in 1941 (Piaget's supposed males of *D. equi* are nymphs); the male of this species is hardly smaller than the female and therefore not likely to be easily overlooked. In such instances suspicion that parthenogenesis must be normal is inevitable, and it has now been shown (Matthysse, 1944) that this is true in the case of *Damalinia bovis*.

Great differences in the proportions of the sexes are by no means confined to distantly related groups of species. *Damalinia ocellata* is so closely related to *D. equi* that they were long thought to be the same, yet in the former species and a very closely related new species (also from a zebra) males comprise 29% and 43% of the population in fairly adequate samples, as against a male proportion much under 1% in populations of *D. equi*. Similarly, in most species of *Geomydoecus* males are quite common, but in a batch of about three hundred adults and many hundred nymphs of *G. scleritus* sent to me unsorted by the American Museum of Natural History this was far from being the case, not a single male being found.

Buxton (1941 c) discusses the enormous differences in the sex-ratio of populations of *Pediculus humanus capitis* from different individual crops of hair, and shows that, when the total number of lice is low, unisexual infestations are common. It is to be assumed that purely male populations are either infestations which are very new (and doomed to annihilation if not reinforced by females) or those in which nymphs have not yet given rise to females. The only definite correlation which he has been able to discover in this connection is one between unusually dense infestations and a high proportion of male lice: he considers (Buxton, 1941 c, p. 231) that this may be due to injury to the females by the males when opportunities for encounters between the sexes and consequent attempts (successful or otherwise) to pair are too frequent.

It is probable that instances of a small excess of females in natural populations are brought about by the male being shorter-lived, but this factor is certainly insufficient to account for such cases as those of *Damalinia americana*, *D. bovis* and *D. equi*. The occurrence of unisexual families is already known in the case of *Pediculus humanus* (Hindle, 1919; Buxton, 1939, p. 35 and fig. 19), and it seems nearly certain that these instances of an enormous excess of females over males must be brought about by the vast majority of families consisting solely of females. Matthysse (1944) notes that males of *D. bovis*, always rare, "are most numerous in rapidly increasing populations".

* Kéler (1940, p. 48) gives the proportion of males to females in *Trichodectes melis* as 1.4:1 (=58% males), but does not say on how many specimens these proportions are based.

Because very little time has been available to me for work on lice, my counts of nymphal populations are few, and I have felt obliged to reduce the number still further by *rejeeting* those species in which the total figures are very small, and also those counts in which the amount of debris was so large that it is practically certain that the counts of nymphs are much too low. I have also

TABLE IV.—Ratios of adults to nymphs in natural populations of mammal-lice.

ANOPLURA.			
Species.	Adults.	Nymphs.	Adults : nymphs.
<i>Haematopinus burchelli</i> ..	32	71	1 : 2.2
<i>Pediculus humanus capitis</i> , a	4245	14197	1 : 3.3
ISCHNOCERA.			
<i>Damalinea adenota</i> ..	103	213	1 : 2.1
<i>Damalinea annectens</i> ..	120	318	1 : 2.7
<i>Damalinea conectens</i> ..	103	124	1 : 1.2
<i>Damalinea spinifer</i> ..	348	751	1 : 2.2
<i>Damalinea victoriae</i> ..	593	949	1 : 1.6
<i>Felicola rostratus</i> ..	2456	3136	1 : 1.3

a. Buxton, 1941 b.

rejected counts in which the material was derived from dry skins and was not treated with caustic potash prior to examination, because in such material many of the shrivelled-up nymphs are so inconspicuous that they are almost certain to be overlooked. Even with these exceptions the counts of nymphs (Table IV) are probably a good deal too low in some instances, but the nymph-population appears normally to be very roughly twice the population of adults.

(7) EFFECT ON THE HOST.

The direct effect of the presence of Mallophaga is very small unless they are in large numbers, but if this latter be the case they may cause considerable irritation in their peregrinations of the host's body. Most of our information in this connection refers to birds, though serious irritation is recorded as being caused to certain domestic mammals, including horses, sheep and cattle. It has been suggested with a great degree of probability that birds take dust-baths to rid themselves of Mallophaga, and this suggestion is supported by the fact that the habit of taking such baths appears to be commonest among certain of the most heavily-infested groups of birds, though it must be admitted that the habit is apparently absent in some heavily infested groups. Eichler (1938 a, pp. 299-302) has discussed the possibility that the extraordinary habits of certain birds of picking up ants and placing them among their feathers ("active anting") or of placing themselves with outstretched wings on an ant-hill ("passive anting"), may serve to kill their Mallophaga by means of formic acid, or even to permit (in the case of passive anting) of the ants seizing and destroying these ectoparasites; in this connection it is perhaps significant that passive anting has been observed chiefly among crows, which are among the lousiest of birds, and active anting among starlings, which are also usually very lousy; also that (with one exception) no mammals whose diet consists largely of ants are known to be louse-infested. At the same time it must be pointed out that it is by no means certain that the object of the habit is to destroy lice; McAtee (1938) and Chisholm (1944), after reviewing all the records, are not convinced that this is the case, and Col. Meinertzhagen informs me that he does not find ant-eating species of woodpeckers less heavily infested than those of their relatives which do not eat ants. A form of passive anting has been recorded in man (Nuttall, 1917 c, p. 184), soldiers placing their shirts on ant-hills to get rid of the lice, and Debreuil (1917) gives an amusing account of a French tramp using the same method. Heavily-infested mammals sometimes endeavour

to rid themselves of Mallophaga by scratching, and there is evidence (p. 432) that in at least one case this is partially successful. The fact that the dog on which Eichler found an estimated population of 20000 Mallophaga suffered from a defect that prevented effective scratching (Eichler, 1940*d*) is highly suggestive in this connection. The use by certain mammals of mud-baths, and the habit of rubbing themselves against trees, are also doubtless methods by which some lice are eliminated, though probably primarily directed against other ectoparasites.

Direct injury to the plumage or pelage of the host by Mallophaga is usually very slight (though serious damage to the wool of sheep and the feathers of pigeons has been recorded) because the proportion of a feather eaten is generally too small seriously to affect its efficiency before it is due to be shed and a louse-population has to be enormous before the number of hairs eaten can impair the efficiency of a covering of fur. The record (J. M. Harrison, 1931, p. 354) of a jay "rendered flightless by depluming lice" is not convincing, nor is the instance (Thompson, 1936*a*, p. 356) of a blackbird whose breast was denuded of feathers, because if the nakedness had been produced by lice it is probable that the shafts of the feathers would have been left. Although various authors, noting the greater abundance of Mallophaga on sickly than on healthy poultry, have attributed the ill-health or death of the birds to the attacks of the lice, there is little evidence as to whether the abundance of these parasites is the cause or an effect of the state of ill-health (though it doubtless aggravates it) and the evidence rather points to the latter explanation. Moreover, heavy louse-infestations in poultry are commonly accompanied by heavy infestations with parasitic mites, which are blood-suckers and definitely injurious, so that it is not easy to separate the effects attributable to the two groups of parasites. Eichler (1940*c*, p. 260) claims that the death of a heavily-infested fox was due to the infestation, but his evidence is not conclusive.

As would be expected from their feeding-habits, Mallophaga are of little importance as vectors of disease. Veintemellas (see *Rev. appl. Ent.*, (B), 24, p. 313) records successful transmission of typhus from guineapig to guineapig by the amblycerous *Trimenopon hispidum*, while Colas-Belcour and Nicolle (1938) found that in some instances more than 50% of the individuals of this species could be shown to have ingested blood, and that they sometimes contained rickettsias in the gut, particularly if blood was present. These authors also review (p. 639) a few other records of the presence of rickettsias in Mallophaga, including the ischnoceros louse of the horse. Rickettsias have also been observed in *Menacanthus stramineus*, an amblycerous parasite of poultry. Dutton (1905, pp. 140, 142-146) records an unnamed menoponid which (from his figure) was evidently *Dennyus minor*, another of the Amblycera, as a vector of a bird-infesting nematode worm (*Filaria cypseli*). The immature stages of one of the tapeworms of the dog were first observed in *Trichodectes canis*, and Zimmermann (1937) produces evidence which suggests that the louse is the normal vector of this species of tapeworm. *Damalinia* (*Werneckiella*) *equi*, the trichodectid parasite of horses, has been reported to produce a dermatitis which resembles mange, and Spencer (1940) records an observation which suggests that *Trichodectes canis* may produce a similar condition in the coyote. *Damalinia equi* has also been accused (Eichler, 1940*a*, p. 35) of being a vector of infectious anaemia of the horse.

We know nothing whatever about the effect of *Haematomyzus* on the elephant but, since the parasite is somewhat small in proportion to its host and does not possess piercing mouth-parts, it seems improbable that the host is even aware of its presence.

The case of the sucking lice is very different. Any insect which feeds on blood and injects toxins in the process of feeding must inevitably cause some weakening of its host, especially if the parasite is present in large numbers; when,

in addition, the blood-sucker inserts into its host the organisms of some disease, the situation of the host is unenviable. Diseases of man which are transmitted mainly or exclusively by sucking lice include two forms of typhus, trench fever, relapsing fever, and probably trachoma; impetigo may be caused indirectly. There seem to be rather few recorded instances of disease being conveyed by sucking lice, in natural conditions, to mammals other than man:—*Haemodipsus* is known to carry tularaemia among wild rabbits, and *Polyplax* is known to transmit both this disease and murine typhus among rodents; surra in horses and Indian buffalos, hog-cholera and impetigo in swine, trypanosomiasis in rats and canine leishmaniasis are known or believed to be transmissible by sucking lice. *Dipetalonema reconditum*, a nematode worm belonging to the family Filariidae and parasitic in dogs, is recorded as being transmitted by *Linognathus setosus*, and it is probable that this list will be greatly extended by future workers. In the case of the sucking lice there seems to be no doubt that lousiness is often the cause of weakness, though in other cases it is probably usually a symptom of this condition.

(8) NATURAL ENEMIES.

The principal enemy of lice is undoubtedly their host, whose efforts to eliminate these irritating lodgers have just been described. Apart from the host, lice appear to have but few enemies. Ants are known to destroy them* and the manner in which the host sometimes takes advantage of this fact is described on p. 414; those birds (*Buphagus*, for example) which specialize in picking ticks off large mammals also destroy a few lice (Moreau, 1933). The question of competition between different groups of lice, or between lice and other groups of ectoparasites is dealt with in a later section of this paper (p. 430).

Parasites of lice are also not numerous. Parasitic fungi of the family Laboulbeniaceae are known from many lice; they cause atrophy of the fat-body, but whether their presence has a really serious effect on the louse appears not to be known. The structures described and figured by Müller (1932, pp. 33–35, fig. 1), and believed by him to be nematode cysts, are actually the spermathecae of female lice, as has been noted by Kéler (1938*a*, p. 66). Mites of the genus *Myialges* are known to occur on Mallophaga (Thompson, 1936*e*, p. 316; 1939*a*), but these mites are parasites of birds, and Thompson (1936*e*, p. 320) doubts their being true parasites of insects, considering it more probable that they attach themselves to Hippoboscidae and Mallophaga for the purposes of oviposition and transport. To the list of parasites of lice must be added *Herpetomonas pediculi*, together with the causative organisms of diseases transmitted by lice, which have been listed in the previous section; of these, *Rickettsia prowazeki* and *R. muricola* are known to be definitely harmful to the louse (Buxton, 1939, pp. 58, 62).

(9) SYMBIOTIC ORGANISMS.

Like many other insects with specialized feeding habits, lice possess symbionts whose function appears to be to aid in the digestion of food. Eichler (1936, pp. 493–495) has summarized our knowledge of the symbionts of Mallophaga, and Florence (1924) reviews most of what is known with regard to those occurring in Anophora. In both these groups of lice symbiotic intracellular Bacteria are found, which occupy modified cells in definite areas of the body of the louse, and for the distribution of which from louse to louse there appear to be special provisions. Their symbiotic nature has been doubted, but Aschner (1934 and earlier papers) shows that louse nymphs from which they have been

* It is possibly significant in this connection that only one of the ant-eating mammals, *Orycteropus afer*, is known to be infested by lice. According to Lang (1922, p. 327) this exception would only be apparent, for he states that this "ant-eater" does not eat ants but termites, but Patrizi (1947) records finding huge numbers of true ants in the stomach of an *Orycteropus*.

eliminated only survive for a short period. These Bacteria occur in many Ischnocera, but are not known from the Trichodectidae and are usually absent in the Amblycera, though present in *Menacanthus stramineus*. Eichler (1936, p. 495) states that it is those groups in which keratin is the main diet which possess symbionts, but keratin is the main diet of almost all the Mallophaga, and actually there is much more evidence in favour of a correlation with the occasional or normal imbibing of blood, for all the groups of lice known to possess bacterial symbionts have this habit, the Anoplura are exclusively blood-feeders, and similar symbionts occur in other groups of blood-sucking arthropods (ticks, mites, the bed-bug and several genera of blood-sucking Diptera).

The importance of these symbionts to our present theme is that Florence (1924, p. 402) produces evidence which suggests the possibility that their inability to flourish in a louse nourished with blood not that of its normal host may be one cause of the difficulty which lice experience in establishing themselves on a strange host. This would explain very well the observed fact that the Amblycera are often less specific than other groups of lice.

Eichler also quotes the presence of rickettsias in certain Amblycera and Ischnocera, including *Trichodectes*, as a possible example of incipient symbiosis, but there is apparently no special provision for the passage of these from louse to louse, each individual having to acquire infection anew from the blood of its host, so they are probably better regarded as parasites, though some of the species of *Rickettsia* (*R. pediculi* and *R. quintana*) found in *Pediculus humanus* are known to be harmless to the louse. A member of the Bacteria which occurs not infrequently in the copulatory organs of *Pediculus* is also believed to be harmless.

(10) TRANSFER FROM HOST TO HOST.

Lice normally do not willingly leave their host except during close contact of the latter with another host, preferably of the same species; any lice which do accidentally become separated from their host have but a poor chance of survival in natural conditions. That eggs will not hatch if kept at temperatures widely different from that of the host, and that adult and nymphal lice cannot, under these conditions, long retain the ability to resume normal life on the host is of great importance, for it means that the dropping of hairs or feathers with lice or their eggs upon them is not a means by which transfer from host to host can easily occur. The ability of lice to survive long periods of cold if daily fed and warmed is irrelevant in this connection, because in nature the daily feed and warming would be lacking, and lice on a dead host would normally pass into a state of akinesis from which only a stimulus such as the warmth and smell of a living host in the closest proximity would arouse them.* In the tropics and subtropics, lice on a dead host would often be exposed to lethal temperatures if they left the shelter of the host's hair. In general, the sensory responses of lice, at least as exemplified by *Haematopinus* (Weber, 1929) and by *Pediculus* (Nuttall, 1919a; Wigglesworth, 1941), are such as to deter them from leaving their living host except during close contact with a similar host. Their negative responses to bright light and to changes of humidity must tend to keep them within the shelter of their host's covering (whether this be clothing, hair or feathers) while their positive responses to a rough texture and to temperatures approximating to those of the surface of their hosts (perhaps also their positive response to the presence of other lice and their eggs) would tend in the same direction. Most important of all for our present purpose, however, is their positive response to the smell of their host, for this is to some degree specific, the *Haematopinus* of the pig reacting more strongly to the smell of a pig than to that of a dog, and *Pediculus humanus* more strongly to that of man than to that of a dog or a rabbit. It would be of great interest to follow up this observation

* Weber (1929, p. 594) has shown that the maximum distance at which the *Haematopinus* of the pig is attracted to its host is only about 30 cm.

and discover how close the relationship between hosts must be before this factor ceases to operate.

Close contact of the sort which favours transfer of lice from host to host occurs normally during copulation, during the care of the young, and in the association between predator and prey; in the more gregarious mammals transfer of a few lice may occur during momentary accidental contacts between members of the same herd. It will be noted that, with the exception of the association between predator and prey, all the most favourable opportunities for the natural transfer of lice from host to host are intra-specific.

Use by different species of mammals of the same rubbing-tree or of the same mud-wallow furnishes an obvious method by which inter-specific transfer of lice could take place, as also does the taking over by one species of the burrow or nest made by another, but in all these instances it would be necessary for the interval of time to be short or the lice would not have retained the capacity to resume normal life. Another possible method of transfer is the use by seals of basking-rocks frequented by other species (see Neumann, 1907*b*), and Eichler (1944) records the experience of a colleague of his who took shelter from a storm in a hollow tree and became infested by 350 specimens of *Pediculus*. Transfer by wind has been observed (Nuttall, 1917*c*, p. 103), but it is probably rarely effective except in the case of man, who is vastly more gregarious than most other mammals.

A further method by which transfer may occur must be mentioned for its interest, though it is probably seldom of importance to those groups of lice which occur on mammals. This is phoresy—the utilization by Mallophaga (or other insects) of more mobile insects to provide transport. Thompson (1933, p. 605; 1935, p. 162; 1936, pp. 309–312; 1939, pp. 441–444; 1947) records or quotes a number of instances of this phenomenon, the more mobile insects including particularly Hippoboscidae, mosquitos (two records only, to which Eichler (1944, p. 319) adds a third) and a flea; he also points out the rarity of such records. Clay and Meinertzhagen (1943), who review all the then known instances of this phenomenon so far as Hippoboscidae are concerned, show that in most cases the Mallophaga attach themselves to the roots of hairs or the veins of the wings (*i.e.*, not to areas where any food supply is available), and suggest (p. 14) that the lice “use the fly as a lifeboat” during the cooling of the host after death. Mitzmain (1912) records finding 620 nymphs of *Haematopinus tuberculatus* on 1800 specimens of a *Lyperosia* in the Philippines, the lice being attached to the legs of the fly. This is by far the largest-scale instance of phoresy recorded for lice, and it seems obvious that in this instance the phenomenon must be of real importance to the louse concerned. Transport of *Pediculus humanus* by house-flies has also been reported (Nuttall, 1917*c*, pp. 103–104). The lice which attached themselves to blood-sucking insects might well have found themselves transported in comfort to a new host, but those which were found on two dragon-flies and on a bee would certainly have found that they had caught the wrong bus, and the chances of those on the house-flies would not have been good.

As to what fate would await the lice on reaching a new host we have sufficient knowledge to suggest probabilities. The flea was a specific parasite of the badger and carried a badger-louse, so this louse would presumably merely have resumed normal life, as would any of the other lice which had the good fortune to be transported to another individual of the host-species to which they were adapted (the mosquitos carried deer-lice and were of a species which feeds mainly on deer). Those lice which were carried to a host widely different from that which constituted their normal habitat would probably die of starvation or poison (p. 422). Perhaps the most interesting consideration is what would happen to lice transferred to an abnormal host so nearly related to their original one that they were able to find suitable food; in this instance they would be likely to

find the host already parasitized by lice nearly related to themselves, and a hint of what might happen is provided by the work of Bacot (1917) and of Keilin and Nuttall (1919), who showed that crosses between the two subspecies of *Pediculus humanus*, though fertile *inter se*, tended to produce an abnormal proportion of males and many gynandromorphs; such a weakened strain would not be likely to survive indefinitely. Bacot also showed (1917, p. 253) that a high proportion of females of *P. h. humanus* mated with males of *P. h. capitis* died as a result.

The prospects of lice which become separated from their normal host are, as we have seen, extremely poor, but they are not quite hopeless. If the lice attach themselves to other insects there is a fair chance that the insect may be specific to their normal host. Failing this, there is the chance that the lice may arrive, either by phoresy or by one of the other possible methods of transfer, on a host which can provide suitable food and which is either not infested with lice or lightly infested with lice too distantly related to the new arrivals for crossing, with its resultant dangers, to be possible. Remote as this chance is, it obviously sometimes comes off, for the instances of establishment of a louse-species on unrelated hosts mentioned on pp. 420 and 421 are conclusive evidence of this. Their very small number indicates the remoteness of the chance of success.

(11) HOST-SPECIFICITY.

To any group of ectoparasites, like the fleas and ticks, of which the members must pass through some stage of their life-history off the host, an extreme degree of adaptation to one kind of host is an obvious disadvantage; in the few members of such groups which have become narrowly adapted to one host the disadvantage is usually minimized either by passing the free stages in the host's dwelling, by great profusion of egg-production, or by both. The lice, spending their entire life on the body of the host, have been free to develop a very high degree of host-specificity and have taken the fullest advantage of this freedom. Owing to the brevity of the period which they can survive off their host in natural conditions, the death of the host means almost certain death to the whole louse-community which dwells upon it, so that absence of host-specificity would involve such a minute lessening of the almost certain imminence of annihilation of the community that it would in no adequate degree lessen the advantages to be gained by a narrow specialization to life on one host-species. Furthermore, it must be recognized that mammals of one species, like birds of a feather, often flock together, and that the converse is also true. Except between predator and victim, close bodily contact between mammals of different species is very rare in natural conditions, so that interspecific transfer of parasites is rarely possible and absence of specificity would very seldom be of any advantage to lice.

The very marked host-specificity exhibited by the Trichodectidae (and also by the mammal-infesting Amblycera) has been noted by many authors, but it is somewhat obscured by erroneous records, by misidentifications of lice, and by the recording of subspecies of hosts as full species, so that its very extreme nature is often not realized. Each species of Trichodectidae occurs normally as a rule, on only one species of host, but occasionally on several hosts which, though very closely related, are not conspecific. Because by far the greater part of my collecting has been done in circumstances in which contamination was excluded, my own experience forms an unusually good illustration of the host-distribution of this group. Setting aside skins in museums, where contamination is always probable, I have successfully examined for Trichodectidae fifty forms of wild mammals which Allen's Checklist treats as specifically distinct; in most cases many specimens have been available and in many instances the hair has been dissolved, so that practically every louse was obtained. Among these mammals I have encountered six instances of the

occurrence of the same trichodectid on two forms which Allen treats as species, the pairs of hosts concerned being *Kobus ellipsiprymnus* and *K. defassa*, *Rhynchotragus guentheri* and *R. kirkii*, *Adenota kob* and *A. vardoni*, *Raphicerus campestris* and *R. sharpei*, *Tragelaphus scriptus* and *T. spekii*, and *Ichneumia albicauda* and *Civettictis civetta*; in addition I have collected the same *Damalinea* from several species of Cephalophini. I have given reasons (pp. 528, 531) for my belief that the members of each of the first two of these pairs are not specifically distinct, and I can see no particular reason why the two forms of *Adenota* should not be regarded as conspecific. In the remaining instances, except that of the *Ichneumia* and the *Civettictis* the hosts concerned are at least extremely closely related. The case of the occurrence of the same species of *Felicola* on *Ichneumia* and *Civettictis* (which has the further complication that the species found on the domestic cat is also apparently the same) is entirely different, because *Ichneumia* and *Civettictis* belong to different subfamilies, while the cat belongs to a different family. This case will be discussed again in another connection (p. 423); here I only wish to mention that such cases are excessively rare: I only know of one other well-authenticated case of the natural occurrence of the same species of Mallophaga on two hosts which are so widely sundered in a genetical sense, this being Werneck's record of the occurrence of guinea-pig parasites on *Sylvilagus brasiliensis*. With regard to genera of Mallophaga on mammals, the only marked anomaly is the occurrence of *Heterodoxus* on marsupials and on the domestic dog (see p. 547). On examining an unknown louse one can tell, with little risk of error, from what sort of mammal it was taken, but it is impossible to tell from what part of the world it came except by considering the distribution of the group of hosts. To this rule there is one large exception: the Gyropidae occur on a wide variety of hosts in South America and are not found elsewhere.

It seems clear that in South America specificity in the Mallophaga of certain groups of hosts is much less marked than elsewhere, all the South American Canidae and Felidae which have been examined sharing the same trichodectids with other members of their families in the same region. But in other host-groups, such as the rodents, specificity is as marked in South America as in other parts of the world.

The specificity of some of the Trichodectidae of the Hyracoidea (hyraxes, dassies or rock-rabbits) differs markedly from that of any group of lice on other hosts by being more extreme. In some respects our knowledge of the hyrax-Mallophaga is exceptionally good, though it is marred by the fact that (largely owing to the great difficulty of identifying hyraxes) a high proportion of the records refer to material obtained from skins in museums, this resulting in a certain number of instances of contamination and (much more serious) others in which we may suspect contamination but are unable to be sure. On the other hand, misidentifications of the Mallophaga are practically absent, since they have recently been excellently monographed (Werneck, 1941c) and mis-determinations corrected. There are sufficient completely authentic records to give us a very clear outline of the picture, though we know almost nothing about the parasites of hyraxes outside East and South Africa.

Allowing for certain discrepancies probably attributable to incorrect assignment of subspecies of hyraxes to species (Hopkins 1945, p. 6), host-specificity in *Dendrohyrax*, and in *Heterohyrax* and *Procavia* in East Africa as far south as Nyasaland, is not unlike what we find on other groups of mammals, though there are a few instances in which a subspecies of the host has developed a peculiar subspecies of the parasite. In South Africa, conditions are similar as regards all the genera and subgenera of lice except *Procavicola s. str.*, though there has perhaps been a certain amount of interchange of parasites between *Procavia* and *Heterohyrax*. In this subgenus of Mallophaga, however, we encounter conditions of host-specificity absolutely different from those found in the lice of any other group of mammals, for nearly every form of *Procavia*

capensis and *Heterohyrax syriacus* found in South Africa has its own specific form of *Procavicola s. str.* Moreover, these lice are species, not subspecies, for though the females are inseparable the differences in the male genitalia are often such as to render cross-mating difficult or even impossible.

It is possible that the explanation may be that the forms of *Procavia* and *Heterohyrax* found in South Africa should be regarded as species, but I think it much more probable that the reason is simply that the hyraxes are so conservative a group that their evolution has lagged behind even that of their lice, whereas in almost all other groups of mammals the lice have evolved more slowly than their hosts. A somewhat similar phenomenon is exhibited by the Mallophaga of birds belonging to the order Tinamiformes, and it seems significant that the Tinamiformes are also an unusually archaic and conservative group.

The presence of a unique anomaly in the host-associations of lice of hyraxes in South Africa is suggested by evidence which points towards the possibility that in the case of *Procavia capensis coombi* and *P. c. letabae* the species of *Procavicola* with which a given individual is infested may be governed rather by locality than by subspecies of host (Hopkins, 1945, p. 3). Unfortunately the whole of the louse-material on which this suggestion is based is derived from museum skins, and such an interesting anomaly ought not to be accepted as fact without the fullest proof. If such proof is eventually forthcoming (as I believe will be the case) the only possible explanation seems to be that a subspecies of *Procavia capensis* may acquire the physiological characteristics of a different race before acquiring its external characteristics.

If we turn to the birds, the same general picture is presented as in the mammals, though not so clearly because of the relative backwardness of our systematic work on bird-Mallophaga. It seems possible that in some groups of birds the units infested with the same Mallophaga may be genera rather than species, though conditions are often found to be precisely the same as in the mammals if the systematic work is adequate. Leaving this aside, however, I know of no well-authenticated case of the natural occurrence of any one species of Mallophaga on two bird-hosts which are not very closely related, and (omitting cases in which the louse-genera need dividing) of only a very few instances of the occurrence of the same genus on birds belonging unquestionably to different orders; the only one which is definitely inexplicable on the basis of phylogeny is the well-known and certainly authentic case of the occurrence of the genus *Perineus* on the albatrosses and petrels (Procellariiformes) and on the skuas of the family Stercorariidae (Charadriiformes). In fact, among the whole of the Mallophaga we know only four instances in which the apparently permanent occurrence of a parasite on two host-forms in common cannot be accounted for by the parasite having been present on the common ancestor of the two forms.

Among the Anoplura there is reason to believe that host-specificity may not have developed to quite the same degree, as is natural in the phylogenetically younger group, but even here there appear to be only two well-authenticated instances of the definite and permanent establishment of a parasite genus on two widely-separated groups of hosts.* One of these instances is the occurrence of *Polyplax* on rodents and on shrews, and the other is the occurrence of *Pediculus* on the higher members of the Old World Anthropeida and on certain of the New World ceboid monkeys. The former instance is conceivably not so anomalous as it seems, since we know nothing of the origins of the rodents, though I do not myself believe this to be the explanation; the latter case is discussed on p. 538. There are a few other authenticated instances of lice occurring on unrelated hosts, but in these it is by no means certain that the infestation is permanently established. In addition there are many instances in which a louse appears to be common to a number of closely-related hosts.

* For reasons given on pp. 547 and 554, I do not consider the occurrence of *Linognathus* on carnivores and ungulates to be an exception.

Considering the lice of birds and of mammals as a whole, there are only some six or eight authenticated cases of the permanent occurrence of a louse species or genus on two or more hosts which are not closely related to one another. Opportunities for transfer are not lacking, as will be shown below, yet the transferred lice are obviously normally unable to establish themselves on the new host. It is interesting to note that this usual inability of lice to establish themselves on a strange host has been employed in the control of *Pediculus humanus*, the people of Ruthenia putting their lousy clothing on horses to eliminate the lice (Hall, 1917, p. 504); although Hall doubts the efficacy of this method it would almost certainly be successful, for the lice would be attracted thermotropically to the horse and would not be able to survive on a host so remote in a phylogenetic sense from that on which they habitually occur.

There are evidently several reasons for the fact that lice normally cannot flourish on an abnormal species of host, of which the most important is perhaps "that the chemical constitution of blood, skin and plumage of the unnatural host is such that its body not only does not provide an attractive source of food and shelter, but may possibly provide actual lethal conditions for the straggling parasite" (Baker, 1931, p. 191). Very few attempts to feed Mallophaga on the hair or feathers of an abnormal host seem to have been made, but Wilson (1934, p. 309) showed that nymphs of a chicken-lice fed on heron-feathers all died, usually at the next moult, whereas other nymphs kept in the same conditions but fed on chicken-feathers remained healthy. Eichler (1936, p. 481) obtained similar results with pigeon-lice fed on heron-feathers, while later (1940c, p. 260) he successfully established the dog-*Trichodectes* on a fox. For the Anoplura there is rather more evidence. Nuttall (1917c, p. 113) and Buxton (1939, p. 32) summarize a number of attempts by various workers to feed *Pediculus humanus* on hosts other than man; in many instances the lice refused to feed, in others the lice fed but died very shortly thereafter, while in most of the other cases there is no record of any attempt to ascertain whether the strange meal had any deleterious effect on the lice. Ewing (1933b, p. 366) fed on man specimens of a *Pediculus* from a spider-monkey, of *Pedicinus* from an Old World monkey, and of the *Linognathus* of the dog; all the lice which fed died very soon after the meal, and in one instance the blood appeared to be only partly digested. Ewing deduced from the results of his experiments that "when impelled by hunger and the desire for warmth" lice "will accept as host the mammal available"; this, while doubtless largely true if ability to obtain blood is to be the test of acceptance of a host, seems to me to be a most misleading way of expressing the facts. Ability to suck blood from an abnormal host of is extremely little value to a species if the process results in death a few hours later. Davis and Hansens (1945) were able to rear two successive generations of *Pediculus humanus capitis* on a rabbit, but they note that there was a heavy mortality and the individuals of the second generation thus reared were too few to enable pairings to be obtained.

There is one very interesting exception to the normal rule that the blood of a phylogenetically remote host is fatal to lice, for Noeller (1916, p. 778, quoted by Nuttall, 1917, p. 112) found human lice capable of living and breeding on pigs, while Florence (1921, p. 645) found that *Haematopinus suis* fed readily on man. The special interest of these records is that there is other parasitological evidence that the physiological composition of man is very much like that of the pig from the parasite's point of view; both are, for instance, normal hosts of *Pulex irritans*, *Tunga penetrans*, certain species of *Auchmeromyia*, and *Ornithodoros moubata*, while the nematode worms of the genus *Ascaris* found in the two hosts are morphologically indistinguishable. It must be noted, however, that none of these organisms show the same type of host-specificity as is found in the lice, and the case is doubtless one of an accidental similarity in skin-texture and probably in the composition of the blood. Furthermore, there is

evidence which suggests that the exceptional immunity to the deleterious effects of strange blood apparently exhibited in this particular case may be only partial, for Alessandrini (1919) found that nymphs of *Pediculus humanus* fed on pigs produced an abnormally high proportion (80%) of females.

It seems extremely probable that another factor which hinders successful transfer of lice is the texture of the hair of the host. Dr. Werneck allows me to quote a series of experiments he performed on this point :—he confined specimens of a trichodectid in petri dishes with hair of a rabbit, and also with hair of a rabbit and of the normal host. Eggs were laid freely on the hair of the normal host, but none were laid on the rabbit-hair, though the lice confined with only rabbit-hair laid many eggs on the glass of the dish. The difficulty is probably mechanical, for it has often been observed that lice are unable to walk well on hair of a widely different texture from that to which they are accustomed. The case of *Felicola subrostratus*, occurring on the domestic cat, a mongoose and a civet, is a partial exception in this connection, for the domestic cat has much finer hair than that of *Ichneumia albicauda* or *Civettictis civetta*, though these latter both have fur of very similar texture.

Further experiments on the ability of lice to establish themselves on abnormal hosts would be of value, but any worker who carries them out should remember the necessity of proving that the infestation has become established; for this purpose the occurrence of a louse in large numbers on an abnormal host in artificial conditions is not enough, even though all stages be present, and it is necessary to prove that successful breeding is taking place.

It is, of course, certain that the original lice cannot have been at all specific in their choice of hosts, or they could not have changed over from a free-living existence, like that of their relatives the Psocoptera, to an exclusively parasitic life upon vertebrates. Moreover, it is likely that establishment of lice on a strange host was much easier before hosts themselves had diverged far from one another. But this catholicity of choice of host has very long been lost, and in geologically recent times transfer of these parasites from one group of hosts to another on any large scale can be ruled out. Our inevitable lack of knowledge as to the period at which the present strongly specific host-associations of the Phthiraptera began to become established is, of course, a serious weakness in making deductions from the present distribution of the group. But the extreme rarity of exceptions to the general rule, coupled with the fact that the lice of different orders (and even families) of modern birds are usually generically distinct, suggests strongly that the specific nature of the association became established at latest not long after the emergence of the main groups of modern birds. In the Upper Eocene period the main modern orders and families of birds were already well-established, so it seems probable that at that period transfer of lice between unrelated hosts had already become very difficult. The excessively rare instances in which geologically recent transfer of a parasite has resulted in its establishment on the new host do not seriously affect the general argument.

(12) STRAGGLING AND CONTAMINATION.

We have seen that permanent establishment of a louse on an abnormal host is extremely rare, but it might be expected that temporary establishment would be very common. Actually this, also, is very rare, though a quite different impression would be obtained by reading the older literature on the Phthiraptera without first having had long experience in collecting lice by a good technique. It is of the first importance that we should recognize the true nature of erroneous records if our knowledge of louse-distribution is to rest on firm foundations, and it is necessary in discussing such errors to distinguish between straggling, contamination, and plain mislabelling.

The extent to which mislabelling may vitiate our records is, I think, not

realized, and it is often difficult to distinguish from contamination.* Mislabelling has been rather frequent in my own experience because I could give only an extremely limited amount of time to this work, so that much had to be left to Africans who were not always as careful as one could wish. But this type of error is easy to detect if sufficient material is available and if abnormal records are examined with a suspicious eye. When, for instance, one finds a tube of parasites supposed to be from a house-rat to contain gerbil-lice, gerbil-fleas and gerbil-mites, there is not much doubt as to what has happened, especially when one finds in the same batch a tube of parasites supposed to be from a gerbil and containing parasites characteristic of the house-rat. Such records should, in my opinion, never be published, and we ought to examine all those which already burden the literature and endeavour to eliminate them. They are particularly deceptive because they have all the appearances of natural infestations. It is highly significant in this connection that Mr. D. H. S. Davis personally made collections from 138 louse-infected individuals of 7 species of rats in Sierra Leone, and encountered no instances of apparent straggling; similarly, in my own collections from rats I have never encountered lice on a host to which the species of louse was not normal on those occasions on which I was able to carry out the work myself and thus reduce the likelihood of mislabelling and other forms of carelessness.

I define contaminations as those instances of occurrence of lice on an abnormal host in which the phenomenon is due to the direct intervention of man. They can be divided into two groups, according to whether the intervention took place before or after the death of the host. Of these the *ante-mortem* group is the more troublesome because the lice may be alive and the infestation appear to be a natural one, but the *post-mortem* group is much more frequent. The *ante-mortem* group is due to artificial approximation of the hosts in zoos and in similar circumstances. One of the best examples of this group is the record (Fenstermacher and Jellison, 1932) of a porcupine-lice infesting a monkey. The authors record that the monkey's cage was next door to one containing heavily-infested porcupines, but (underestimating the mobility of lice) they consider that the presence of nymphs on the monkey proves that the infestation was established; this could only have been proved by removing the monkey to a cage remote from the porcupines and ascertaining whether the infestation persisted. Such instances are of interest with regard to the bionomics of lice and the possibility of secondary infestations of groups of mammals with parasites derived from another group, but they should be thoroughly confirmed and they have no place in a host-list of the lice, which should be confined as far as possible to occurrences in natural conditions. There is no reason whatever to believe that, *in nature* monkeys are ever infested with porcupine-lice.

As regards the mobility of lice, a border-line case in which the hosts were dead but the parasites alive is of some interest. On one occasion I offered rewards to Africans to induce them to bring in small Carnivora from which I might obtain the lice, and I then unexpectedly had to be away for a day. On my return I found many corpses of four species of small Carnivora laid out on the floor of the office, and I believe that both adults and nymphs of every species of louse present could have been recorded from every species of host, to say nothing of *Pediculus humanus* (derived from the Africans) which was present on at least two species of the corpses. Incidentally, most of the lice were alive and active, and after I had made a preliminary examination of the corpses I could have added considerably to the list of ectoparasites recorded from man!

* An unusually excellent example of one or the other of these phenomena is provided by Werneck (1936, p. 542), who notes the erroneous nature of a batch of records of a specific goat-parasite from an opossum and five different species of birds. In one very famous museum there is a series of a *Harrisoniella*, a genus strictly confined to albatrosses, labelled as having been collected from pigs in Roumania, where albatrosses do not occur.

Instances of *post-mortem* contamination are exceedingly common in the literature and abound in the writings of Piaget, a very large part of whose material was obtained from skins preserved in museums. These contaminations usually come about through a few lice being shaken out of one skin on to another, and are often not difficult to detect because the number of specimens of the lice is usually very small. Instances in my own experience include the finding of two or three specimens of a mongoose-parasite on two hyrax-skins sent to me in the same parcel as the skin of the mongoose, many specimens of hyrax-parasites on skunk-skins and *vice-versa* (due to the same cause), and a pair of *Geomydoecus* on another hyrax-skin in a museum; the last case is particularly instructive because the hosts of *Geomydoecus* are all American, whereas the hyraxes are all Ethiopian. Another source of *post-mortem* contamination is, as already mentioned, failure to clean the work-bench thoroughly between the examinations of two different hosts. The records (Ferris, 1920-1935, p. 319) of *Eulinognathus denticulatus* from *Rattus* (*Mastomys*) *coucha* and *Rattus rattus* are undoubtedly due to this cause; I regret that I am myself responsible for these records, because I did not notice until after the lice had been sent to England that we did not get records of *Eulinognathus* or of *Delopsylla* (the characteristic flea of *Pedetes* in East Africa) from rats unless a *Pedetes* had been examined just previously. Records which are due to *post-mortem* contamination obviously have no interest whatever and they should never be published if detected in time.

In a former paper (Hopkins, 1939) I used the word straggling to include all occurrences of lice on abnormal hosts, using "artificial straggling" for the cases now called contamination, but I now consider that the word straggling ("Vagismus" of Kéler, 1938 a, p. 60) should be restricted to natural occurrences. In this restricted sense it is an exceedingly rare phenomenon and even very close association, in nature, between two closely-related hosts does not normally result in their becoming mutually infested with lice from each other. A large pile of rocks (Umi Rocks) in northern Uganda is inhabited by two species of hyraxes, of each of which I have examined half a dozen specimens, all heavily infested with lice; not once did I find on either species of hyrax even a single louse normal to the other. Baker (1931, pp. 190, 191) notes that "owls and other birds of prey provide excellent opportunity for the establishment of parasites of their prey upon themselves; yet I know of no record in the literature of the occurrence of a mammal louse upon such bird hosts and no record of the establishment of a species from a passerine bird. Cuckoos should provide an admirable illustration of straggling, if stragglers become established, because of the certain infection of the young in the nest. There is, however, no record of lice of foster parents on cuckoos—only records of true cuckoo-infesting species." The experience of other workers fully supports Baker's remarks. Colonel Meinertzhagen kindly permits me to state that out of 579 predatory or parasitic birds which he has examined (341 hawks and eagles, 162 owls, 27 skuas and 49 cuckoos) he has only found 10 (6 hawks, 1 owl, 1 skua and 2 cuckoos) bearing lice not normal to their groups, the instance of one of the cuckoos being particularly interesting because the single *Brüelia* found on it was attached to a hippoboscid fly; my own experience is quite similar, for I have examined some 30 cuckoos, a few owls and about 200 birds of prey in East Africa and Britain, have never found mammal-lice on a predatory bird nor lice belonging to other bird-groups on cuckoos, and have only once encountered bird-lice from prey on a predatory bird (this instance being the possibly genuine occurrence of a few specimens of *Actornithophilus*, characteristic of Charadriiformes, on a hawk), but Eichler (1944, p. 311) states that the pigeon-lice *Columbicola* occurs rather regularly on peregrine falcons. With regard to other birds whose nesting-habits resemble those of cuckoos the evidence is scanty and inconclusive: Ewing (1933 b, p. 369) considers that *Molothrus ater* is like the cuckoos in harbouring its own specific parasites and not those of the foster-parents, whereas

Eichler (1936, p. 482) has drawn an entirely contrary deduction from the collections made by Geist (1935, p. 97) from this bird; it is to be noted that all the lice recorded by Geist belong to groups in which specific determinations, in the present state of systematics, are little more than guess-work, and it may well prove eventually that the lice really belong to species confined to *Molothrus*.

Genuine straggling is also extremely rare in the case of mammals. I do not know of a completely authenticated published case of the occurrence on a predatory mammal of a louse of its prey, though a few, including Paine's record (1912 b, p. 438) of four specimens of a deer-parasite on a wild dog, have the appearance of being genuine. I have myself examined scores of predatory mammals in East Africa, and have never encountered a single louse which appeared to be derived from their prey.

That straggling should be so extremely uncommon is most surprising, for one would expect predators to pick up sufficient lice from their prey for the finding of such lice on them to be a common event even if the lice were unable to survive the transfer for more than a few days. The fact remains, however, that such instances are exceedingly uncommon.

In the host-list which follows I have used the word "erroneous" to cover the whole range of abnormal records, from the natural occurrence of a single louse on a host on which survival is evidently impossible to instances of mislabelling, but not including those cases in which there is evidence suggesting that the louse is established; where possible I have suggested the type of error which seems to have been involved in each case. I have deliberately used "erroneous" rather than the more non-committal "abnormal" because of my firm belief that the vast majority of such records are due entirely to errors in our collecting-technique.

(13) PRIMARY AND SECONDARY INFESTATIONS.

In the two preceding sections I have emphasized the extremely specific nature of the host-distribution of lice, both because it is not often realized by those who have not specialized on the group, and because of its great importance with regard to the possibility of unrelated hosts becoming infested from one another. This latter possibility is the only alternative to accepting the belief that the possession of species, genera and families of lice in common by different hosts is evidence of different degrees of community of descent of the hosts themselves.

Those instances in which almost every member of a given group of mammals is infested with lice closely related to those found on other members of the group may be called primary infestations, since in such cases it seems unreasonable to doubt that the louse-infestation dates from at least the period when the group of hosts diverged from its parent stock. As has been pointed out, these primary infestations constitute by far the greater part of all those known to us.

Secondary infestations are exceedingly rare (p. 420). They comprise those instances in which the occurrence on a given host or group of hosts of a particular species or group of lice cannot be explained by the phylogeny of the hosts, so that the infestation must necessarily have originated after the divergence of the host-unit from its parent stock. The best example of secondary infestation of mammals which has come within my own experience is that of the African civet (*Civettictis civetta*), the white-tailed mongoose (*Ichneumia albicauda*) and the domestic cat with the same species of *Felicola*, which is established by a number of completely reliable records.

If for orders, families and other groups of hosts we substitute faunal regions, continents and smaller geographical divisions, then infestations with lice form a very good parallel with the types of distribution shown by free-living animals or by plants, the fauna and flora of any given area being nearly always composed

mainly of autochthonous elements ("primary infestations") with a proportion of extraneous forms ("secondary infestations"), of which some have arrived in the area by natural means ("stragglers") and others have been accidentally or deliberately brought in by man ("contaminations"). The main difference is that in the case of the lice the secondary element is very much smaller than in the case of free-living forms. In the free-living forms we often have fossil evidence that the absence of a given group in a given area merely means that it was once present and has become extinct, like elephants and the ginkgo tree in Europe, and in the case of the lice I hope to show that a similar explanation will fit many of the observed facts better than any other. This matter is discussed in the next section.

(14) SECONDARY ABSENCE.

Various authors (Kellogg and Ferris, 1915*b*, pp. 52-53, for instance) have remarked on the absence of Mallophaga, Anoplura, or both, from certain groups of mammals, but the idea that this absence may be secondary appears not to have occurred to any previous writer except Clay, although secondary absence is only a special form of the well-known phenomenon of discontinuous distribution, which is frequent among free-living organisms. Clay (1941, p. 120) remarks of the distribution of the genus *Chelopistes* (late *Virgula*): "This distribution cannot indicate any close affinities between the families and sub-families mentioned above but may possibly be due to the fact that the genus was once widespread throughout the Galliformes and has since died out in the intervening genera." In many instances this explanation of the absence of one or more of the groups of lice on a given group of animals is the only one which will satisfactorily explain the observed facts, but failure to appreciate this has misled certain authors into putting forward theories with regard to louse-distribution which I believe to be entirely unsupported by the evidence. In these circumstances I find it necessary to give a number of examples of the phenomenon.

Perhaps the most striking instance is that of the distribution on birds of the closely-related mallophagan families Ricinidae and Laemobothriidae. Of the genera included in these two families, *Ricinus* is found on a few of the many families of Passeriformes (finches etc.) but not on other families, and also on Trochiliformes (humming-birds); *Trochiloectes* (which is perhaps inseparable from *Ricinus*) on humming-birds; *Laemobothrion* on Falconiformes (hawks and vultures) and Strigiformes (owls); *Eulaemobothrion* on Ralliformes (coots and rails), one family of the Ciconiiformes (ibises) and on the hoatzin (somewhat doubtfully included in the Galliformes). The author who would argue from the above distribution any specially close relationship between the groups of birds concerned would need to be a great deal bolder than I am, and the suggestion that this sporadic distribution among (and even within) the orders of birds represents the remnant of a once nearly universal infestation seems irresistible. That the different groups concerned should all have acquired their Ricinidae or Laemobothriidae either from an ancestor common to them and not to other bird-groups or secondarily from each other seems almost impossible.

Turning to mammals, Trichodectidae are found on every large group formerly included in the ungulates except the Suina, and on every large group of the Carnivora (*s.l.*) except the seals. Anoplura occur on all the large groups of the ungulates, but (like the Trichodectidae) appear to be absent on a few small groups, including the Tapiridae and the Rhinocerotidae; they occur in abundance on the seals but on no other Carnivora except the Canidae. It is hardly possible to argue that Trichodectidae attached themselves to the ungulates after the divergence of the Suina, the Tapiridae and the Rhinocerotidae from the main stock, because they occur on an ungulate stock (that of the hyraxes) which appears to be still older; they must, therefore, have once been present on these groups and have become extinct. The absence of Anoplura

on all Carnivora except seals and Canidae seems also to be explicable in no other way, since these are among the oldest groups of the Carnivora. The absence of Trichodectidae from the seals is doubtless due to their aquatic habits, and seems to me to be certainly another instance of secondary absence. A number of other cases are mentioned in the discussion of the host-list. Such absences of a given group of lice from a whole group of hosts are, of course, explicable by the lice having become extinct at a date when the host-group was represented by a single ancestral species. It has been suggested that the ungulates are not a natural group, the Artiodactyla being nearer related to the Carnivora than to the Perissodactyla; if this is correct the fact would tend to strengthen my argument.

Even among genera and species of hosts there are many instances of apparently anomalous absences. An excellent example is the absence of *Prolinognathus* on hyraxes of the genus *Dendrohyrax* although the genus is often very common on *Procavia* and *Heterohyrax*. A still better instance is provided by the African squirrels of the genus *Xerus* (p. 461), both of which have been examined so frequently that we may feel a reasonable degree of certainty that we know their louse-fauna. A glance through the list of squirrels (pp. 454-465) will show that a great variety of genera normally possess an *Enderleinellus* and a *Neohaematopinus* (with sometimes a *Hoplopleura* as well); each of the species of *Xerus* has lost one of these two genera, but the lost genus is different in each case, *X. inauris* lacking *Enderleinellus* whereas *X. erythropus* lacks *Neohaematopinus*. I consider this last instance completely conclusive evidence that absences of lice may be secondary, and I believe that a great number of apparent anomalies in louse-distribution are due to this factor. It seems worth recording that Bedford in South Africa and myself in Uganda failed to find *Trichodectes canis* on dogs, since it suggests strongly that this cosmopolitan and often abundant species has become secondarily absent in Africa.

A glance at the pages of the host-list dealing with land-Carnivora (pp. 496-508) and those dealing with Artiodactyla and Perissodactyla (pp. 520-534) will at once show the extremely sporadic nature of the distribution of the natural groups of Trichodectidae which I have here called subgenera (see p. 437); the distribution of the various groups of *Felicola* on mongooses (pp. 504-506) is particularly interesting in this connection. Such a state of affairs could be accounted for by secondary infestation on a huge scale, by parallelism (the explanation I suggested in earlier papers) or by the hypothesis that at one time most of the ungulates and carnivores had multiple infestations of the type common among the hyraxes, and that in almost all instances all but one of the original species of Trichodectidae on a given host has died out. The theory of secondary infestation is confronted by the fact that the group of Carnivora among which multiple infestations are least rare (the mongooses) includes precisely those forms whose mammalian prey does not normally include the groups which are infested with Trichodectidae, and my faith in the suggestion that the explanation is parallelism has been shattered by the amazing resemblance between *Damalinea neglecta*, found on *Ammotragus lervia* (a sheep) and the species found on the Equidae, which seems to me to be far too close to be accounted for by anything except very near relationship. I now believe that subsequent to the original infestation of mammals by lice there was a period during which there was multiplication of species and genera to a degree that we might never suspect but for such residual cases as that of *Dendrohyrax arboreus adolphi-friederici*, though this explanation involves invoking secondary absence on an entirely unexpected scale. I revert to this subject in the next section of this work.

There are several ways in which extinction of a group of parasites on a given group of hosts could come about, of which the most obvious is the acquisition by the hosts of habits or a structure (such as relative or absolute hairlessness) that render them unsuitable to the parasites. The relative hairlessness of pigs

and hippopotamuses seems an adequate reason for their lack of the hair-eating Trichodectidae, and when hairlessness is combined with a completely aquatic mode of life, as in the Sirenia and Cetacea, we certainly need look no further for the cause of the absence of all lice from these groups of hosts. It seems extremely probable that another factor in this class may be some chemical alteration in the blood or hair that renders these unsuitable as food. Unfortunately the most suggestive instance in this connection is not fully established, but it seems worth mentioning nevertheless: I have examined by the dissolving technique the skins of seven spotted hyaenas and three striped hyaenas, and many scores of the former species have been examined by searching, but no lice of any kind have been found on either species. Since Trichodectidae occur on all other groups of land-carnivores which have been examined (including the aard-wolf, which is very nearly related to the Hyaenidae) this apparent absence must, if confirmed, necessarily be secondary, and I suggest that it is perhaps due to changes in the blood and hair of hyaenas attributable to their diet. The absence of lice from mammals whose food consists largely of ants (see p. 416, footnote) is perhaps attributable to this diet, but the fact that certain ant-eating birds are infested much weakens this suggestion.

The ease with which a group of parasites could become extinct on certain hosts is clearly indicated by those not infrequent cases in which a species of louse occurs on only a small proportion of the individuals of its host-species. In the by no means extreme case of *Damalinia annectens*, belonging to the Ischnocera, I examined by the dissolving technique sixteen skins of the host, of which eight were louse-free, six more produced a maximum of five specimens, and only one was heavily infested (Hopkins, 1943 *a*, p. 26). We have seen above (pp. 410–411) that youth and ill-health are factors often associated with heavy infestations of lice (both Mallophaga and Anoplura); if we assume an epizootic passing through a largely uninfested population and selecting out for destruction the weakly and the young, it is easy to see that the result might be the elimination of all heavily-infested individuals and the consequent extinction of the chewing louse of the host in question. Extinction of a sucking louse by such a means would be still easier, because the disease might be one transmitted by the louse itself.

Hindle (1916; 1919) records many examples of unisexual broods of *Pediculus humanus*, and Buxton (1939, p. 45) notes that a particular strain of this species "brought itself close to extinction by producing 190 males to 3 females". If such a tendency were to become widespread in a louse-species it is obvious that complete extinction of the species might easily result, especially as too high a proportion of males is directly injurious to the females (Buxton, 1939, p. 46).

In some instances the absence of lice from certain individuals of a louse-infested species is doubtless due to chance, these individuals not having happened to become infested, but in the case of man there is direct evidence that individual insusceptibility exists. Buxton (1941 *a*, p. 194) and MacLeod and Crauford-Benson (1941, p. 290) observed cases of such insusceptibility and the latter authors tested the observations by experiment and showed that certain individuals constitute an unfavourable environment for *Pediculus humanus*; Riley and Johannsen (1932, p. 129) record an instance of hungry lice refusing to feed on one of two brothers, though they fed readily on the other. In man this insusceptibility is rare, but it is reasonable to assume that among other mammals there may be instances in which insusceptibility is the rule, or even universal. We know very little about the causes of insusceptibility, but it seems possible that this factor may have played an important part in the extinction of lice upon certain groups of hosts. A highly suggestive point with regard to insusceptibility is that there is much evidence (Ferris, 1920–1935, p. 598; Werneck, 1937 *d*, pp. 162, 163) that captivity greatly favours the

occurrence of lice on monkeys, perhaps by breaking down their relative insusceptibility. Similarly it has been shown (Crauford-Benson, 1941, p. 355) that cattle kept under cover are more heavily infested by lice than are those in the open.* These observations suggest the possibility that the fact that a given louse may become established on a captive animal to which it is not normal may not be evidence that the host-species could be successfully colonized by the louse in natural conditions. Kartman (1942 : 1943) summarizes most of the little that is known on the subject of the causes of insusceptibility, and shows that in captive white rats there is a strong positive correlation between heavy infestations with lice and deficiency of certain vitamins in the diet; such deficiencies, therefore, may be one cause of the break-down of relative natural immunity which is sometimes observed in captive mammals. Joyeux and Sautet (1939, p. 619) record an instance in which a dog proved an unfavourable host for *Linognathus setosus*, an experimental infestation dying out in the course of a few weeks, and also (p. 620) cases in which natural infestations of dogs with the same louse died out or greatly diminished after the development of a furfuraceous dermatitis; they suggest that in the latter instance the lice are unable to penetrate the scales caused by the dermatitis and therefore cannot feed. Shull (1932) states that breeds of cattle with a greasy skin are less susceptible to infestation with Trichodectidae than those with a dry skin.

There is much evidence which suggests that yet another cause of extinction of lice on a given host-group may be competition between different groups of ectoparasites, which need not necessarily be lice. Although I find it impossible to suggest how Mallophaga and Anoplura could come into competition unless the former destroy the eggs of the latter, there is evidence which suggests very strongly that abundance of members of one group is usually inconsistent with abundance of members of the other. The most satisfactory examples of this phenomenon are to be found among the rodents (pp. 454-496) where it will be noted that the families and genera which are heavily infested with Mallophaga seldom or never have Anoplura; although the Old World rodents never have Mallophaga the difference is not solely geographical, for examination of the list will show that the prevalence of apparent incompatibility of the two groups of lice extends to New World families and genera also. The same phenomenon is to be found to some degree among other host-groups infested by both Mallophaga and Anoplura, for Dr. Werneck kindly informs me that he has not yet encountered both Mallophaga and Anoplura on the same individual monkey, and my examinations of large numbers of hyraxes and antelopes have shown that species, and even individuals, infested with large numbers of one of these groups of lice usually harbour few or no members of the other (Tables II and V). Particulars of the proportions of these two groups on a number of skins of *Procavia* and *Heterohyrax* are given in Table V, *Dendrohyrax* being omitted because Anoplura do not occur on this genus. The table includes all individuals for which full particulars are available and from which a "reasonable sample" of lice was obtained, "reasonable sample" being defined for this purpose as not less than ten lice. In order to exclude differences attributable to the technique employed I have confined the table to skins examined by brushing, but it is not to be assumed that all the skins were examined with equal thoroughness, so that the lice obtained do not necessarily represent the same proportion of the total population on the skin in each instance. The very strong tendency for one group to be dominant almost to the exclusion of the other emerges clearly from these figures; as might be expected, it is much less marked if the total louse-population is small.

Some unpublished work performed by Dr. Werneck and mentioned by his kind permission is direct evidence of similar competition within the Mallophaga;

* On the other hand, there is much evidence suggesting that, in certain other mammals and in birds, captivity favours loss of lice,

TABLE V.—Proportions of Mallophaga and Anoplura found by brushing individual skins of hyraxes. Skins from which a total of less than ten lice was obtained are omitted.

	Particulars of host.	Total lice.	Percentage of Mallophaga.
T.M. 3043	(<i>letabae</i>)	10	100
T.M. 3276	(<i>letabae</i>)	10	100
T.M. 8318	(<i>welwitschii</i>)	10	100
T.M. 8329	(<i>tsumebensis</i>)	10	90
T.M. 9618	(<i>windhuki</i>)	10	100
T.M. 9620	(? <i>reuningi</i>)	10	100
T.M. 2097	(<i>capensis</i> ssp.)	11	82
T.M. 7795	(<i>vanderhorsti</i>)	11	55
T.M. 9613	(<i>windhuki</i>)	11	82
T.M. 8319	(<i>welwitschii</i>)	12	33
T.M. 7535	(near <i>ruddi</i>)	13	31
T.M. 7793	(<i>capensis</i> ssp.)	13	85
T.M. 8324	(<i>welwitschii</i>)	13	15
T.M. 4776	(<i>granti</i>)	14	100
T.M. 5882	(<i>letabae</i>)	14	86
T.M. 9327	(near <i>natalensis</i>)	14	100
T.M. 9617	(<i>windhuki</i>)	15	80
T.M. 9615	(<i>windhuki</i>)	16	81
T.M. 3568	(<i>coombsi</i>)	17	82
T.M. 3570	(<i>coombsi</i>)	17	100
T.M. 2146	(<i>klaverensis</i>)	18	33
T.M. 9614	(<i>windhuki</i>)	18	95
T.M. 8335	(<i>reuningi</i>)	19	95
T.M. 9331	(<i>griquae</i>)	19	0
T.M. 2006	(<i>natalensis</i>)	20	100
T.M. 9326	(near <i>capensis</i>)	20	50
T.M. 3044	(<i>granti</i>)	22	100
T.M. 3570	(<i>coombsi</i>)	22	100
T.M. 6759	(<i>albaniensis</i>)	22	73
T.M. 7797	(<i>vanderhorsti</i>)	23	83
S.A.M. 18899	(<i>capensis</i>)	23	87
T.M. 5883	(<i>letabae</i>)	24	100
T.M. 3983	(<i>granti</i>)	27	100
T.M. 8339	(? <i>schantzei</i>)	28	100
T.M. 8338	(<i>schantzei</i>)	29	72
T.M. 1804	(<i>coombsi</i>)	30	100
T.M. 6756	(<i>albaniensis</i>)	30	97
T.M. 1546	(<i>coombsi</i>)	39	62
T.M. 1805	(<i>coombsi</i>)	39	88
T.M. 5331	(<i>ruddi</i>)	43	100
T.M. 2144	(<i>marlothi</i>)	44	0
T.M. 4489	(? <i>letabae</i>)	45	100
T.M. 6749	(<i>albaniensis</i>)	45	98
T.M. 5881	(? <i>letabae</i>)	46	96
T.M. 5886	(<i>ruddi</i>)	50	100
T.M. 6752	(<i>albaniensis</i>)	53	100
S.A.Z.S. T.M. 577	(<i>capensis</i> ssp.)	55	95
T.M. 3489	(<i>coombsi</i>)	56	93
T.M. 9323	(very near <i>capensis</i>)	57	100
T.M. 2145	(<i>klaverensis</i>)	63	51
T.M. 1547	(<i>coombsi</i>)	64	97
T.M. 3573	(<i>granti</i>)	70	100
T.M. 7575	(<i>coombsi</i>)	73	100
T.M. 7575	(<i>coombsi</i>)	73	100
T.M. 3574	(<i>granti</i>)	77	99
T.M. 4488	(? <i>letabae</i>)	83	100
T.M. 9295	(<i>johnstoni</i>)	84	85
T.M. 6755	(<i>albaniensis</i>)	87	100
T.M. 8336	(? <i>reuningi</i>)	90	63
T.M. 4775	(<i>granti</i>)	91	100
T.M. 3981	(<i>letabae</i>)	96	100
T.M. 3569	(<i>coombsi</i>)	99	98
T.M. 5335	(<i>otjiwarongensis</i>)	99	12
T.M. 6757	(<i>albaniensis</i>)	108	95
T.M. 8333	(<i>waterbergensis</i>)	120	77
T.M. 2150	(<i>klaverensis</i>)	126	98
T.M. 2005	(<i>natalensis</i>)	150	97
T.M. 8334	(<i>waterbergensis</i>)	178	49
S.A.M. 19448	(<i>capensis</i>)	183	97
T.M. 4344	(<i>coombsi</i>)	250	98
T.M. 1548	(<i>coombsi</i>)	289	75
T.M. 9294	(<i>johnstoni</i>)	349	97

he found that the louse-population of normal guinea-pigs is made up roughly of 85% *Gliricola*, 10% *Gyropus* and 5% *Trimenopon*; if the animals are prevented from scratching themselves the proportion of *Trimenopon* greatly increases and after some time the other two genera completely disappear, but if the same experiment is performed with a guinea-pig not infested with *Trimenopon* the other two genera multiply exceedingly. It is an everyday observation that abundance of one species of Mallophaga on a host with a multiple infestation is often accompanied by rarity or absence of the other species, and the absence of *Trichodectes* on dogs in Africa (p. 428) may be due to the fact that neglected dogs in this continent are often very heavily infested with *Heterodoxus spiniger*. Thompson (1940) notes that there are no records of these two species from the same dog, and this is also my experience.

Thompson (1938 *c*, pp. 331–332) has observed an apparent incompatibility between the presence of fleas and that of mites or lice on the same individual rat, and competition provides a probable explanation of the absence of lice on the Chiroptera, since bats are often very heavily infested by ectoparasitic mites, fleas and Diptera. Although in Thompson's observations (which I can confirm) mites and lice often occurred on the same rat, my own observations show that a heavy infestation with one of these groups of parasites is, at least usually, incompatible with the presence of large numbers of individuals of the other group on the same specimen of the host.

Because of the possibility of secondary absence, cases of sporadic occurrence of a given group of parasites on a given group of hosts need to be considered with especial care; they may represent a primary infestation, which dates from the very remote period when the hosts were represented by a common ancestor but which has largely died out, or they may be instances of secondary infestation of relatively recent date. The factors which should guide us in assessing such instances are the degree of relationship between the different hosts and that between the different parasites.

(15) GEOGRAPHICAL FACTORS.

It is rarely the case that geography plays any direct part in determining the distribution of lice, this being far more dependent on the ancestry of the host than on any other factor. Yet the geographical factor cannot be entirely ignored, and it apparently acts in at least two different ways.

We have seen that it is normal for different subspecies of the same host-species to be infested by the same lice, but that there are some completely authenticated exceptions. Taking the hyraxes as an example, the simplest form these exceptions may take is illustrated by cases such as the occurrence of *Procaricola neumanni* on *Dendrohyrax validus*, the island and mainland subspecies of the host bearing subspecifically distinct forms of the parasite. In other instances, such as the forms of *Procaricola s. str.* on the various subspecies of *Procavia capensis*, the parasites are sufficiently different to be regarded as specifically distinct but are still obviously of not far distant common descent. Such differences in the parasites may originate from subspecific differences in the hosts or may be due to the same factors which commonly cause free-living animals from different areas to differ from one another. That the latter factors may be important in the case of lice is suggested by the case of *Procavia capensis coombi*, discussed on p. 421. In all instances which come into this category the parasites that replace one another are closely related and often not more than subspecifically distinct, the differences between them having clearly arisen through modification of one original stock.

In the second set of instances in which geography appears to have affected louse-distribution the case is entirely different because the species that replace one another are not closely related and are often generically distinct. This phenomenon does not seem to have been explicitly recognized, but Peers

(1935 b, p. 148) came very close to doing so when he noted the probability that his *Philopterus migratorii* occurs only on the eastern form of *Turdus migratorius*, because *migratorii* is a *Penenirmus* and generically distinct from the species which Peters calls *Philopterus subflavescens* and which he records from three other subspecies of the host. It is obviously a development of the very familiar fact that individuals of a host which is infested with several genera of Mallophaga seldom bear heavy infestations of more than one of them. The phenomenon is very clearly illustrated by the louse-fauna of hyraxes, where it is plain that the fauna occurring on ancient hyraxes must have been much richer than that of most present-day members of the group. The most obvious case is in the genus *Procavia*, in which nearly every form possesses a *Procavicola* s. str. except in Southwest Africa, where numerous specimens of *Procavia capensis windhuki*, *P. c. reuningi* and *P. c. waterbergensis* have been examined without a *Procavicola* being found. Still more striking is the instance afforded by *Eurytrichodectes*, now confined to one subspecies of *Dendrohyrax arboreus*, but so distinct from all other Trichodectidae that it must surely have occurred on the original *Dendrohyrax* and probably on the original stock of the Procaviidae. I believe that this hypothesis that the ancestors of the Ferungulata once had much richer louse-infestations than we find on their modern representatives and that these infestations have been thinned out by extinction resulting in secondary absence, provides the only satisfactory explanation for such anomalies as the sporadic occurrence of the *Suricatoecus* group on Carnivora belonging to both Canoidea and Feloidae and the fact that the Trichodectidae of North American Mustelidae nearly all belong to the *Neotrichodectes* group, whereas in Europe this group is unknown and the Mustelidae (except *Meles* and *Lutra*) are all infested by members of the *Stachiella* group. When today we find a mammalian host bearing a number of genera and species of lice (as do *Dendrohyrax arboreus* and *Atilax paludinosus*) we are apt to consider this condition as being abnormal, but I suggest that to a large extent such a condition is earlier than the presence of only one or two louse genera and species, and that to this extent it is the latter condition which should be considered abnormal.

Kéler (1940, p. 47) seems to suggest that the fact that Mallophaga of mammals are very rich in species only in warm and hot climates may have a climatic explanation, mentioning that it is against expectation because one would expect Mallophaga to be more numerous in the denser fur of mammals of cool climates than in the sparser covering of tropical species. But I do not consider the fact that there are more species of Trichodectidae in certain tropical areas than in some cool regions to be an exception to the general rule that louse-distribution is governed solely by host-distribution; *in proportion to the number of host-species of suitable groups* Trichodectidae are hardly (if at all) fewer in temperate regions than in the tropics. The mammalian fauna of Europe, for instance, is overwhelmingly composed of members of groups (Chiroptera, Insectivora and Muridae) that do not have Mallophaga either in tropical or in cool regions, and on the groups which normally are infested with Mallophaga we generally find one species of Trichodectidae per host-species in both sets of climatic conditions. Multiple infestations with Trichodectidae are rare in most host-groups, whether in hot or in cool conditions; here, again, there does not seem to me to be any real difference between conditions in tropical and in temperate areas, for among the deer (e.g.) the only known cases of multiple infestations are those of the two North American species of *Odocoileus*, occurring in temperate conditions, each of which is infested by two species of Trichodectidae, while in the Procaviidae, on which multiple infestations are normal, *Procavia c. capensis*, occurring in the temperate conditions of the extreme south of Africa, is infested by three species of Trichodectidae as against the two that are normal for tropical species of the genus such as *Procavia johnstoni lopesi*.

III. A HOST-LIST OF THE LICE OF MAMMALS.

PROCEDURE FOLLOWED IN COMPILING THE LIST.

The difficulties of compiling a critical host-list of mammal-lice are considerable and I am conscious that I have not entirely succeeded in overcoming them, but an uncritical list would be valueless because of the numerous erroneous records that burden the literature, most of which are due to contamination, mislabelling, and misidentifications of either the host or the parasites. Nuttall (1917 c p. 112) writes, of contaminations of *Pediculus humanus* on domestic animals, that finding lice on these hosts has "no more significance than if they were found on a hearthrug or chair unless it can be shown that they breed upon other hosts than man", yet such records are often repeated by author after author until it would almost seem that the occurrence is normal. Denny's record of *Linognathus setosus* on a ferret, for example, has been copied so many times that Ewing (1929, p. 139) includes the ferret without comment in a list of the hosts of this louse, although Denny's record is obviously due to contamination. As my list is intended to be as complete as possible, I have not felt justified in omitting even obviously erroneous published records, but I have relegated most of them to notes and I hope that future authors will ignore them, for they are completely valueless and misleading.

In order to miss as few records as possible I have tried to see all the literature in which records of mammal-lice are contained, except the huge bulk of economic literature dealing solely with well-known lice of man and his domestic animals. In this endeavour I have certainly failed, because many records (some of which would be valuable as confirmation) are published in obscure local lists which seldom find their way into the reviews. Records from a few papers which I have been unable to consult have been taken from Ferris (1920-1935), from the 'Zoological Record', and from the 'Review of Applied Entomology'.

It is very unfortunate that many descriptions or records of lice are based on a few specimens collected from captive animals or from skins in museums. Many of these lice have subsequently been obtained from hosts in natural conditions and the accuracy or otherwise of the original records has been established, but many others are still only known from material of such suspect provenance. If we remember that in scores of instances a louse is known only from three or four specimens, sometimes derived from skins of as many different species of hosts, it is clear that many errors must remain, only to be cleared up by extensive collecting from wild hosts.

It is obvious that (subject to certain reservations in respect of museum skins and captive hosts) the more frequently a given louse has been obtained from a given species of host the greater becomes the probability that the louse is a normal parasite of the host concerned, particularly if it occurred in numbers. For this reason I have recorded the number of occasions on which each louse has been taken on a given host-species, regarding each host-individual as one "record", and I have also given the number of individuals of the louse which were obtained in the few instances in which this information is available. I have used a special symbol to indicate that I consider the genuine occurrence of the louse on the host under which it is listed to be established, but the brief summary of the evidence which I give in each instance will enable the reader to form his own judgment on this point. The symbol has been used rather sparingly, so that its absence does not necessarily imply that I consider the record doubtful. It is also obvious that, if the possibility of mislabelling has been excluded, a single record of a louse in large numbers from a wild host is worth many records from museum skins or captive animals. It is because I know the exact circumstances of the records, and not because I regard myself as less liable to error than others, that a number of my own records from single hosts are indicated

as being reliable* ; many other records of my own have been rejected for a similar reason—that, knowing the circumstances, I know that a mistake was extremely probable. In many instances the figures I give of louse-infestations from skins in the Transvaal Museum examined by Bedford will be found to be higher than the figures for the same skins quoted by the latter. This is because a leave spent in South Africa gave me the opportunity to re-examine many of these skins and obtain further material from them. A few records of my negative results from dissolved skins have been included in spite of the numbers being far too small to suggest that lice are really absent on these hosts, because these records may be of use to other workers.

The conditions in which monkeys are normally kept in zoos, with animals of different species often cuddling up to one another and hunting each other's lice, are ideal for the occurrence of contamination, and it is amazing that this contamination is apparently so limited in scope—that there appear, for instance, to be no records of the genus *Pedicinus* from any of the American monkeys which constitute the Ceboidea. But I have not felt able to accept the fact of there being several records of a louse from captive specimens of a monkey as constituting more than extremely weak confirmation of the authenticity of the occurrence. Furthermore, the skin of such a captive may later find its way into a museum with its original data and without any indication that it had been in captivity. For these reasons, while accepting as "wild" all museum-skins with data suggesting that the animals had never been in captivity, I have tried to differentiate by calling such specimens "wild skins". Records in which the lice were collected from a freshly-killed wild host, or from the skins of such hosts if these had not been in contact with other skins, are stated to be from "wild hosts". Records from wild skins are, of course, much less reliable than those from wild hosts. Some of Bedford's records which have the appearance of being from wild hosts are actually from wild skins, but it is often impossible to be sure in which class his records fall and I have given doubtful cases the benefit of the doubt.

Domesticated mammals also form a peculiarly difficult problem, as pointed out by Fahrenholz (1939 a). Not only are records from these hosts especially liable to be due to contamination, but the hosts themselves are probably in some cases of polyphyletic origin. Definite instances in which this latter factor appears to have affected the louse-fauna of such hosts are provided by the pigs (p. 521), the goats (p. 533) and perhaps the sheep (p. 533). The difficulty of elucidating such records is greatly increased by the almost invariable habit of authors of mentioning only vernacular names for domesticated hosts, coupled with the impossibility of deducing the form concerned from the geographical data. An ox in East Africa, for instance, may equally well be *Bos taurus*, *Bos indicus*, or a cross between the two. Very much more collecting, carried out with much more care than has usually been the case hitherto, will be required before we can hope to have anything like adequate knowledge of the lice which infest our domestic mammals.

With regard to the classification of the hosts, I have followed Simpson (1945) down to the genus. Below the genus there is no comprehensive list, but I have followed Ellerman (1940, 1941) for rodents, with a few small alterations suggested by Dr J. E. Hill for American groups. G. M. Allen (1939) has been my guide for African mammals other than rodents, but I have made a few small modifications for reasons mentioned in each case. Other groups have been worked in with the aid of mammalogical friends, but I take responsibility for the final version. Except in the case of the Hyracoidea, there are very few instances in which different subspecies of one host-species are infested with different lice,

* For the sake of brevity I have sometimes used the phrase "reliable record" in the host-list, without giving details. This phrase implies that the host was wild, contamination was excluded, and the louse-species occurred in sufficient numbers to exclude the possibility that the case was one of straggling.

so (in order to keep the list within bounds) I have normally ignored subspecies except in this group of hosts. As mentioned on p. 392, I take a conservative view of what constitutes a species, but I have not thought it desirable to alter the accepted arrangement with regard to host-species except in a few instances which are explained in the list.

Misidentifications of the hosts do not usually cause much difficulty, because most modern collectors of lice from the more difficult groups of mammals have taken the trouble to get the hosts accurately determined, but a few erroneous records are undoubtedly due to this factor. Spencer (1939), for instance, notes that the white-tailed deer of the hunter is often not the white-tailed deer of the biologist; nor is the presence of a subspecific name always proof of accurate determination, because this may merely have been added by someone who knows that this subspecies occurs in the area concerned. I have omitted records from incompletely identified hosts except actual type-hosts (*i.e.* the hosts from which the types of a louse were obtained) together with many records in which the parasite was not fully identified. The monkeys form a specially difficult problem because their synonymy is extremely complicated and the same name has often been used for different species at different periods, so that a guess has frequently had to be made as to the sense in which a given author was probably using a given name, but the importance of this factor is easily exaggerated because it only seriously affects the earlier records, all of which are from captive hosts and therefore in any case somewhat unreliable. Ferris and Bedford have set the excellent example of recording museum-numbers of their material in the more difficult groups of mammals, and this has enabled a number of host-determinations to be completed or corrected. I have followed their example wherever possible, using abbreviations (listed at the end of this section) for the various museums in which skins have been examined.

Misdeterminations of the parasites are extremely common because of the unsatisfactory state of our systematics, particularly with regard to the Mallophaga. Ferris will serve as an example for the very reason that he is an exceptionally careful author and good systematist: in 1930 he examined a collection of Mallophaga from African hyraxes, and figured them so excellently that all the species are easy to recognize; omitting the four species he described (all of them correctly) as new, he identified five species and only one of his determinations is correct. If a systematist of the calibre of Ferris can make so many mistakes, what can be expected of those of lesser grade? Again and again in his great monograph of the sucking lice (1920–1935) Ferris remarks that further material will probably cause what he is at present forced to regard as one variable species to be split up into numerous species or subspecies. In a number of instances this process of splitting has begun, but in far more this is not the case. Because of the certainty that this process will proceed further, I have indicated the type-host of each louse by placing an asterisk against the name of the latter; records without the asterisk must be read as meaning only that a louse of the same type as that named has been found on the host in question. Where a louse found on a given host has been recorded as a given species of the parasite and also split off specifically or subspecifically, only the name of the segregate is given (usually in subspecific form), regardless of the fact that it may now be regarded as a synonym, and records under the former name are regarded as applying to the latter. An example will make this point clearer: *Haematopinus asini* was described from the ass, *H. macrocephalus* from the horse and *H. minor* from the zebra, and Ferris regards all three as synonymous. For the purpose of the host-list I have assumed all records of *H. asini* from the horse and zebra to refer to *H. asini macrocephalus* and *H. a. minor* respectively, without this procedure implying any expression of opinion as to whether Ferris is right in considering them the same. Similarly, nearly all the known lice of the Mustelinae, for instance, have at some time or other been misidentified as

Trichodectes retusus, and I have assumed records under this name to refer to the specific louse of the host concerned.

The question of the number of genera into which the Trichodectidae should be divided is one of great difficulty, on which it is possible to hold very different views with an almost equal basis of logic. Taking the Mallophaga of the mongooses as an example, there is no question that they are divisible into natural groups and that, for instance, *Felicola acutirostris*, on *Atalax paludinosus*, is much more closely related to species found on other mongooses than it is to *Felicola laticeps*, also found on *Atalax*. But these groups are not sharply defined and, for this reason, I contend, mainly on grounds of convenience, that they should not be called genera or even subgenera (Hopkins, 1941 *b*, 1942 *b*, 1943 *a*). A quite similar difficulty is encountered among the Trichodectidae of the ungulates (except those of the hyraxes, in which there is no doubt that the main groups are genera) and frequently in the Anoplura. In the host-list I have used a conservative generic arrangement, partly because such an arrangement shows better the relationships between the forms found on different groups of hosts, which is one of my main objects, but I have conceded subgeneric rank to many groups which seem likely to be accepted by systematists whose views on this point differ from mine.

The status and identity of the forms of *Pediculus* found on New World monkeys (principally on the genus *Ateles*) constitute an extremely complex problem. The earliest name concerned is *Pediculus quadrumanus* (Murray, 1877), which authors seem agreed to regard as a synonym of *Pediculus humanus*. Next comes *Pediculus consobrinus* Piaget, 1880; the surviving specimen of this species in the British Museum is *Pediculus humanus* and Ferris (1920-1935, p. 586) apparently regards this specimen as the type, but Ewing (1938, p. 21) correctly points out that as it does not agree with Piaget's figure it cannot be the type (which is perhaps still at Leyden); Ewing does not, however, adopt the name *consobrinus*, though he had used it in an earlier paper (1926, p. 21). The next name is *Pediculus affinis* Mjöberg 1910, but the name is preoccupied and Ferris (1916 *b*, p. 136) renamed the species *Pediculus mjobergi*, under which name he discussed all the *Ateles*-lice in his monograph (Ferris, 1920-1935, pp. 588-598). Ewing, however (1938, p. 22), states that Mjöberg's figures indicate that *P. affinis* Mjöberg (and therefore *P. mjobergi* Ferris) is a synonym of *Pediculus humanus*, and consequently he employs the name *Pediculus lobatus* Fahrenholz, 1916, over which *P. mjobergi* has three months' priority. Furthermore, Ewing (1926; 1938) considers that there are a number of species of *Ateles*-lice, which he would place in a separate subgenus from *Pediculus humanus*, whereas Ferris (1920-1935, p. 598) not only considers them all conspecific but is even not entirely convinced that this species is distinct from *P. humanus*. It is interesting to note that Ewing later (1938, p. 18) shows a leaning towards the suppression of his special subgenus for these lice. In these circumstances I have adopted the earliest undisputed name (*P. lobatus* Fahrenholz) for these lice. I consider that Ewing, more especially in his later paper, has established a case for the existence of several apparently rather unstable forms which I think are best regarded as subspecies of *Pediculus lobatus*. The latter species is extremely closely related to the *Pediculus* of man, and I consider that to erect a special subgenus for it is grossly to exaggerate the importance of the differences. I have, therefore, accepted all the forms described or recognized by Ewing, but have placed them all as subspecies of *lobatus*, and I have accepted Ewing's claim to be able to determine eggs of *Pediculus*; I have included in my list as *P. lobatus* (without subspecific name) all the records given by Ferris unless Ewing has identified material from the same host as one of the forms he maintains, in which case the records given by Ferris are omitted; the omission is not very important because all these records are from captives.

The *Pediculus* of man presents a somewhat similar problem, whether more than one subspecies of *Pediculus humanus* should be recognized being a matter

of opinion. Nuttall and Ferris recognize only one form worthy of a name; Fahrenholz and Ewing would divide both the head-louse and the body-louse into a number of subspecies stated to be characteristic of the different races of man. The matter was discussed in great detail by Ferris (1920-1935, pp. 543-588), and I have departed from his arrangement only to the extent of recognizing the head-louse and body-louse as environmental forms which are normally so limited to their particular regions on the host as to seem to me to be worthy of subspecific rank.

The correct nomenclature of the lice of domestic pigs is also in dispute and introduces a question of unusual interest, problems of nomenclature being normally extremely dull. *Haematopinus suis* was known to Linnaeus in 1746 and the name is valid from 1758. Ferris (1920-1935, pp. 433-434) has correctly pointed out that all the early records, including those of Linnaeus, are of lice from domestic pigs, and consequently uses the name *suis* for the lice now found on the domestic pigs of Europe. Fahrenholz, however (1939 c), points out that at the time when Linnaeus wrote the domestic pigs of Europe were a domesticated form of *Sus scrofa*, hardly (if at all) modified at that time by infusion of the blood of oriental pigs, which were first imported into Europe during the eighteenth century. He considers that in Linnaeus's time the lice of domestic pigs in Sweden must have been the species now found on the European wild boar (*i.e.* *Haematopinus apri* Goureau), to which he accordingly applies the name *H. suis* (Linnaeus); his contention finds considerable support in the fact that lice from the domestic pigs of southern Europe, where the admixture of oriental blood is apparently small, are much nearer to *apri* than are those from modern pigs in north and central Europe. This arrangement is close to that proposed by Ewing (1934 b), but (although Fahrenholz is very probably right) I think the adoption of his arrangement would lead to much confusion and I have not used it in my list; I have omitted *Haematopinus sardiniensis* Fahrenholz (from *Sus scrofa nana*), which appears to be the same as *H. suis* (Linn.) in Fahrenholz's sense, and *H. suis germanus* Fahrenholz, which the latter later considered to be only a variety of *H. chinensis*. I also consider that the existence of intermediates indicates that all the form of *Haematopinus* from the genus *Sus* should be regarded as subspecies of *H. suis*. The problem of the forms of lice found on swine needs much more elucidation, particularly the collecting of far more material from wild hosts.

The abbreviations and symbols employed in the host-list are given below:—

Amb.	Amblycera.
An.	Anoplura or sucking lice.
Bo.	Boopidae.
Gyr.	Gyropidae.
Hae.	Haematopinidae.
Isc.	Ichnocera.
Neo.	Neolinognathidae.
Ped.	Pediculidae.
Phil.	Philopteridae.
Rhy.	Rhyncophthirina.
Tric.	Trichodectidae.
Trim.	Trimenoponidae.
A.M.N.H.	American Museum of Natural History, New York.
B.M.	British Museum (Natural History), London.
C.M.M.	Coryndon Memorial Museum, Nairobi.
F.C.M.	Field Columbian Museum, Chicago.
S.A.M.	South-African Museum, Cape Town.
T.M.	Transvaal Museum, Pretoria.
U.S.N.M.	United States National Museum, Washington.
*	The host concerned is the type host of the louse against whose name the symbol is placed.
†	The natural occurrence on the host concerned of the louse against whose name this symbol is placed appears to be established.

Class **MAMMALIA.**Subclass **PROTOTHERIA.**Order **MONOTREMATA.** (Egg-laying Mammals.)

No lice have been recorded from any of the Tachyglossidae (Porcupine "Anteaters") or Ornithorhynchidae (Duck-billed Platypus) which constitute this subclass. It is improbable that sufficient specimens have been adequately examined to give any indication as to whether this apparent freedom from lice is genuine.

Subclass **THERIA.**Infraclass **METATHERIA.**Order **MARSUPIALIA.** (Marsupials.)Superfamily **DIDELPHOIDEA.**Family **DIDELPHIDAE.** (Opossums.)Subfamily **Didelphinae.**Genus **MONODELPHIS.**Subgenus **Peramys.****MONODELPHIS DOMESTICUS** (Wagner).

*†*Cummingsia peramydis* Ferris (synonym: *horrida*) (Amb., Trim.). Four records, including U.S.N.M. skin no. 20251 and two wild hosts (in numbers on the latter).

Genus **MARMOSA.** (Murine Opossums.)**MARMOSA INCANA** (Lund). (Grey Opossum.)

**Cummingsia intermedia* Werneck. One record of numerous specimens from a wild host.

Genus **METACHIRUS.****METACHIRUS OPOSSUM** (Linn.). (Quica Opossum.)

Records of *Trimenopon hispidum*, *Gryopus ovalis* and *Gliricola porcelli* from this host all refer to one captive individual and are certainly due to contamination (Werneck, *in litt.*).

Dr. Werneck tells me that he has been unable to obtain lice, in nature, from the larger opossums.

Superfamily **DASYUROIDEA.**Family **DASYURIDAE.**Subfamily **Phascogalinae.**Genus **PHASCOGALE.** (Broad-footed Pouched "Mice.")Subgenus **Antechinus.****PHASCOGALE TAPOATAFU** Meyer. (Brush-tailed Pouched "Mouse.")

†*Boopia spinosa* Harrison and Johnston. Two records, one from U.S.N.M. skin 8500 almost certainly reliable. Described from *Wallabia bicolor*, but this is almost certainly erroneous.

Piaget's record of *Trichodectes penicillatus*, which he described from material supposedly obtained from this host in Rotterdam Zoo, is due either to mislabelling or contamination, the name being a synonym of *Holakartikos crassipes* and the louse a goat-parasite. A single record of *Heterodoxus longitarsus*, though apparently from a wild host, is also very probably erroneous.

PHASCOGALE FLAVIPES Waterhouse. (Yellow-footed Pouched "Mouse.")

**Phacogalia brevispinosa* (Harrison and Johnston). (Amb., Bo.) One record of a single female from a captive host.

Subfamily DASYURINAE.

Genus DASYURUS. (Native "Cats.")

DASYURUS QUOLL (Zimmermann). (Eastern Native "Cat.")

**Boopia uncinata* Harrison and Johnston. (Amb., Bo.) Two records.

DASYURUS GEOFFROYI Gould. (Black-tailed Native "Cat.")

†*Boopia uncinata* Harrison and Johnston. Several records, apparently from wild hosts.

DASYURUS HALLUCATUS Gould. (Little Northern Native "Cat.")

Boopia uncinata Harrison and Johnston. One record of three pairs, apparently from a wild host.

Superfamily PERAMELOIDEA.

Family PERAMELIDAE. (Bandicoots.)

Genus PERAMELES. (Long-nosed Bandicoots.)

PERAMELES NASUTA Geoffroy.

*†*Boopia phanocerata* Harrison and Johnston. Four records, including one "in enormous numbers" from a wild host.

Genus THYLACIS. (Short-nosed Bandicoots.)

THYLACIS TOROSUS (Ramsay). (Brindled Short-nosed Bandicoot.)

Boopia phanocerata Harrison and Johnston. One record, apparently from a wild host.

THYLACIS MACROURUS (Gould). (Larger Northern Bandicoot.)

A single record of two males of *Boopia uncinata* is probably due to contamination.

Superfamily CAENOLESTOIDEA.

Family CAENOLESTIDAE.

Subfamily *Caenolestinae*.

Genus OROLESTES.

OROLESTES INCAE Thomas.

**Cummingsia maculata* Ferris. One record of three males and one female from U.S.N.M. skin 194427.

Superfamily PHALANGEROIDEA.

Family PHASCOLOMIDAE.

Genus PHASCOLOMIS. (Wombats.)

PHASCOLOMIS HIRSUTUS (Perry). (Common Wombat.)

Boopia tarsata Piaget. One record from a captive host.

PHASCOLOMIS URSINUS (Shaw). (Island Wombat.)

**Boopia tarsata* Piaget. Three records, different sources, captive hosts.Piaget's record of *Colpocephalum truncatum*, a bird-parasite, from this host could be due to straggling but is much more probably contamination.

Genus LASIORHINUS. (Hairy-nosed Wombats.)

LASIORHINUS LATIFRONS (Owen).

**Boopia dubia* Werneck and Thompson. One record of 18 specimens, apparently from a wild host.

Family *MACROPODIDAE*.Subfamily *Macropodinae*. (Kangaroos and Wallabies.)Genus *THYLOGALE*. (Pademelons or Scrub Wallabies.)*THYLOGALE BILLARDIERI* (Desmarest). (Tasmanian or Rufous-bellied Pademelon.)*Heterodoxus forcipatus* (Mjöberg). (Amb., Bo.) One record, apparently from a wild host.*THYLOGALE COXENII* (Gray). (Cape York Pademelon.)**Heterodoxus forcipatus* (Mjöberg). One record, no details.*THYLOGALE STIGMATICA* Gould. (Northern Red-legged Pademelon.)*Heterodoxus longitarsus* (Piaget). Two records, apparently wild hosts, one certainly a misdetermination.*THYLOGALE THETIS* (Lesson). (Red-necked Pademelon.)*Heterodoxus forcipatus* (Mjöberg). Two records (one as *H. longitarsus*) from apparently wild hosts.Genus *PROTEMNODON*. (Large Wallabies.)*PROTEMNODON AGLIS* (Gould). (Sandy Wallaby.)*Heterodoxus longitarsus* (Piaget). One record, apparently wild host.*PROTEMNODON BICOLOR* (Desmarest). (Black-tailed Wallaby.)**Boopia nota-fusca* Le Souëf. One record, probably from a captive.*†*Heterodoxus macropus* Le Souëf and Bullen (synonym: *ualabati*). Three records. Described from material collected from "Kangaroos, Wallabies etc.", but Paine's redescription of material from this host is a restriction.*†*Latumcephalum lesouëfi* Harrison and Johnston. (Amb., Bo.) Three records, including one in great numbers from a captive.*Boopia spinosa* Harrison and Johnston was described from a single pair from a probably captive host; the record is doubtless due to contamination, the true host being apparently *Phascogale tapoatafu*. Records of a single female of *Boopia tarsata*, two females of *Latumcephalum macropus*, two males (and seven females) of *Heterodoxus spiniger*, and two females and a nymph of *Paraheterodoxus insignis* are all probably cases of contamination.*PROTEMNODON DORSALIS* (Gray). (Black-striped Wallaby.)**Boopia minuta* Le Souëf. One record, probably from a captive. A paratype female is indistinguishable from *nota-fusca*, but males may be different.*Heterodoxus longitarsus* (Piaget). One record, apparently wild host.**Latumcephalum macropus* Le Souëf. One record, probably from a captive. Originally from "Wallabies", later restricted to present host.*PROTEMNODON RUFOGRISEA* (Desmarest). (Red-necked Wallaby.)*Heterodoxus longitarsus* (Piaget). Two records, one from a captive, the other apparently a wild host. Doubtless misdetermination.Genus *MACROPUS*.Subgenus *Osphranter*.*MACROPUS ROBUSTUS* (Gould). (Dusky Wallaroo.)*Boopia notafusca* Le Souëf. One record of three females.*†*Paraboopia flava* Werneck and Thompson. Two records, different sources, apparently wild hosts.*Heterodoxus longitarsus* (Piaget). One record, apparently wild host.

Subgenus *Megaleia*.

MACROPUS RUFUS (Desmarest). (Great Red Kangaroo.)

*†*Boopia grandis* Piaget. Three records, different sources.*Heterodoxus longitarsus* (Piaget). One record, host apparently wild.

Mjöberg (1910 b, p. 26) states that he described *Boopia peregrina* (a synonym of *B. grandis*) from "einige Exemplare von einer *Lutra pruneri* aus Indien ('soeben frisch angekommenes Thier') (Coll. Mus. Zool. Hamburg, 4, viii. 1895)." As the whole genus *Boopia* is confined to marsupials, the record is almost certainly due to mislabelling. Incidentally, there appears to be no such otter as *Lutra pruneri*.

Subgenus *Macropus*.

MACROPUS MAJOR Shaw. (Great Grey Kangaroo.)

**Boopia mjobergi* Werneck and Thompson. One record of three females and a nymph.*†*Heterodoxus longitarsus* (Piaget). Three records, different sources, two of which apparently refer to wild hosts.One record of two specimens of *Boopia grandis* is probably due to contamination.

Genus DENDROLAGUS. (Tree Kangaroos.)

DENDROLAGUS LUMHOLTZI Collett. (Lumholtz's Tree Kangaroo.)

*†*Dendrolagia pygidialis* Mjöberg. (Amb., Bo.) Two records from wild hosts.Subfamily *Potoroinae*.

Genus AEPYPRYMNUM. ("Rat"-Kangaroos.)

AEPYPRYMNUM RUFESCENS (Gray). (Rufous "Rat"-Kangaroo.)

*†*Paraheterodoxus insignis* Harrison and Johnston. (Amb., Bo.) Four records, one from a captive, the others without details.

The single record of *Boopia bettongia*, which Le Souëf described from this host, is almost certainly due to contamination, the species being the same as *B. phanoerata*, which occurs on the bandicoot, *Perameles nasuta*.

Infraclass EUTHERIA.

Cohort UNGUICULATA.

Order INSECTIVORA.

Superfamily TENRECOIDEA.

Family POTAMOGALIDAE.

Genus POTAMOGALE.

POTAMOGALE VELOX Du Chaillu. (Insectivorous "Otter.")

I have dissolved one skin of this species without finding any lice.

Superfamily CHRYSOCHLOROIDEA.

Family CHRYSOCHLORIDAE.

The Golden "Moles" are so rare that it is not surprising that I can find no published records of any of them having been examined for lice, unless the remark of Bedford (1932 a, p. 470) that no parasites have been recorded from the South African species should be read in this sense. I have dissolved the hair of two specimens of *Chlorotalpa stuhlmanni* (Matschie) and failed to find parasites of any kind.

Superfamily ERINACEOIDEA.

Family ERINACEIDAE.

Subfamily *Erinaceinae*.

Genus ERINACEUS.

ERINACEUS EUROPAEUS Linn. (European Hedgehog.)

A single record (Bezzi, 1898) of *Trichodectes melis* from this host is almost certainly due to mislabelling. A single male of *Haemodipsus ventricosus* recorded by Enderlein (1904 c, p. 221) was either a straggler or a contamination, probably the latter.

Superfamily MACROSCELIDOIDEA.

Family MACROSCOLIDIDAE.

Genus NASILIO.

NASILIO BRACHYRHYNCHUS (A. Smith). (Short-nosed Elephant-Shrew.)

Neolinognathus elephantuli Bedford. (An., Neo.) One record from U.S.N.M. skin 181461.

Genus ELEPHANTULUS.

ELEPHANTULUS RUPESTRIS (A. Smith).

*†*Neolinognathus elephantuli* Bedford. Several records from wild hosts.

ELEPHANTULUS RUFESCENS (Peters).

**Neolinognathus praelautus* Ferris. Two records, from U.S.N.M. skins 181488 and 182612.

Genus PETRODROMUS.

PETRODROMUS TETRADACTYLUS Peters. (Four-toed Elephant-Shrew.)

Neolinognathus elephantuli Bedford. One record from U.S.N.M. skin 141526.

Superfamily SORICOIDEA.

Family SORICIDAE.

Subfamily Soricinae. (Red-toothed Shrews.)

Genus SOREX.

SOREX ARANEUS Linn. (European Common Shrew.)

*†*Polyplax r. reclinata* (Nitzsch). (An., Hae.) Several records from wild hosts.

A solitary record of a single specimen of *Hoplopleura acanthopus* may refer to a straggler, but more probably a contamination.

SOREX OBSCURUS Merriam. (Dusky Shrew.)

An erroneous record of *Trichodectes (Neotrichodectes) interrupto-fasciatus* Kellogg and Ferris is probably due to mislabelling.

Subfamily Crocidurinae. (White-toothed Shrews.)

Genus CROCIDURA.

CROCIDURA LEUCODON (Hermann). (European White-toothed Shrew.)

**Polyplax reclinata leucodontis* Jancke. One record, no details.

CROCIDURA HORSFIELDI Tomes. (Ceylon White-toothed Shrew.)

**Ancistroplax crocidurae* Waterston. (An., Hae.) One record of a short series.

CROCIDURA MANNI Peters.

Polyplax reclinata (Nitzsch). One record, no details.

Genus SUNCUS. (Musk Shrews.)

SUNCUS CAERULEUS (Kerr). (Indian Musk Shrew.)

**Polyplax deltoides* Fahrenholz. Two records, including U.S.N.M. skin 201120.

The single record of *Polyplax asiatica*, described by Ferris from this host, is extremely doubtful; the type-series consisted of two specimens from this host and three from a rodent, *Nesokia indica*, and the latter is almost certainly the true host. A single record of *Polyplax spinulosa* is also almost certainly erroneous; it is from the same specimen as *P. asiatica* and both records are probably due to an error in labelling.

SUNCUS LUZONENSIS (Peters). (Luzon Musk Shrew.)

Polyplax reclinata (Nitzsch). One record from a skin, probably mis-determination of *P. deltoides*.

Subfamily *Scutisoricinae*.

Genus SCUTISOREX. (Hero or Armoured Shrews.)

SCUTISOREX CONGICUS Thomas.

Polyplax reclinata (Nitzsch). Two records, different sources, including U.S.N.M. skin 48477 and a wild host.

Family TALPIDAE. (Moles.)

Subfamily *Talpinae*.

Genus TALPA.

TALPA EUROPAEA Linn. (European Mole.)

A single record of *Geomydoecus copei* Werneck is a perfect example of contamination, the host being European and the parasite-genus exclusively American.

Subfamily *Scalopinae*.

Genus SCALOPUS.

SCALOPUS AQUATICUS (Linn.). (Eastern American Mole.)

*†*Haematopinoides squamosus* (Osborn). (An., Hae.) (synonym: *abnormis*).

Many records from two subspecies, including U.S.N.M. skins 19616, 67601 and 91588. Host of original specimens misidentified as *Geomys*.

Genus SCAPANUS.

SCAPANUS, sp. or spp.

Ferris (1916c, p. 98) records having examined "a few fresh specimens and many skins" of *Scapanus* without finding lice. A record of four specimens of *Geomydoecus californicus* is quite definitely contamination from *Thomomys bottae* (see Werneck, 1945a, p. 96).

Order DERMOPTERA.

Family CYNOCEPHALIDAE.

Genus CYNOCEPHALUS.

Subgenus Galeopterus. (Colugos or "Flying Lemurs.")

CYNOCEPHALUS VARIEGATUS (Audebert).

*†*Hamophthirus galeopitheci* Mjöberg. (An., Hae.) One record from a freshly-collected wild host.

Mjöberg's material was from "*Galeopithecus* sp." from Fesseltan, North Borneo, but Mr. Hayman informs me that all Bornean members of this family are subspecies of *variegatus*.

Order CHIROPTERA. (Bats.)

Although several lice have been recorded from bats, the records are all erroneous and no Phthiraptera are known to occur naturally on members of this order. The supposed sucking louse, *Acanthophthirus etheldredae* Perkins (1925), from *Pipistrellus pipistrellus*, is a mite, and the supposed chewing louse, *Trichobius parasiticus* Gervais (1842), from *Desmodus rotundus*, is a member of the Diptera. The record (Ferris, 1920-1935) of *Hoptopleura maniculata* and *Neohaematopinus echinatus* from *Scotophilus wroughtoni* is almost certainly due to mislabelling. The record (Dudich, 1923) of *Enderleinellus sphaerocephalus* from *Miniopterus schreibersi* may possibly have been due to natural straggling, but many of Dudich's other records are obvious cases of contamination. The alleged finding (Gerberg and Goble, 1914) of single specimens of a bird-lice on *Hemiderma perspicillata* and of a *Geomydoecus* (a genus of rodent-infesting Trichodectidae) on *Leptoncyteris nivalis* is entirely without significance and the occurrences are at most cases of straggling; the instance of the *Geomydoecus* is particularly instructive, for the hosts of this genus are all burrowers and I fail to see how a burrowing rodent could come into any sort of natural contact, even indirect, with a living bat.

Order PRIMATES.

Suborder PROSIMII.

Infraorder Lemuriformes.

Superfamily TUPAIOIDEA.

Family TUPAIIDAE. (Tree "Shrews.")

Subfamily Tupaiinae.

Genus ANATHANA.

ANATHANA ELLIOTTI (Waterhouse). (Eastern Ghat Tree "Shrew.")

**Docophthirus acinetus* Waterston. (An., Hae.) One record, of two males and two females.

Superfamily LEMUROIDEA.

Family LEMURIDAE.

Subfamily Lemurinae.

Genus LEMUR.

LEMUR MACACO Linn. (Black Lemur or Red Lemur.)

Dr. Werneck has examined the Type of *Trichodectes abnormis* Ewing, described from a single male found on a skin of this host (U.S.N.M. skin 63338) and informs me that it is a contamination derived from a fox; it is a synonym of *ulpis*.

LEMUR MONGOZ Linn. (Mongoose Lemur.)

**Trichophlopterus ferrisi* Eichler. (Isch., Phil.) One record, five males and six females from U.S.N.M. skin 83961. Not distinguishable from *T. babakotophilus*.

Family INDRIDAE.

Genus PROPITHECUS.

PROFITHECUS DIADEMA Bennett. (Diademed Sifaka.)

*†*Phthirpediculus propithecii* Ewing. (An., Hae.) Three records; a few specimens from U.S.N.M. skins 63352 and 63354, and numbers from U.S.N.M. skin 63351.

Trichophlopterus babakotophilus Stobbe. One record.

Genus INDRI.

INDRI INDRI (Gmelin). (Indri Lemur.)

**Trichophlopterus babakotophilus* Stobbe. One record of a pair; no details as to status of host.

Infraorder Lorisiformes.

Family LORISIDAE.

Subfamily Lorisinae.

Genus NYCTICEBUS.

NYCTICEBUS COUCANG (Boddaert). (Slow Loris.)

*†*Loriscicola mjobergi* (Stobbe). (Isch., Tric.) (synonym: *brachycephala*). Three records from different subspecies and different sources, including U.S.N.M. skin 114151.

Genus PERODICTICUS.

PERODICTICUS POTTO (P. L. S. Müller). (Potto.)

I have dissolved two skins and brushed seven skins and one freshly killed animal, all *P. potto ibeanus* Thomas, without finding any lice.

Subfamily *Galaginae*.

Genus GALAGO.

GALAGO SENEGALENSIS E. Geoffroy. (Bush-baby.)

*†*Lemurphthirus galagus* Bedford. (An., Hae.) Five records from several different sources. Obtained in numbers from one wild skin.

GALAGO DEMIDOVII Fischer.

†*Lemurphthirus galagus* ssp. 105 specimens obtained by brushing one wild skin; contamination excluded.

Suborder ANTHROPOIDEA.

Superfamily CEBOIDEA.

Family CEBIDAE.

Subfamily Aotinae.

Genus AOTES. (Dourocoulis.)

AOTES BOLIVIENSIS Elliot. (Bolivian Dourocouli.)

**Gyropus aotophilus* (Ewing). (Amb., Gyr.) A single nymph from a wild skin and three males and five females from another wild skin.

AOTES INFULATUS (Kuhl).

†*Gyropus aotophilus* (Ewing). Three records from wild skins.

AOTES TRIVIRGATUS (Humboldt). (Three-banded Dourocouli.)

†*Gyropus aotophilus* (Ewing). Many specimens from a wild skin.

Subfamily Pitheciinae.

Genus PITHECIA.

Subgenus Pithecia.

PITHECIA MONACHUS E. Geoffroy. (Hairy Saki.)

**Pediculus lobatus pseudohumanus* Ewing. (An., Ped.) One record from a captive (now U.S.N.M. skin 255542).

A single female *Gyropus aotophilus* from a wild skin should provisionally be regarded as a contamination.

Subgenus Cacaiao.

PITHECIA RUBICUNDUS (I. Geoffroy). (Red Uakari.)

Pediculus lobatus pseudohumanus Ewing. One record from a captive.

Subfamily Alouattinae.

Genus ALOUATTA. (Howler Monkeys.)

ALOUATTA CARAYA (Humboldt). (Central Brazilian Black or Straw-coloured Howler Monkey.)

†*Cebidicola semiarmatus* (Neumann). (Isc., Tric.) Several records, apparently wild hosts.

ALOUATTA BEELZEBUL (Linn.). (Amazon Black and Red Howler Monkey.)

Cebidicola semiarmatus (Neumann). Two records, apparently from wild hosts.

Pediculus lobatus Fahrenholz. Two records from museum skins.

ALOUATTA PALLIATA (Gray). (Mantled Howler Monkey.)

A single record of *Pediculus lobatus* Fahrenholz is probably a case of contamination.

ALOUATTA URSINA (Humboldt). (Brown Howler Monkey.)

*†*Cebidicola semiarmatus* (Neumann). Four records from apparently wild hosts.

A single record of *Cebidicola armatus* (Neumann), though from an apparently wild host is probably a case of contamination.

ALOUATTA SENICULUS (Linn.). (Red Howler Monkey.)

†*Cebidicola semiarmatus* (Neumann). Four records from apparently wild hosts.

Subfamily *Cebinae*.

Genus *CEBUS*. (Ringtailed or Capuchin Monkeys.)

CEBUS CAPUCINUS (Linn.). (White-throated Capuchin.)

Pediculus lobatus Fahrenholz. Three records from captives.

Ewing regards specimens of *P. l. chapini* from a captive specimen of this host as contaminations.

CEBUS FATUELLUS (Linn.). (Crested Capuchin.)

**Pediculus lobatus pseudohumanus* Ewing. Three records from captives.

A single female of *Gyropus uotophilus* obtained from a wild skin is almost certainly a contamination.

Subfamily *Atelinae*.

Genus *ATELES*. (Spider Monkeys.)

ATELES PANISCUS (Linn.). (Red-faced Spider Monkey.)

†*Pediculus lobatus lobatus* Fahrenholz. Several records, including Werneck's from a definitely wild host. Possibly the same as *P. consobrinus* Piaget, described from this host and discussed on p. 437.

There is one record of *Pediculus humanus* as a contamination on this host.

ATELES ATER F. Cuvier. (Black Spider Monkey.)

**Pediculus lobatus chapini* Ewing. Four records from captives, including U.S.N.M. skin 200153.

ATELES DARIENSIS Goldman. (Panama Black Spider Monkey.)

Pediculus lobatus atelophilus Ewing. One record from a captive.

ATELES MARGINATUS E. Geoffroy. (White-whiskered Spider-Monkey.)

A single record of *Pediculus humanus* from a captive is due to contamination from man.

ATELES PAN Schlegel. (Guatemala or Schlegel's Spider Monkey.)

Pediculus lobatus atelophilus Ewing. One record, possibly wild host (now U.S.N.M. skin 61284.)

**Pediculus lobatus lobatus* Fahrenholz. Ewing (1938) regards only the original record as referring to this form and evidently considers the record erroneous.

ATELES GEOFFROYI Kuhl. (Brown-sided Spider Monkey.)

*†*Pediculus lobatus atelophilus* Ewing. Many records, including eggs from wild hosts (now U.S.N.M. skins 12138, 12150, 12151 and 61209).

Ewing regards specimens of *P. l. chapini* from a captive specimen of this species as "stragglers", i.e. contaminations.

ATELES HYBRIDUS I. Geoffroy. (Colombian Spider Monkey.)

Pediculus lobatus atelophilus Ewing. One record from a captive.

Genus BRACHYTELES.

BRACHYTELES ARACHNOIDES (E. Geoffroy). (Woolly Spider Monkey.)

*†*Cebidicola armatus* (Neumann). Two records (one of large numbers) apparently from wild hosts.

Family CALLITHRICIDAE.

Genus CALLITHRIX. (Marmosets.)

CALLITHRIX SANTAREMENSIS (Matschie). (Santarem Marmoset.)

Single records of *Harrisonia uncinata* Ferris and *Gliricola pintoii* Werneck are from a skin in a museum. Werneck (1935 *d*, p. 373; 1936 *b*, p. 488), in recording the occurrences, states his belief that they are due to contamination and is certainly right, both the lice (the *Gliricola* represented by a pair and some nymphs) being now known to occur naturally on *Proechimys oris* (see p. 493).

Genus LEONTOCEBUS. (Tamarins.)

LEONTOCEBUS NIGRICOLLIS (Spix). (Black and Red Tamarin.)

A record of *Pediculus l. lobatus* from two captives which had been in close contact with exceptionally heavily infested *Ateles paniscus* is unquestionably a case of contamination.

Superfamily CERCOPITHECOIDEA.

Family CERCOPITHECIDAE.

Subfamily Cercopithecinae.

Genus MACACA.

MACACA SYLVANUS (Linn.). (Barbary Macaque.)

*†*Pedicinus albidus* (Rudow). (An., Ped.) Three records, one from a wild skin (U.S.N.M. no. 196984.)

MACACA CYCLOPSIS Swinhoe. (Formosa Macaque.)

Pedicinus obtusus (Rudow). Two records (Neumann, 1913), perhaps from wild hosts.

MACACA NEMESTRINA (Linn.). (Pig-tailed Macaque.)

Pedicinus obtusus (Rudow). Two records from wild skins (U.S.N.M. nos. 104439 and 124286), and one from a captive.

Pedicinus eurygaster (Burmeister). Two records, same skins.

MACACA MULATTA (Zimmermann). (Bengal Macaque or Rhesus Monkey.)

*†*Pedicinus obtusus rhesi* Fahrenholz. Six records, two from wild skins including U.S.N.M. no. 63471. Ferris considers this inseparable from *obtusus*.

*†*Pedicinus eurygaster piageti* Stroebelt. Four records, one from a wild skin. Ferris considers this inseparable from *eurygaster*.

The record (Fenstermacher and Jellison) of *Eutrichophilus setosus* on this host is an obvious case of contamination.

MACACA SILENUS (Linn.). (Lion-tailed Macaque or Wanderoo.)

**Pedicinus obtusus paralleliceps* Mjöberg. One record from a captive. Ferris considers this inseparable from *obtusus*.

Pedicinus eurygaster (Burmeister). One record from a captive.

MACACA SINICUS (Linn.). (Ceylon Bonnet Macaque.)

Pedicinus obtusus (Rudow). One record from a captive.

**Pedicinus eurygaster* (Burmeister). One record from a captive.

MACACA IRUS F. Cuvier. (Crab-eating Macaque.)

(*)*Pedicinus obtusus longiceps* Piaget. Original record from a captive of this species and one of *Presbytis cristatus* (p. 450). Three records from wild skins, including U.S.N.M. nos. 114559 and 125319. Ferris considers this inseparable from *obtusus*.

Pedicinus eurygaster (Burmeister). Seven records from captives and one from a wild skin (U.S.N.M. no 144675).

MACACA sp.

Fahrenholz (1921, p. 363) mentions a *Trichodectes latifrons* from "Macacus sp." This is mentioned here only to point out that it is a *nomen nudum* and the record erroneous, the specimens being dog-lice.

Subgenus Cynopithecus.

MACACA NIGER (Desmarest). (Black or Celebes Macaque.)

Pedicinus obtusus (Rudow). One record from a captive.

Subgenus Lyssodes.

MACACA SPECIOSUS F. Cuvier. (Stump-tailed Macaque.)

Pedicinus obtusus (Rudow). One record, apparently from a wild host.

MACACA FUSCATUS (Blyth). (Japanese Macaque.)

Pedicinus obtusus (Rudow). One record, apparently from a wild host.

Genus CERCOCEBUS.

CERCOCEBUS ALBIGENA (Gray). (Grey-cheeked Black Mangabey.)

Pedicinus sp. nov. near *patas*. One record (2 males, 2 females, 2 nymphs) from a wild skin. Six other skins were dissolved and no lice found. Contamination was not wholly excluded.

Genus PAPIO.

PAPIO DOGUERA (Pucheran). (Anubis Baboon.)

†*Pedicinus hamadryas* Mjöberg. Three records, one from a wild host (contamination excluded) and two from wild skins.

Genus COMOPITHECUS.

COMOPITHECUS HAMADRYAS (Linn.). (Hamadryas or Sacred Baboon.)

**Pedicinus hamadryas* Mjöberg. Original record from "*Hamadryas* sp." in captivity. There is only one other (doubtful) species of the *hamadryas* group, but the occurrence may have been due to contamination.

Fahrenholz's *Trichodectes hamadryas*, supposed to be from this species (Fahrenholz, 1921, p. 363), is a *nomen nudum*. According to Kéler (1941b,) it is a deer-lice.

Genus CERCOPITHECUS.

CERCOPITHECUS NICTITANS (Linn.). (White-nosed or Red-tailed Monkey)

Pedicinus obtusus (Rudow). One record from a captive.

Pedicinus eurygaster (Burmeister). One record from a captive.

CERCOPITHECUS AETHIOPS (Linn.). (Black-faced Monkey.)

Pedicinus obtusus (Rudow). Two records, one from a wild host.

CERCOPITHECUS MITIS Wolf. (Diadem Guenon or Blue Monkey.)

Pedicius patas (Fahrenheit). Three records from wild skins, including U.S.N.M. 162844.

CERCOPITHECUS MONA (Schreber). (Mona Guenon.)

**Pedicius obtusus breviceps* Piaget. One record from a captive. Ferris considers this inseparable from *obtusus*.

Pedicius eurygaster (Burmeister). One record from a captive.

CERCOPITHECUS DIANA (Linn.). (Diana Monkey.)

Pedicius obtusus (Rudow). One record, no details but host probably a captive.

Genus ERYTHROCEBUS.

ERYTHROCEBUS PATAS (Schreber). (Hussar Monkey or Red Monkey.)

**Pedicius patas* (Fahrenheit). Two records, one from a wild skin (U.S.N.M. no. 162844).

Subfamily Colobinae.

Genus PRESBYTIS.

PRESBYTIS ENTELLUS (Dufresne). (Hanuman Langur.)

Pedicius ancoratus Ferris. Two records from wild skins (U.S.N.M. nos. 63470 and 191986); only a single female from the second.

Pedicius obtusus (Rudow). One record, London Zoo.

Single records of *Pedicius eurygaster* and *P. pictus* from captives in the London Zoo are due to contamination.

PRESBYTIS RUBICUNDUS (Müller). (Maroon Langur.)

Pedicius ancoratus Ferris. One record from a wild skin (U.S.N.M. no. 145334).

PRESBYTIS OBSCURA (Elliot). (Dusky Langur.)

Pedicius obtusus (Rudow). One record, wild skin (U.S.N.M. no. 124113).

PRESBYTIS CRISTATUS (Raffles). (Sumatran Langur.)

*†*Pedicius ancoratus* Ferris. Three records from wild skins (U.S.N.M. nos. 113170, 123070 and 124713).

**Pedicius o. obtusus* (Rudow) (synonym: *longiceps*). Three records from captives.

PRESBYTIS PYRRHUS (Horsfield). (Negro Langur.)

Pedicius ancoratus Ferris. One record from a wild skin (U.S.N.M. no. 201549).

Genus SIMIAS.

SIMIAS CONCOLOR Miller. (Pagi Island Langur.)

Pedicius eurygaster (Burmeister). One record from a wild skin (U.S.N.M. no. 201549).

Genus NASALIS.

NASALIS LARVATUS (Wurmb). (Proboscis Monkey.)

Pedicius obtusus (Rudow). One record, from apparently wild host.

Genus COLOBUS. (Colobus or Guereza Monkeys.)

COLOBUS POLYKOMOS (Zimmermann). (Black-and-white Colobus).

*†*Pedicinus pictus* Ferris. Many records from wild hosts and wild skins, including U.S.N.M. skin 163125.

Werneck (1946 *a*) discusses the supposed occurrence of *Procavicola colobi* (Kellogg) (Isch., Tric.) on this host and produces evidence that makes it nearly certain that the original record was due to mislabelling (note the complete absence of signs of desiccation of the specimens) and a second record to contamination (note that the specimens included other hyrax-parasites and had been dry). It is to be remembered that hyraxes are often so heavily infested with Mallophaga that gross contamination can easily occur when their dry skins come into contact with those of other mammals. That I have dissolved 25 skins of the supposed host without encountering *P. colobi* is not conclusive but points in the same direction. There is a very strong probability that the true host of the louse is a subspecies of *Dendrohyrax validus*.

The single record of *Pedicinus obtusus colobi* Fahrenholz, described from a captive colobus, is probably due to contamination, since there are no records of forms of *obtusus* from wild specimens of any African monkeys. Ferris considers the form inseparable from *obtusus s. str.*

Superfamily HOMINOIDEA.

Family PONGIDAE. (Apes.)

Subfamily Hylobatinae. (Gibbons.)

Genus HYLOBATES.

HYLOBATES CONCOLOR (Harlan). (Grey Gibbon.)

**Pediculus humanus friedenthali* Fahrenholz. One record, no details, presumably captive host. See note below.

Genus SYMPHALANGUS.

SYMPHALANGUS SYNDACTYLUS (Desmarest). (Siamang Gibbon.)

**Pediculus humanus assimilis* Fahrenholz (synonym: *oblongus*). One record, Berlin zoo.

The status of both of Fahrenholz's lice as parasites of gibbons is exceedingly doubtful. Ferris (1920-1935, p. 587), after examining specimens of *assimilis*, decided that both forms were merely *P. humanus*; it is to be presumed that they had been derived, as a contamination, from man. Ewing (1933 *a* p. 168) records his having "searched several scores of study skins of gibbons . . . without finding as much as a single egg or louse specimen."

Subfamily Ponginae. (Great Apes.)

Genus PAN.

PAN TROGLODYTES (Blumenbach). (Chimpanzee.)

*†*Pediculus schäffi* Fahrenholz (synonym: *simiae*). Six records of adults of which one possibly and one certainly from wild hosts, and four records of eggs from wild skins.*Phthirus pubis* (Linn.). (An., Ped.) One record, possibly from a wild host. See note after next genus.

Genus GORILLA.

GORILLA GORILLA (Savage and Wyman). (Gorilla.)

**Phthirus gorillae* Ewing. Known only from eggs and first-stage nymphs from two wild skins (U.S.N.M. nos. 239883 and 239884). See note below.

The occurrence of *Phthirus* on the great apes in nature is entirely probable but badly needs confirmation. The record from the chimpanzee is from a host in its own country (Belgian Congo, see Bedford, 1936 *c*, p. 105), but if the host was a captive, about which there is no information, could very easily be due to contamination from man. The records from the gorilla are still more unsatisfactory; it is to be noted that Ewing's material consisted of eggs and first-stage nymphs only, and may very well have been derived from the porters who carried in the skins, for in Africa all loads are normally carried on the head and *Phthirus* is not uncommon on the head-region in man. The differences between *P. gorillae* and *P. pubis* given by Ewing are not very convincing.

Family *HOMINIDAE*.Genus *HOMO*.*HOMO SAPIENS* Linn. (Man.)*†*Pediculus humanus humanus* Linn. (synonyms: *albidior*, *chinensis*, *corporis*, *marginatus*, *nigritarum*, *nigrescens*, *tabescentium* and *vestimenti*). Abundant.*†*Pediculus humanus capitis* De Geer (synonyms: *americanus*, *angustus*, *cervicalis*, *maculatus* and *pubescens*). Abundant.*†*Phthirus pubis* (Linn.) (synonyms: *chavesi*, *ferus* and *inguinalis*). Abundant.There is one record (Ewing, 1938, p. 24) of *Pediculus pseudohumanus* from man.

Order EDENTATA.

Suborder XENARTHRA.

Infraorder Pilosa.

Superfamily MYRMECOPHAGOIDEA.

Family MYRMECOPHAGIDAE.

Dr. Werneck kindly informs me that he has examined large numbers of ant-eaters without finding any lice.

Superfamily BRADYPODOIDEA.

Family BRADYPODIDAE. (Tree-sloths.)

Genus BRADYPUS.

BRADYPUS TRIDACTYLUS Linn. (Three-toed Sloth or Ai.)**Lymneon cummingsi* Eichler. (Isc., Tric.) A single pair from a probably recently-captured host. See note at end of Bradypodidae." *Gyrogonus* " *hispidus* Burmeister, described from a single specimen found on a skin of this host, is a contaminating *Trimenopon* derived from *Cavia* sp., probably *porcellus* (information kindly supplied by Dr. S. Kéler).*CHOLOEPUS DIDACTYLUS* (Linn.). (Two-toed Sloth or Unau.)**Lymneon gastrodes* (Cummings). One record of a male, three females and a nymph from British Guiana, no details *re* status of host.The status of *Lymneon* is not satisfactory, though Eichler's record greatly strengthens the case for the genus containing true sloth-parasites. Ewing (1924 c, pp. 36, 37) records examining several scores of skins and several freshly-killed sloths without finding so much as an egg of a louse, and Werneck (1936 b, p. 460) mentions having examined large numbers of skins and living or recently-dead sloths with similar results. At least superficially, *Lymneon* shows a close resemblance to *Procavicola* (from Procaviidae), but I have not seen specimens. It seems most unlikely that the specimens are contaminations from Procaviidae since these mammals are confined to the Ethiopian Region, Syria and Palestine, while both the records of *Lymneon* are Neotropical.

Infraorder Cingulata.

Superfamily DASYPODOIDEA.

Family DASYPODIDAE. (Armadillos.)

Dr. Werneck tells me that he has examined large numbers of armadillos without finding any lice.

Order PHOLIDOTA.

Family MANIDAE. (Pangolins.)

There are no published records of examinations of pangolins for lice. I have searched three specimens of *Manis* (*Phataginus*) *tricuspis* Rafinesque without finding any lice.

Cohort GLIRES.

Order LAGOMORPHA.

Family OCHOTONIDAE. (Pikas or Mouse-Hares.)

Genus OCHOTONA.

OCHOTONA SCHISTICEPS (Merriam). (Grey-headed Pika.)

Ferris (1916c, p. 98) records examining about 15 fresh specimens and several skins of subspecies *albata*, as well as several skins of the nominotypical form, with negative results.

OCHOTONA THIBETANA (Milne-Edwards). (Tibetan Pika.)

**Hoplopleura ochotonae* Ferris. (An., Hae.) One record from U.S.N.M. skin 144032.

OCHOTONA DANURICA Pallas. (Mongolian Pika.)

Hoplopleura ochotonae Ferris. One record from U.S.N.M. skin 176274.

OCHOTONA ROYLEI (Ogilby). (Himalayan Pika.)

Hoplopleura ochotonae Ferris. One record from a skin.

Family LEPORIDAE. (Hares and Rabbits.)

Subfamily Leporinae.

Genus LEPUS.

Subgenus Lepus.

LEPUS CALIFORNICUS Gray. (Black-tailed Jack "Rabbit.")

*†*Haemodipsus setoni* Ewing. (An., Hae.) Many records, different sources, including U.S.N.M. skins 60907, 123846 and 123847.

A record of two individuals of *Linognathus setosus* is doubtless due to contamination.

LEPUS TOWNSENDII Bachman. (White-tailed Jack "Rabbit.")

Haemodipsus? setoni Ewing. One record.

LEPUS WASHINGTONI Baird. (Western Varying Hare or Snowshoe Rabbit.)

A single record of one individual of *Linognathus setosus* is doubtless due to contamination.

LEPUS ARCTICUS Ross. (Arctic Hare.)

Haemodipsus setoni Ewing. One record.

LEPUS EUROPÆUS Pallas. (European Common or Brown Hare.)

†*Haemodipsus lyriocephalus* (Burmeister). Four records, different sources.

A single erroneous record of *Damalinia tibialis* is probably due to mislabelling.

LEPUS TIMIDUS Linn. (European Blue or Mountain Hare.)

*†*Haemodipsus lyriocephalus* (Burmeister). Numerous records.

LEPUS CAPENSIS Linn. (Cape Hare.)

†*Haemodipsus* sp. nov. One reliable record (five males and six females from a skin of ssp. *crawshayi*).

LEPUS SAXATILIS F. Cuvier. (South African Desert Hare.)

**Haemodipsus africanus* Bedford. One record of a single female.

"LEPUS CANNABINUS."

Ponton's "*Trichodectes leporis*", supposedly from this host, is a bird-parasite and does not even belong to the Ischnocera. No mammal of this name apparently exists.

Subgenus Poëlagus.

LEPUS MARJORITA (St. Leger). (Uganda Grass Hare.)

One fresh skin dissolved; no lice found.

Genus SYLVILAGUS. (Cottontails, Brush "Rabbits", Swamp "Rabbits.")

SYLVILAGUS FLORIDANUS (Allen).

A single record of four specimens of *Geomydoecus californicus* is almost certainly a case of mislabelling.

SYLVILAGUS PALUSTRIS (Bachman).

An erroneous record of *Trichodectes* (*Neotrichodectes*) *osborni* (Kéler) is probably due to mislabelling.

SYLVILAGUS BRASILIENSIS (Linn.). (Brush "Rabbit.")

†*Trimenopon hispidum* (Burmeister). (Amb., Trim.)

†*Gyropus ovalis* Burmeister. (Amb., Gyr.)

†*Gliricola porcelli* (Schrank). (Amb., Gyr.)

The above parasites are all undoubtedly derived from *Cavia* and must originally have been stragglers, but they have evidently become established. Dr. Werneck informs me that, not only do these hares easily become infested with *Cavia*-parasites in the laboratory, when the parasites live and reproduce as if on their normal host, but also he has killed several heavily-infested hares in open grassland far from human dwellings, where the obvious source of infestation was the wild species of *Cavia* inhabiting the same ground.

Genus ORYCTOLAGUS. (True Rabbits.)

ORYCTOLAGUS CUNICULUS (Linn.). (Rabbit.)

*†*Haemodipsus ventricosus* (Denny). Very many records.

Records of *Linognathus setosus* from rabbits are almost certainly due to contamination from dogs employed in retrieving them. Werneck is unquestionably right in considering his record of *Pedicinus eurygaster* from a tame rabbit in a laboratory to be due to contamination from a monkey.

Order RODENTIA.

Suborder SCIUROMORPHA.

Superfamily APLODONTOIDEA.

Family APLODONTIDAE.

Genus APLODONTIA.

APLODONTIA RUEFA (Rafinesque). (Sewellel or Mountain "Beaver.")

Ferris (1915 c, p. 98) records having examined a number of specimens of this species with negative results.

Superfamily SCIUROIDEA.

Family SCIURIDAE.

Subfamily *Sciurinae*.

Tribe SCIURINI.

Genus SCIURUS.

Subgenus *Sciurus*.

SCIURUS VULGARIS Linn. (European Red Squirrel.)

*†*Enderleinellus nitzschi* Fahrenholz (synonym: *sphaerocephalus* Nitzsch). (An., Hae.) Numerous records from different sources, including U.S.N.M. skin 115218.

*†*Neohaematopinus sciuri* Jancke. (An., Hae.) At least four records from three sources.

Subgenus *Tenes*.

SCIURUS ANOMALUS Guldenstaedt. (Persian Squirrel.)

Enderleinellus nitzschi Fahrenholz. One record (1 male 3 females) from U.S.N.M. skin 13511.

**Neohaematopinus syriacus* Ferris. Single specimens from U.S.N.M. skins 13511 and 152748.

Subgenus *Neosciurus*.*carolinensis* group.

SCIURUS CAROLINENSIS Gmelin. (North American Grey Squirrel.)

*†*Enderleinellus longiceps* Kellogg and Ferris. Several records, different sources, including U.S.N.M. skin 23691.

*†*Hoplopleura sciuricola* Ferris. (An., Hac.) Many records, different sources, including U.S.N.M. skin 23691.

†*Neohaematopinus sciurinus* (Mjöberg) Many records from wild hosts and one from U.S.N.M. skin 23691.

aureogaster group.

SCIURUS AUREOGASTER F. Cuvier.

Enderleinellus extremus Ferris. Two records (4 pairs and 2 males 3 females) from skins of different subspecies, probably including U.S.N.M. skin 73297.

Neohaematopinus sciurinus (Mjöberg). One record from U.S.N.M. skin 73297.

SCIURUS POLIOPUS (Fitzinger).

Enderleinellus extremus Ferris. One record of a pair, probably from U.S.N.M. skin 68182.

Neohaematopinus sciurinus (Mjöberg). One record from U.S.N.M. skin 68182.

SCIURUS NELSONI Merriam.

Enderleinellus mexicanus Werneck. One record (4 males 5 females) from U.S.N.M. skin 51156.

Neohaematopinus sciurinus (Mjöberg). One record from U.S.N.M. skin 51156.

SCIURUS COLLIAEI Richardson.

Enderleinellus mexicanus Werneck. One record (1 male 7 females) from U.S.N.M. skin 91245.

Neohaematopinus sciurinus (Mjöberg). One record from U.S.N.M. skin 91245.

SCIURUS TRUEI Nelson.

**Enderleinellus mexicanus* Werneck. One record (1 male, 6 females and 19 nymphs) from U.S.N.M. skin 96795.

SCIURUS SOCIALIS Wagner.

**Enderleinellus extremus* Ferris. One record of 9 males and 16 females, probably from a wild host. The number is large enough to suggest that the record is reliable.

SCIURUS GRISEOFLAVUS (Gray).

Enderleinellus extremus Ferris. One record of 2 males and 4 females, probably from a skin.

SCIURUS VARIEGATOIDES Ogilby.

*†*Enderleinellus hondurensis* Werneck. Three records (in considerable numbers) from U.S.N.M. skins 14253, 77906 and 90168.

Stobbe's queried record of *Geomydoecus geomydis* from this host is doubtless due to contamination.

deppei group.

SCIURUS DEPPEI Peters.

Enderleinellus extremus Ferris. One record of a male and two females, probably from U.S.N.M. skin 100048.

Neohaematopinus sciurinus (Mjöberg). One record of 4 males and 2 females, probably from a skin.

Subgenus *Otosciurus*.

SCIURUS ABERTI Woodhouse. (Tassel-eared Squirrel.)

Enderleinellus longiceps Kellogg and Ferris. One record of 3 pairs from U.S.N.M. skin 19023, 25819.

Neohaematopinus sciurinus (Mjöberg). One record from U.S.N.M. skin 168301.

SCIURUS KAIBABENSIS Merriam. (Kaibab Squirrel.)

Enderleinellus longiceps Kellogg and Ferris. One record (4 pairs) from U.S.N.M. skin 168301.

Hoplopleura sciuricola Ferris. One record from U.S.N.M. skin 168301.

Subgenus *Hesperosciurus*.

SCIURUS GRISEUS (Ord). (Californian Grey Squirrel.)

**Enderleinellus kelloggi* Ferris. Two records, apparently from wild hosts.

Hoplopleura sciuricola Ferris. One record from a wild host.

*† *Neohaematopinus sciurinus griseicolus* Ferris. Four records, apparently wild hosts.

Subgenus *Parasciurus*.

SCIURUS NIGER Linn. (American Fox-Squirrel.)

*† *Enderleinellus longiceps* Kellogg and Ferris. Three records, different sources, including U.S.N.M. skin 70023.

*† *Neohaematopinus sciurinus* (Mjöberg) (synonyms: *antennatus* Osborn and *macrospinosus*). Many records from different sources.

SCIURUS OCLATUS Peters.

Enderleinellus longiceps Kellogg and Ferris. One record (10 males 15 females) from U.S.N.M. skin 54235.

Neohaematopinus sciurinus (Mjöberg). One record from U.S.N.M. skin 54235.

SCIURUS ALLENI Nelson.

Enderleinellus arizonensis Werneck. One male from U.S.N.M. skin 116931.

Enderleinellus longiceps Kellogg and Ferris. One pair from U.S.N.M. skin 116931.

Neohaematopinus sciurinus (Mjöberg). One record from U.S.N.M. skin 11691 (? 116931).

It is probable that one of the two species of *Enderleinellus* on this host represents contamination, though there are fully-authenticated cases of the occurrence of two or more species of one louse-genus even on the same individual host.

SCIURUS NAYARITENSIS Allen.

Enderleinellus arizonensis Werneck. One male from U.S.N.M. skin 90947.

Enderleinellus longiceps Kellogg and Ferris. Two pairs from U.S.N.M. skin 90947.

See note on *Sciurus alleni*.

SCIURUS APACHE Allen. (Apache Squirrel.)

Enderleinellus arizonensis Werneck. Two males and one female from U.S.N.M. skin 132347.

Neohaematopinus sciurinus (Mjöberg). One record from the same skin.

SCIURUS ARIZONENSIS Coues. (Arizona Grey Squirrel.)

**Enderleinellus arizonensis* Werneck. One record (2 males and 6 females) apparently from a wild host.

Hoplopleura sciuricola Ferris. One record, no details.

Subgenus *Guerlinguetus*.*hoffmani* group.

SCIURUS HOFFMANI (Peters).

Enderleinellus ? extremus Ferris. One record, probably from a skin.

Neohaematopinus sciurinus (Mjöberg). One record from a skin.

SCIURUS GRISEOGENA (Gray).

**Enderleinellus venezuelae* Ferris. Two records (6 pairs and 3 pairs) from different subspecies, probably skins.

Hoplopleura sciuricola Ferris. One record from F.C.M. skin 17621.

SCIURUS NESAEUS Allen.

**Enderleinellus insularis* Werneck. One record of 4 males and 3 females, probably from F.C.M. skin 16606.

Hoplopleura sciuricola Ferris. One record from F.C.M. skin 16606.

SCIURUS GERRARDI Gray.

Enderleinellus venezuelae Ferris. One record of a pair, probably from F.C.M. skin 18732.

Neohaematopinus sciurinus (Mjöberg). One record from F.C.M. skin 18732.

SCIURUS SPLENDIDUS Gray.

Hoplopleura sciuricola Ferris. One record from U.S.N.M. skin 107224.

aestuans group.

SCIURUS AESTUANS Linn.

*†*Enderleinellus brasiliensis* Werneck. Many records.

Hoplopleura sciuricola Ferris. One record.

SCIURUS INGRAMI Thomas.

Hoplopleura sciuricola Ferris. One record from a wild host.

pucherani group.

SCIURUS IGNITUS (Gray).

Hoplopleura sciuricola Ferris. One record from U.S.N.M. skin 194488.

Subgenus *Hadrosciurus*.

SCIURUS IGNIVENTRIS Wagner.

**Enderleinellus urosciuri* Werneck. One record of 1 male and 5 females.

SCIURUS PYRRHONOTUS Wagner.

Hoplopleura sciuricola Ferris. One record from U.S.N.M. skin 194486.

SCIURUS LANGSDORFFI Brandt.

Hoplopleura sciuricola Ferris. Two records from wild hosts.

Genus *MICROSCIURUS*.

MICROSCIURUS MIMULUS (Thomas). (American Pigmy Squirrel.)

**Enderleinellus microsciuri* Werneck. Two records, 3 pairs from U.S.N.M. skin 172947 and 4 males from F.C.M. skin 18876.

Tribe *TAMIASCIURINI*.Genus *TAMIASCIURUS*.

TAMIASCIURUS HUDSONICUS (Erxleben). (American Red Squirrel or Chickaree.)

Enderleinellus nitzschi Fahrenholz. Two records (1 male and 5 females) from skins of different subspecies.

†*Hoplopleura sciuricola* Ferris. Many records from two subspecies.

†*Neohaematopinus sciurinus* (Mjöberg). Seven records from wild hosts.

TAMIASCIURUS DOUGLASHII (Bachman). (Pacific Chickaree.)

†*Enderleinellus nitzschi* Fahrenholz. Three records, different sources, one a wild host.

†*Hoplopleura sciuricola* Ferris. Three records, different sources, at least one a wild host.

*†*Neohaematopinus sciurinus semifasciatus* Ferris. Two records from wild hosts of different subspecies. Ferris later considered this form inseparable from *sciurinus*.

TAMIASCIURUS FREMONTI (Audubon and Bachman). (Rocky Mountain or Boomer Chickaree.)

Enderleinellus nitzschi Fahrenholz. One record of 3 females from a skin.

Tribe *FUNAMBULINI*.Genus *FUNAMBULUS*.

FUNAMBULUS PALMARUM (Linn.). (Indian Striped Palm-squirrel.)

**Enderleinellus platyspicatus* Ferris. One record of 3 females, probably from U.S.N.M. skin 114084.

**Hoplopleura maniculata* (Neumann). One record, apparently from a wild host.

**Neohaematopinus echinatus* (Neumann). One record, apparently from a wild host, and one male from U.S.N.M. skin 114084.

Genus *PROTOXERUS*.

PROTOXERUS STANGERI (Waterhouse). (African Giant Forest-squirrel.)

Enderleinellus heliosciuri Ferris. Two records (1 male 2 females and 3 females), probably from skins.

Genus *PARAXERUS*. (African Scrub-squirrels.)

cepapi group.

PARAXERUS OCHRACEUS (Huet). (Olive Scrub-squirrel.)

**Enderleinellus minutus* Werneck. One male from F.C.M. skin 16747.

**Enderleinellus zonatus* Ferris. Two records (1 male 3 females and 1 male) from different subspecies, including U.S.N.M. skin 182776.

†*Neohaematopinus heliosciuri* Cummings. Four records, including F.C.M. skin 16747 and U.S.N.M. skins 182776 and 182795.

Neohaematopinus suahelicus Ferris. Two records, from F.C.M. skin 16747 and U.S.N.M. skin 182776.

PARAXERUS PALLIATUS (Peters).

**Enderleinellus paraxeri* Werneck. One male and seven females from U.S.N.M. skin 182804. A record of *E. zonatus* from U.S.N.M. skin 141472 also probably refers to *paraxeri*.

*†*Neohaematopinus heliosciuri* Cummings. Six records, including U.S.N.M. skin 182794 and T.M. skin 6278.

**Neohaematopinus suahelicus* Ferris. Two records, U.S.N.M. skins 141472 and 182804.

boehmi group.

PARAXERUS ALEXANDRI (Thomas and Wroughton). (Alexander's Striped Scrub-squirrel.)

†*Neohaematopinus heliosciuri* Cummings. One reliable record.

Genus HELIOSCIURUS.

Subgenus Heliosciurus.

HELIOSCIURUS GAMBIANUS (Ogilby).

*†*Enderleinellus heliosciuri* Ferris. Six records, from several subspecies.

**Neohaematopinus keniae* Ferris. A single male, almost certainly from a skin, and one male and three females from a wild host.

Subgenus Aethosciurus.

HELIOSCIURUS RUWENZORII (Schwann).

Enderleinellus heliosciuri Ferris. A single male, probably from U.S.N.M. skin 172921.

Neohaematopinus keniae Ferris. A single male from U.S.N.M. skin 172921.

Tribe CALLOSCIURINI.

Genus CALLOSCIURUS. (Oriental Tree-squirrels.)

Subgenus Tamiops.

CALLOSCIURUS MACLELLANDI (Horsfield). (Striped Himalayan Squirrel.)

Hoplopleura erismata Ferris. One record from U.S.N.M. skin 124254.

CALLOSCIURUS VESTITUS Miller.

**Hoplopleura distorta* Ferris. One record from U.S.N.M. skin 199559.

Subgenus Callosciurus.

tenuis group.

CALLOSCIURUS PROCERUS Miller.

Neohaematopinus sciurinus (Mjöberg). One record from U.S.N.M. skin 104699.

erythraeus group.

CALLOSCIURUS FERRUGINEUS (F. Cuvier). (Bay Squirrel.)

**Hoplopleura erismata* Ferris. One record from U.S.N.M. skin 201408.

Neohaematopinus sciurinus Mjöberg. One record from the same skin.

CALLOSCIURUS FINLAYSONI (Horsfield). (Finlayson's Squirrel.)

Neohaematopinus sciurinus (Mjöberg). Two records from skins of different subspecies (U.S.N.M. nos. 201383 and 201395).

caniceps group.

CALLOSCIURUS CANICEPS Gray. (Golden-backed Squirrel.)

*†*Enderleinellus malaysianus* Ferris. Four records from skins of different subspecies (U.S.N.M. nos. 83495, 104386, 123922 and 124147).

Hoplopleura erismata Ferris. One record from U.S.N.M. skin 83495.

Neohaematopinus sciurinus (Mjöberg). One record, U.S.N.M. skin 83495.

prevosti group.

CALLOSCIURUS PREVOSTI (Desmarest). (Prevost's Squirrel.)

Enderleinellus malaysianus Ferris. A pair from U.S.N.M. skin 142319.

Neohaematopinus sciurinus (Mjöberg). One record from U.S.N.M. skin 142319.

hippurus group.

CALLOSCIURUS JUVENCUS (Thomas).

Neohaematopinus sciurinus (Mjöberg). One record from a skin.

Genus MENETES.

MENETES BERDMOREI (Blyth).

**Enderleinellus menetensis* Ferris. A pair from U.S.N.M. skin 201426.

Neohaematopinus sciurinus (Mjöberg). One record from U.S.N.M. skin 201426.

Genus LARISCUS.

LARISCUS INSIGNIS (F. Cuvier). (Striped Oriental Ground-Squirrel.)

**Enderleinellus larisci* Ferris. Five males and four females from U.S.N.M. skin 153683.

Neohaematopinus sciurinus (Mjöberg). One record from U.S.N.M. skin 121644.

Genus DREMOMYS.

DREMOMYS PERNYI (Milne-Edwards). (Red-cheeked Oriental Ground-Squirrel.)

**Enderleinellus dremomydis* Ferris. Two females from a skin.

Genus SCIUROTAMIAS.

SCIUROTAMIAS DAVIDIANUS (Milne-Edwards).

**Enderleinellus sciurotamiasis* Ferris. One record of two pairs, probably from U.S.N.M. skin 200873.

**Hoplopleura emarginata* Ferris. Many specimens from U.S.N.M. skin 200873.

Genus NANNOSCIURUS. (Oriental Pigmy Squirrels.)

NANNOSCIURUS MELANOTIS (Müller and Schlegel).

**Enderleinellus nannosciuri* Ferris. A pair from a skin.

Tribe XERINI.

Genus ATLANTOXERUS.

ATLANTOXERUS GETULUS (Linn.). (North African Ground-Squirrel.)

*†*Neohaematopinus pectinifer* (Neumann) (synonym: *setosus*). Three records (one of 50 specimens from a wild host), different sources.

Genus XERUS.

Subgenus Euxerus.

XERUS ERYTHROPUS (E. Geoffroy). (Central African Side-striped Ground-Squirrel.)

*†*Enderleinellus (Hoplophthirus) euxeri* Ferris. Many records from wild hosts.

Subgenus Geosciurus.

XERUS INAURIS (Zimmermann). (South African Ground-Squirrel.)

*†*Neohaematopinus faurei* (Bedford). Many records from wild hosts.

Doubtfully referred to Tribe XERINI.

Genus SPERMOPHILOPSIS.

SPERMOPHILOPSIS LEPTODACTYLUS (Lichtenstein).

**Neohaematopinus citelli* (Cummings) (synonym: *spermophili*). One record, probably from a wild host.

Tribe MARMOTINI.

Genus MARMOTA.

monax group.

MARMOTA MONAX (Linn.). (Woodchuck.)

*†*Enderleinellus (Cyclophthirus) suturalis marmotae* Ferris. Five records from two subspecies.

flaviventris group.

MARMOTA FLAVIVENTRIS (Audubon and Bachman). (Yellow- or Red-bellied Marmot.)

*†*Neohaematopinus marmotae* Ferris. Many records from wild hosts.

"*Philandesia*" *foxi* Ewing, described from a male from this host and a female from a rat, turns out to be a *Menacanthus* derived from a bird. It is possible that the bird had been eaten by the marmot.

caudata group.

MARMOTA AUREA (Blanford).

Neohaematopinus ? marmotae Ferris. One male from U.S.N.M. skin 62116.

marmota group.

MARMOTA MARMOTA (Linn.). (Alpine Marmot.)

Piaget described *Gyropus turbinatus* from material supposed to have been obtained from this host, but the record is at best contamination, the name being a synonym of *G. ocalis* Burmeister and the true host the guinea-pig.

Genus CYNOMYS. (Prairie-"Dogs", Prairie-Marmots.)

Subgenus Leucocrossuromys.

CYNOMYS LEUCURUS Merriam. (Northern White-tailed Prairie-"Dog.")

Enderleinellus (Cyclophthirus) suturalis (Osborn). Two records, of which one is from a skin.

Neohaematopinus laeviusculus (Grube). One record from a skin.

CYNOMYS GUNNISONI (Baird). (Southern White-tailed Prairie-"Dog.")

Enderleinellus (C.) suturalis (Osborn). One record from a skin.

Genus CITELLUS. (Susliks, Gophers or Spermophiles.)

Subgenus Citellus.

pygmaeus group.

CITELLUS RUFESCENS (Keyserling and Blasius).

Neohaematopinus laeviusculus (Grube). One record, perhaps from a wild host.

citellus group.

CITELLUS DAURICUS (Brandt).

Enderleinellus (Cyclophthirus) suturalis (Osborn). One record of 3 males probably from a skin.

CITELLUS EVERSMAINI (Brandt).

Enderleinellus (C.) suturalis (Osborn). A male and 10 females from U.S.N.M. skin 175306.

*†*Neohaematopinus laeviusculus* (Grube) (synonym: *spermophili* Grube). Five records, different sources, including U.S.N.M. skins 175306 and 199576.

townsendii group.

CITELLUS TOWNSENDII (Bachman). (Townsend's Ground-Squirrel.)

†*Enderleinellus (C.) suturalis* (Osborn). Two records (4 males 12 females and 3 males 8 females) from skins.

richardsoni group.

CITELLUS RICHARDSONI (Sabine). (Yellow Gopher or Picket-Pin Ground-Squirrel.)

Enderleinellus (C.) suturalis (Osborn). One female, probably from a skin.

(*?)*Neohaematopinus laeviusculus montanus* (Osborn). At least two records. See note below.

Osborn's "Western Gray Squirrel" from Fort Collins, Colorado, was almost certainly a *Citellus* and perhaps a form of *richardsoni*. It is the type-host of *Neohaematopinus montanus* (Osborn), which Ferris thinks inseparable from *laeviusculus*.

CITELLUS BELDINGI (Merriam). (Oregon or Western Picket-Pin Ground-Squirrel.)

Enderleinellus (C.) suturalis (Osborn). One record (2 males 11 females) from a wild host.

Neohaematopinus laeviusculus (Grube). One record from a wild host and one from a skin.

parryi group.

CITELLUS COLUMBIANUS (Ord). (Columbian Spermophile or Ground-Squirrel.)

*†*Neohaematopinus laeviusculus columbianus* (Osborn). Many records from wild hosts. Ferris thinks this inseparable from *laeviusculus*.

CITELLUS PARRYII (Richardson). (Arctic Ground-Squirrel.)

Neohaematopinus laeviusculus (Grube). Two records, one certainly from a skin.

CITELLUS OSGOODI (Merriam). (Yukon Valley Ground-Squirrel.)

Enderleinellus (C.) suturalis (Osborn). One record of a male and two females, probably from a skin.

Neohaematopinus laeviusculus (Grube). One record from U.S.N.M. skin 128369.

Subgenus *Ictidomys*.

- CITELLUS TRIDECIMLINEATUS (Mitchill). (Thirteen-striped Ground-Squirrel.)
 †*Enderleinellus* (*C.*) *suturalis* (Osborn). Three records, different subspecies,
 including U.S.N.M. skins 87688 (two pairs) and 132674 (3 females).
Neohaematopinus laeviusculus (Grube). One record, wild host.
- CITELLUS MEXICANUS (Erxleben). (Mexican Ground-Squirrel.)
Neohaematopinus laeviusculus (Grube). One record.

Subgenus *Poliocitellus*.

- CITELLUS FRANKLINII (Sabine). (Franklin's Ground-Squirrel.)
 *†*Enderleinellus* (*C.*) *suturalis* (Osborn). One record from a wild host,
 another (13 males 14 females) from U.S.N.M. skin 179237.
Neohaematopinus laeviusculus (Grube). One record, wild host.

Subgenus *Otospermophilus*.

- CITELLUS VARIEGATUS (Erxleben). (Rock Squirrel.)
 †*Enderleinellus* (*C.*) *suturalis osborni* Kellogg and Ferris. Two records
 (5 pairs and 7 pairs) from different subspecies.
Neohaematopinus laeviusculus (Grube). Two records, one from a skin.
- CITELLUS BEECHEYI (Richardson). (California Ground-Squirrel.)
 *†*Enderleinellus* (*C.*) *suturalis osborni* Kellogg and Ferris. At least four
 records from three subspecies.
Neohaematopinus laeviusculus (Grube). One record.

Subgenus *Ammospermophilus*.

- CITELLUS HARRISII Audubon and Bachman.
Neohaematopinus citellinus Ferris. One record, apparently from a wild
 host.
- CITELLUS NELSONI (Merriam). (White-tailed "Antelope" Ground-Squirrel.)
Enderleinellus (*C.*) *suturalis* (Osborn). Two females from a skin.

Subgenus *Xerospermophilus*.

- CITELLUS TERETICAUDUS (Baird). (Round-tailed Ground-Squirrel.)
Enderleinellus (*C.*) *suturalis osborni* Kellogg and Ferris. One record of
 11 males 13 females, probably from a skin.
 *†*Neohaematopinus citellinus* Ferris. Several records, apparently from
 wild hosts.

Subgenus *Callospermophilus*.

- CITELLUS LATERALIS (Say). (Say's Ground-Squirrel or Big Chipmunk.)
 *†*Enderleinellus* (*C.*) *suturalis occidentalis* Kellogg and Ferris. Three
 records, at least one from a wild host. Ferris thinks this form inseparable
 from *suturalis*.
Neohaematopinus laeviusculus (Grube). One record.
- CITELLUS MADRENSIS (Merriam).
Enderleinellus (*C.*) *suturalis occidentalis* Kellogg and Ferris. One male
 two females from U.S.N.M. skin 95350.

Genus **TAMIAS**. (Chipmunks.)Subgenus **Neotamias**.*alpinus* group.**TAMIAS ALPINUS** Merriam. (Alpine Chipmunk.)*Hoplopleura e. erratica* (Osborn). One record from a wild host.*Neohaematopinus pacificus* Kellogg and Ferris. One record, wild host.*minimus* group.**TAMIAS MINIMUS** Bachman.A single record of *Hoplopleura sciuricola* from a skin is probably due to contamination.*amoenus* group.**TAMIAS AMOENUS** Allen.†*Hoplopleura erratica* (Osborn). Four records from wild hosts.*quadrivittatus* group.**TAMIAS QUADRIVITTATUS** (Say). (Colorado Chipmunk.)*Hoplopleura erratica arboricola* Kellogg and Ferris. One record from a wild host.*Neohaematopinus pacificus* Kellogg and Ferris. One record, wild host.*townsendii* group.**TAMIAS TOWNSENDII** (Bachman). (Pacific Chipmunk.)*Hoplopleura e. arboricola* Kellogg and Ferris. Two records.**Neohaematopinus pacificus* Kellogg and Ferris. One record.**TAMIAS ALLENI** (Howell).**Hoplopleura e. arboricola* Kellogg and Ferris. One record.*Neohaematopinus pacificus* Kellogg and Ferris. One record.**TAMIAS MERRIAMII** Allen. (Merriam's Chipmunk.)*Hoplopleura e. arboricola* Kellogg and Ferris. One record from a wild host.*Neohaematopinus pacificus* Kellogg and Ferris. One record, wild host.Subgenus **Tamias**.**TAMIAS STRIATUS** (Linn.). (Eastern Chipmunk.)(*)†*Hoplopleura e. erratica* (Osborn). Many records, including U.S.N.M. skins 35147 and 135553. Originally described from a single specimen as a contamination on a bird (*Larus* sp.).Fahrenheit's *Enderleinellus tamiasis* was described from material obtained from this host in a zoo and is probably a contamination.Subfamily **Petauristinae**.Genus **PETAURISTA**. (Giant Flying Squirrels.)**PETAURISTA PETAURISTA** (Pallas).**Neohaematopinus batuanae* Ferris. One record from a skin.**PETAURISTA INORNATUS** Geoffroy.**Neohaematopinus petauristae* Ferris. One record from a skin.

Genus SCIUROPTERUS.

SCIUROPTERUS VOLANS (Linn.).

**Enderleinellus replicatus* Redikorzev. Two records, different sources, one of them from a wild host.

Genus GLAUCOMYS.

GLAUCOMYS VOLANS (Linn.). (Smaller American Flying Squirrel.)

Hoplopleura trispinosa Kellogg and Ferris. Two records, one of which is from a skin.

*†*Neohaematopinus sciuropteri* (Osborn). Four records, three from apparently wild hosts.

GLAUCOMYS SABRINUS (Shaw). (Larger American Flying Squirrel.)

**Hoplopleura trispinosa* Kellogg and Ferris. Two records, different localities, one from a wild host.

**Microphthirus uncinatus* (Ferris). (An., Hae.) One record from a wild host.

†*Neohaematopinus sciuropteri* (Osborn). Three records from wild hosts.

Superfamily GEOMYOIDEA.

Family GEOMYIDAE.

Subfamily Geomyinae.

Genus GEOMYS.

tuza group.

GEOMYS TUZA (Barton). (Southeastern Pocket-Gopher or "Salamander.")

(*)†*Geomydoecus scleritus* (McGregor). (Isch., Tric.) Original record from "gopher", Florida. Abundant records from *G. t. tuza* and *G. t. floridanus*.

Dr. J. E. Hill tells me that *Geomys tuza floridanus* must almost certainly have been the host of the original material.

bursarius group.

GEOMYS BURSARIUS (Shaw). (Midwestern Pocket-Gopher.)

*†*Geomydoecus geomydis* (Osborn). Several records of large numbers from wild hosts.

The record of *Haematopinooides squamosus*, described from material purporting to be from this host, is due to misdetermination of the host (see *Scalopus aquaticus*).

breviceps group.

GEOMYS LUTESCENS Merriam.

Geomydoecus geomydis (Osborn). Three males, six females and five nymphs from two individuals.

GEOMYS BREVICEPS Baird. (Texas Pocket-Gopher.)

*†*Geomydoecus texanus* Ewing. Seven records, mostly from wild hosts.

†*Geomydoecus geomydis* (Osborn). Four records, including one of large numbers from skins in A.M.N.H.

Geomydoecus, sp. nov. Six males from skins of ssp. *personatus* in A.M.N.H.

The holotype male of *Geomydoecus chapini* Werneck was found on U.S.N.M. skin 218035 but its presence was probably due to contamination, as also was probably the finding of two males of *Geomydoecus californicus* on skins in A.M.N.H.

Dr. Hill tells me that *G. personatus* and *G. p. fallax* are probably subspecies of *breviceps*.

GEOMYS ARENARIUS Merriam.

†*Geomydoecus californicus* (Chapman). Three records, including one of large numbers from skins in A.M.N.H.

Geomydoecus, sp. nov. near *chapini*. A single male from the same skins.

The above records are possibly due to natural transfer from *Thomomys*.

Genus THOMOMYS.

Subgenus Thomomys.

bottae group.

THOMOMYS BOTTAE (Eyndoux and Gervais). (Western Pocket-Gopher.)

†*Geomydoecus thomomyus* (McGregor). Many records, different sources.

(*)†*Geomydoecus californicus* (Chapman). Many records. Described from material supposedly obtained from "*Perognathus* sp.", from Baja California; *T. bottae* is the only member of the Geomyidae in the area.

A single record of *Geomydoecus geomydis* (4 specimens) is probably due to contamination.

perpallidus group.

THOMOMYS PERPALLIDUS (Merriam).

Geomydoecus geomydis (Osborn). One record, probably misdetermination.

fulvus group.

THOMOMYS BAILEYI Merriam.

Geomydoecus californicus (Chapman). Many specimens from skins in A.M.N.H.

Geomydoecus, sp. nov. near *chapini*. Numerous specimens from the same skins.

talpoides group.

THOMOMYS TALPOIDES (Richardson). (Saskatchewan Pocket-Gopher.)

*†*Geomydoecus thomomyus* (McGregor). Original record from "*Thomomys* sp.", Jefferson, Colorado. At least three records from *talpoides*, different sources.

Dr. Hill kindly informs me that *Thomomys douglasii*, *T. fuscus* and *T. monticola* are all probably subspecies of *T. talpoides*, and that a *Thomomys* from Jefferson must almost certainly have been *T. talpoides fossor* Allen.

Genus CRATOGEOMYS.

CRATOGEOMYS CASTANOPS (Baird).

Geomydoecus ? *geomydis* (Osborn). Many specimens from skins in A.M.N.H.

Genus PLATYGEOMYS.

PLATYGEOMYS GYMNURUS (Merriam).

(?)**Geomydoecus expansus* (Dugés). See note below.

(?)**Geomydoecus copei* Werneck. See note below.

The original record of *expansus* is from "la tuza (*Geomys mexicanus*, Licht. ; *Platygeomys gymnurus*, Merr.)". As pointed out by Werneck (1945, p. 101) "tuza" is the equivalent of "pocket-gopher" and the two Latin names were probably merely mentioned as illustrating the group to which the "tuza" belonged. All other records, including those of the type-series of *copei*, are from "*Geomys mexicanus*", a name which is stated to refer to species belonging to at least two genera.

Genus *MACROGEOMYS*.

MACROGEOMYS HETERODUS (Peters). (Giant Pocket-Gopher.)

Geomydoecus expansus (Dugés). Three records. Very probably mis-determinations.

Family *HETEROMYIDAE*.Subfamily *Perognathinae*.

Genus *PEROGNATHUS*. (Pocket-Mice.)

Subgenus *Perognathus*.

PEROGNATHUS PARVUS (Peale). (Silky Pocket-Mouse.)

Fahrenholzia pinnata Kellogg and Ferris. (An., Hae.) One record from a skin.

PEROGNATHUS FORMOSUS Merriam. (Long-tailed Pocket-Mouse.)

**Fahrenholzia tribulosa reducta* Ferris. One record from a wild host.

Subgenus *Chaetodipus*.

PEROGNATHUS HISPIDUS Baird. (Spiny Pocket-Mouse.)

**Fahrenholzia tribulosa zacatecae* Ferris. One record from U.S.N.M. skin 91875.

PEROGNATHUS PENICILLATUS Woodhouse.

Fahrenholzia tribulosa Ferris. Three females from a skin.

A record of a single male *Geomydoecus californicus* is due to contamination.

PEROGNATHUS CALIFORNICUS Merriam. (California Pocket-Mouse.)

**Fahrenholzia t. tribulosa* Ferris. One record from a wild host.

Unplaced within genus.

PEROGNATHUS sp. (from Baja California).

Geomydoecus californicus (Chapman) was described from a single female, supposedly from a *Perognathus*, but the record is erroneous. The only member of the Geomyidae known to occur in Baja California is a form of *Thomomys bottae*, and this is the true host.

Genus *MICRODIPODOPS*.

MICRODIPODOPS POLIONOTUS Grinnell. (Kangaroo-Mouse or Dwarf Pocket-Rat.)

Fahrenholzia pinnata Kellogg and Ferris. One record from a skin.

Subfamily *Dipodominae*.

Genus *DIPODOMYS*. (Kangaroo-Rats or Sand Rats.)

heermanni group.

DIPODOMYS HEERMANNI Le Conte. (Heerman's Kangaroo-Rat.)

*†*Fahrenholzia pinnata* Kellogg and Ferris. Several records, apparently wild hosts.

"*Perodipus*" *streatori*, type-host of *Polyplax auricularis californiae* Fahrenholz, is probably a misreading of *Peromyscus [maniculatus] streatoris*. This matter is discussed on p. 470.

philippsi group.

DIPODOMYS PHILIPPSI Gray.

Fahrenholzia pinnata Kellogg and Ferris. One record, U.S.N.M. skin 52036.

DIPDOMYS ORNATUS Merriam.

Fahrenholzia pinnata Kellogg and Ferris. One record, U.S.N.M. skin 91939.

merriami group.

DIPDOMYS MERRIAMII Mearns. (Merriam's Kangaroo-Rat.)

Fahrenholzia pinnata Kellogg and Ferris. Two records from skins, including U.S.N.M. skin 26053.

A record (Paine, 1912 *b*, p. 440) of "several specimens" of *Geomysdoecus californicus* (Chapman) from this host is very probably erroneous.

ordii group.

DIPDOMYS ORDII Woodhouse. (Ord's Kangaroo-Rat.)

Fahrenholzia pinnata Kellogg and Ferris. Two records, including F.C.M. skin 6807.

deserti group.

DIPDOMYS DESERTI Stephens. (Big Desert Kangaroo-Rat.)

Fahrenholzia pinnata Kellogg and Ferris. Two records from skins, including U.S.N.M. no. 136616.

Subfamily *Heteromyinae*.

Genus LIOMYS.

pictus group.

LIOMYS PICTUS (Thomas).

**Fahrenholzia microcephala* Ferris. One record, F.C.M. skin 11099.

irroratus group.

LIOMYS IRRORATUS (Gray).

Fahrenholzia microcephala Ferris. From U.S.N.M. skins 29943, 34131 and 91883.

Genus HETEROMYS.

Subgenus *Heteromys*.

HETEROMYS GOLDMANI Merriam. (Spiny Pocket-Rat.)

Fahrenholzia microcephala Ferris. One record, U.S.N.M. skin 14353.

Superfamily CASTOROIDEA.

Family *CASTORIDAE*.Subfamily *Castorinae*. (Beavers.)

Genus CASTOR.

CASTOR CANADENSIS Kuhl. (American Beaver.)

Trichodectes castoris Osborn, supposedly from this host, is actually from a skunk.

Superfamily ANOMALUROIDEA (doubtfully referred to Sciuromorpha).

Family *ANOMALURIDAE*.

Genus ANOMALURUS.

ANOMALURUS FRASERI Waterhouse. (Common Scaly-tail.)

I have dissolved three wild skins of *A. f. jacksoni* De Winton, but found no lice.

Family *PEDETIDAE* (doubtfully *Anomaluroidea*).Genus *PEDETES*.*PEDETES CAFER* (Pallas). (South African Springhaas.)*†*Eulinognathus d. denticulatus* Cummings. (An., Hac.) Many records from wild hosts.*PEDETES SURDASTER* Thomas. (East African Springhaas.)*†*Eulinognathus d. surdasteri* Werneck. Many records from wild hosts.Suborder *MYOMORPHA*.Superfamily *MUROIDEA*.Family *CRICETIDAE*.Subfamily *Cricetinae*Tribe *HESPEROMYINI*.Genus *ORYZOMYS*: (American Rice-Rats.)Subgenus *Oryzomys*.*melanotis* group.*ORYZOMYS ROSTRATUS* Merriam.*Hoplopleura quadridentata* (Neumann). One record, U.S.N.M. skin 92935.

Not allocated to group.

ORYZOMYS ANGOUYA (Desmarest).*Hoplopleura nesoryzomydis* Ferris. From F.C.M. skin 18167.*ORYZOMYS CHAPARENSIS* Osgood.*Hoplopleura hesperomydis* (Osborn). One record from a skin.*ORYZOMYS ELIURUS* Wagner.*Hoplopleura affinis* (Burmeister). One record from a skin.*ORYZOMYS FLAVESCENS* (Waterhouse).*†*Hoplopleura travassosi* Werneck. Numerous records from wild hosts.*ORYZOMYS LATICEPS* (Lund).A record of *Gyropus parasetosus* Werneck, apparently from a wild host, is probably an instance of mislabelling.*ORYZOMYS RATTICEPS* Hensel.*Hoplopleura quadridentata* (Neumann). One record from a skin.*ORYZOMYS XANTHAEOLUS* Thomas.*Hoplopleura nesoryzomydis* Ferris. From F.C.M. skin 19431.Subgenus *Oligoryzomys*.*ORYZOMYS FULVESCENS* (Saussure).*Hoplopleura hesperomydis* (Osborn). From U.S.N.M. skin 58259.*Hoplopleura quadridentata* (Neumann). From U.S.N.M. skin 58259.Subgenus *Nesoryzomys*.*ORYZOMYS INDEFESSUS* Thomas.*Hoplopleura nesoryzomydis* Ferris. One record from skins.*ORYZOMYS NARBOROUGHII* Heller.**Hoplopleura nesoryzomydis* Ferris. One record from skins.

Genus *NECTOMYS*. (Neotropical Water-Rats.)*NECTOMYS* *SQUAMIPES* (Brants).

*†*Hoplopleura quadridentata* (Neumann). Three records, including F.C.M. skins 4908 and 18162.

Dr. Hill informs me that *N. palmipes* is a subspecies of *squamipes*.

Genus *RHIPIDOMYS*.

Ellerman (1941, pp. 364-366) lists the forms of this genus in alphabetical order and suggests the probability that all may prove to belong to "one or perhaps two species."

RHIPIDOMYS *LEUCODACTYLUS* Tschudi.

Hoplopleura angulata Ferris.

RHIPIDOMYS *VENEZUELAE* Thomas.

**Hoplopleura angulata* Ferris. From F.C.M. skin 7048.

RHIPIDOMYS *VENUSTUS* Thomas.

Hoplopleura angulata Ferris. From U.S.N.M. skin 137507.

A single specimen of *Hoplopleura hirsuta* Ferris from U.S.N.M. skin 137507 was most probably a contamination.

Genus *THOMASOMYS*.*THOMASOMYS* *CINEREUS* (Thomas).

Hoplopleura angulata Ferris. From F.C.M. skin 19824.

Genus *REITHRODONTOMYS*. (American Harvest-Mice.)Subgenus *Aporodon*.*mexicanus* group.*REITHRODONTOMYS* *MEXICANUS* (Saussure). (Mexican Harvest-Mouse.)

Polyplax a. auricularis Kellogg and Ferris. (An., Hae.) From U.S.N.M. skin 68685.

Genus *PEROMYSCUS*.Subgenus *Haplomyiomys*.*PEROMYSCUS* *CALIFORNICUS* (Gambel). (Parasitic Mouse.)

**Polyplax painei* Fahrenholz. One record, apparently from a wild host.

Subgenus *Peromyscus*.*maniculatus* group.*PEROMYSCUS* *MANICULATUS* (Wagner). (North American White-footed or Deer-Mouse.)

†*Hoplopleura hesperomydis* (Osborn). Several records, three subspecies, at least two wild hosts.

*†*Polyplax a. auricularis* Kellogg and Ferris. Two records, different subspecies, at least one a wild host.

It is exceedingly probable that "*Perodipus streatori*" (type-host of *Polyplax auricularis californiae* Fahrenholz) is a misreading of *Peromyscus* [*maniculatus*] *streatori*, and that the louse is the same as *P. a. auricularis*, but Fahrenholz does not even mention the number of specimens. A record of two males of *Geomydoecus californicus* is erroneous, doubtless contamination.

PEROMYSCUS *SITKENSIS* Merriam. (Sitka White-footed or Deer-Mouse.)

Polyplax a. auricularis Kellogg and Ferris. One record.

leucopus group.*PEROMYSCUS* *LEUCOPUS* (Rafinesque). (White-footed Mouse.)

**Hoplopleura hesperomydis* (Osborn). One record, probably a wild host.

boylei group.

PEROMYSCUS BOYLEI (Baird). (Brush Mouse.)

Hoplopleura hesperomydis (Osborn). One record.

Genus ONYCHOMYS.

ONYCHOMYS LEUCOGASTER (Wied). (Grasshopper-Mouse.)

Hoplopleura hesperomydis (Osborn). One record from a skin.*Polyptax auricularis* Kellogg and Ferris. One record from a skin.

ONYCHOMYS TORRIDUS (Coues).

Hoplopleura hesperomydis (Osborn). Two records, different subspecies.

Genus AKODON.

Subgenus Akodon.

boliviensis group.

AKODON ARENICOLA (Waterhouse).

Hoplopleura affinis (Burmeister). From U.S.N.M. skin 94161.A single specimen of *Protogyropus normalis* found on a skin of this host was a contamination.

AKODON ARVICULOIDES (Wagner).

†*Hoplopleura affinis* (Burmeister). Four records from skins and two from wild hosts, including F.C.M. nos. 18182 and 18891 and U.S.N.M. no. 121380.

AKODON MOLLIS Thomas.

Hoplopleura affinis (Burmeister). One record from U.S.N.M. skin 181334.*urichii* group.

AKODON AEROSUS Thomas.

Hoplopleura affinis (Burmeister). One record from U.S.N.M. skin 148841.

Subgenus Chroemys.

AKODON PULCHERRIMUS Thomas.

Hoplopleura affinis (Burmeister). Two records from wild hosts.

Genus ZYGODONTOMYS.

ZYGODONTOMYS LASIURUS (Lund).

Hoplopleura affinis (Burm.). One record, wild host.

ZYGODONTOMYS SEORSUS Bangs.

Hoplopleura nesoryzomydis Ferris. One record from U.S.N.M. skin 116671.

Genus OXYMYCTERUS.

OXYMYCTERUS JUDEX Thomas.

**Hoplopleura fonsecai* Werneck. One record of seven adults and some nymphs.*Hoplopleura travassosi* Werneck. One record, wild host.

OXYMYCTERUS PARAMENSIS Thomas.

**Hoplopleura oxymycteri* Ferris. From U.S.N.M. skin 194701.

Genus SCAPTEROMYS.

gnambiquarae group.

SCAPTEROMYS GNAMBIQUARAE Ribeiro.

*†*Gyropus (Tetragyropus) ribeiroi* Werneck. (Amb., Gyr.) Several records, doubtless a secondary infestation, but apparently established.

Genus HESPEROMYS.

HESPEROMYS CALLOSUS (Rennger).

Hoplopleura hesperomydis (Osborn). From U.S.N.M. skin 94164.

HESPEROMYS VENUSTUS (Thomas).

Hoplopleura nesoryzomydis Ferris. One record, wild host.

Genus GRAOMYS.

GRAOMYS GRISEOFLAVUS (Waterhouse).

Hoplopleura affinis (Burmeister). One record from a skin.

Genus PHYLLOTIS.

Subgenus Phyllotis.

PHYLLOTIS ARENARIUS Thomas.

Hoplopleura affinis (Burmeister). One record, wild host.

PHYLLOTIS RICARDULUS Thomas.

Hoplopleura affinis (Burmeister). One record, wild host.

Subgenus Auliscomys.

PHYLLOTIS PICTUS (Thomas).

Hoplopleura affinis (Burmeister). From F.C.M. skin 21140 and U.S.N.M. skin 194544.

PHYLLOTIS MICROPUS (Waterhouse).

Hoplopleura affinis (Burmeister). From U.S.N.M. skin 84290.

Hoplopleura reducta Ferris. From F.C.M. skin 18891.

A pair and a nymph of *Phtheiropoios latipollicaris* from U.S.N.M. skin 84290 were doubtless contaminations.

PHYLLOTIS BOLIVIENSIS (Waterhouse).

Hoplopleura affinis (Burmeister). One record, wild host.

Genus REITHRODON.

REITHRODON CUNICULOIDES Waterhouse.

Hoplopleura affinis argentina Werneck. From U.S.N.M. skin 84199.

A single female *Phtheiropoios latipollicaris* from U.S.N.M. skin 84199 was a contamination.

REITHRODON sp. (from Argentina).

**Hoplopleura affinis argentina* Werneck. One record.

Genus HOLOCHILUS.

HOLOCHILUS BALNEARUM Thomas.

†*Hoplopleura nesoryzomydis* Ferris. Three records from wild hosts.

HOLOCHILUS SCIUREUS Wagner.

†*Hoplopleura nesoryzomydis* Ferris. Three records, wild hosts.

HOLOCHILUS VULPINUS (Lichtenstein).

†*Hoplopleura nesoryzomydis* Ferris. Eight records, wild hosts.

Genus SIGMODON. (Cotton-Rats.)

hispidus group.

SIGMODON HISPIDUS Say and Ord.

*†*Hoplopleura hirsuta* Ferris. Five records from three subspecies.

The supposed provenance of the type-series of *Gliricola panamensis* from this host is probably a case of mislabelling, and I suggest that "*Sigmodon hispidus chiriquensis*" was a slip for "*Proechimys centralis chiriquensis*". The latter name is a synonym of *P. semispinosus panamensis*, the host from which the remainder of the type-series was obtained (see p. 493).

fulviventer group.

SIGMODON OCHROGNATHUS Bailey.

Hoplopleura hirsuta Ferris. From U.S.N.M. skin 96268.
Unplaced.

SIGMODON PERUANUS Allen.

Hoplopleura hirsuta Ferris. From F.C.M. skin 19216.

Genus NEOTOMODON.

NEOTOMODON ALSTONI Merriam.

Polyplax a. auricularis Kellogg and Ferris. One record from U.S.N.M. skin 50656.

Genus NEOTOMA.

Subgenus Neotoma.

floridana group.

NEOTOMA MICROPUS Baird. (Baird's Wood-Rat.)

Neohaematopinus ? neotomae Ferris. One record, probably from a wild host.*albigula* group.

NEOTOMA ALBIGULA Hartley. (White-throated Wood-Rat.)

*†*Neohaematopinus neotomae* Ferris. Several records (at least one of large numbers), apparently from wild hosts.

Subgenus Homodontomys.

NEOTOMA FUSCIPES Baird. (Dusky-footed Wood-Rat.)

†*Neohaematopinus neotomae* Ferris. Several records, apparently from wild hosts.

Subgenus Teonoma.

NEOTOMA CINEREA (Ord). (Bushy-tailed Wood-rat.)

*†*Neohaematopinus inornatus* (Kellogg and Ferris). Many records from two different subspecies, apparently wild hosts.

The single record of *Hoplopleura a. acanthopus* from this host is regarded by Ferris as a case of straggling.

Subgenus Hodomys.

NEOTOMA ALLENI Merriam.

Neohaematopinus neotomae Ferris. One record from U.S.N.M. skin 32706.

Genus XENOMYS.

XENOMYS NELSONI Merriam.

Hoplopleura hirsuta Ferris. One record of a single specimen, probably a contamination.

Tribe CRICETINI.

Genus CRICETULUS. (Dwarf Hamsters.)

Subgenus Cricetulus.

longicaudatus group.

CRICETULUS LONGICAUDATUS (Milne-Edwards).

**Polyplax dentaticornis* Ewing. A single male and a nymph (perhaps not conspecific) from U.S.N.M. skin 172610.*migratorius* group.

CRICETULUS MIGRATORIUS (Pallas).

A single record of *Neohaematopinus citelli* from this host is almost certainly erroneous.

Subgenus Tscherkia.

CRICETULUS TRITON (de Winton).

Hoplopleura affinis (Burmeister). One record from U.S.N.M. skin 172550.

Subfamily Lophiomyinae.

Genus LOPHIOMYS.

LOPHIOMYS IMHAUSI Milne-Edwards. (Maned Rat.)

*†*Bathyergicola lophiomydis* Ferris. Original series from three wild skins, including U.S.N.M. nos. 184114 and 755360; since obtained in large numbers from a wild host.

Subfamily Microtinae.

Tribe LEMMI.

Genus DICROSTONYX.

DICROSTONYX TORQUATUS (Pallas). (Collared Lemming.)

Hoplopleura a. acanthopus (Burmeister). One record.

Genus SYNAPTOMYS.

Subgenus Synaptomys.

SYNAPTOMYS COOPERI Baird. (Cooper's Lemming-Mouse.)

Hoplopleura a. acanthopus (Burmeister). Two records from wild hosts.

Subgenus Mictomys.

SYNAPTOMYS BOREALIS (Richardson). (Lemming-Mouse.)

Hoplopleura a. acanthopus (Burmeister). One record from U.S.N.M. skin 129396.*Polyplax spinulosa* (Burmeister). One record.

Genus LEMMUS.

obensis-trimucronatus group.

LEMMUS OBENSIS Brants.

**Hoplopleura hispida* (Grube) (synonym: *gracilis* Grube). One record of several specimens from a wild host. Ferris considers this to be probably a synonym of *H. a. acanthopus*.

LEMMUS ALASCENSIS Merriam. (Brown Lemming.)

Hoplopleura a. acanthopus (Burmeister). One record from U.S.N.M. skin 107733.

Tribe MICROTINI.

Genus CLETHRIONOMYS.

rutilus group.

CLETHRIONOMYS GLAREOLUS (Linn.). (European Red-backed Mouse or Bank-Vole.)

**Hoplopleura acanthopus edentulus* Fahrenholz. Three records. Ferris considers this a synonym of *H. a. acanthopus*. The original host was determined as *rutilus*, but the locality (near Kronstadt) is outside the range of the latter.

rufocanus group.

CLETHRIONOMYS RUFOCANUS (Sundevall). (Red-backed Mouse or Bank-Vole.)

(*)*Polyplax borealis* Ferris. Described from two males and a female from an apparently wild host which was doubtfully determined as *rufocanus*. According to Ewing this is a synonym of *P. alaskensis*.

CLETHRIONOMYS NIVARIUS (Bailey). (Olympic Peninsula Red-backed Mouse or Bank-Vole.)

Hoplopleura acanthopus (Burmeister). One record from F.C.M. skin 6247.

glareolus group.

CLETHRIONOMYS GAPPERI (Vigors). (Red-backed Mouse.)

Hoplopleura acanthopus (Burmeister). One record from a wild host.

Genus ARVICOLA.

ARVICOLA AMPHIBIUS (Linn.). (Water-rat or Water-Vole.)

*†*Polyplax spiniger* (Burmeister). Many records from different sources. Apparently a synonym of *spinulosa*.

Genus PHENACOMYS.

intermedius group.

PHENACOMYS INTERMEDIUS Merriam.

Polyplax abscisa Fahrenholz. Two records, apparently from wild hosts.

longicaudus group.

PHENACOMYS LONGICAUDUS True.

Polyplax abscisa Fahrenholz. One record, probably from a wild host.

Genus PITYMYS.

PITYMYS SUBTERRANEUS (de Sélys-Longchamps).

**Hoplopleura acanthopus aequidentis* Fahrenholz. One record, no details. Regarded by Ferris as a synonym of *a. acanthopus*.

PITYMYS SAVII (de Sélys-Longchamps).

†*Hoplopleura acanthopus* (Burmeister). Several records, wild hosts.

PITYMYS PINETORUM (Le Conte). (Pine Mouse.)

Hoplopleura acanthopus (Burmeister). Two records, U.S.N.M. skins 31888 and 88733.

Genus *MICROTUS*.Subgenus *Microtus*.*pennsylvanicus* group.

MICROTUS PENNSYLVANICUS (Ord). (American long-tailed Meadow-Mouse or Vole.)

Hoplopleura acanthopus (Burmeister). Two records, wild hosts.

Polyplax abscisa Fahrenholz. One record, apparently from wild host.

Osborn's record of *Hoplopleura erratica* from this host is due either to contamination or mislabelling.

MICROTUS BREWERI (Baird).

Polyplax abscisa Fahrenholz. One female from a skin.

agrestis group.

MICROTUS AGRESTIS (Linn.). (Northern European Field-vole or Short-tailed Field-Mouse.)

†*Hoplopleura a. acanthopus* (Burmeister). Many records, including wild hosts and U.S.N.M. skin 105752.

arvalis group.

MICROTUS ARVALIS (Pallas). (Southern European Field Vole.)

*†*Hoplopleura a. acanthopus* (Burmeister). Numerous records from wild hosts.

californicus group.

MICROTUS CALIFORNICUS (Peale). (Californian Meadow-mouse.)

**Hoplopleura acanthopus americans* Kellogg and Ferris. Two records, from different subspecies. Ferris considers this inseparable from *H. a. acanthopus*.

(*)*Polyplax abscisa* Fahrenholz. Described from one or more males from "Arvicola spec." from California. The host was almost certainly a *Microtus* and may have been *M. californicus*, from which there is one other record of the louse.

longicaudus group.

MICROTUS MORDAX (Merriam).

Polyplax spinulosa (Burmeister). One record. Probably a misdetermination of *P. abscisa*.

nivalis group.

MICROTUS NIVALIS (Martins).

*†*Hoplopleura acanthopus villosa* (Galli-Valerio). Eight records, different sources, including U.S.N.M. skin 124482 and three wild hosts. Ferris considers this a synonym of *H. a. acanthopus*.

MICROTUS sp. (Alaska).

**Polyplax alaskensis* Ewing. A single male from a wild host.

Subgenus *Phaiomys*.

MICROTUS LEUCURUS (Blyth).

**Hoplopleura phaiomydis* Ferris. One record from U.S.N.M. skin 198570.

Genus *LAGURUS*.

LAGURUS LAGURUS (Pallas). (Sage-brush Meadow-Mouse or Vole.)

Polyplax spiniger (Burmeister). One record.

Subfamily *Gerbillinae*.

Genus GERBILLUS.

pyramidum group.

GERBILLUS PYRAMIDUM I. Geoffroy. (Greater Egyptian Gerbil.)

**Polyplax gerbilli* Ferris. One record of a male and three females.

Genus TATERA.

Subgenus TATERA.

indica group.

TATERA INDICA (Hardwicke). (Indian Gerbil.)

*†*Polyplax stephensi* (Christophers and Newstead). Several records from wild hosts.*robusta* group.

TATERA VICINA (Peters).

Polyplax t. taterae* Ferris. A male and two females from F.C.M. skin 16704.Polyplax t. mombassae* Werneck. A single male from a skin.

It seems almost certain that at least one of the above lice must be a contamination.

TATERA NIGRICAUDA (Peters).

(*?)*Hoplopleura (Ctenopleura) neumanni* Fahrenholz. Three records (two from skins, including U.S.N.M. no. 183935).(*?)*Polyplax praecisa* (Neumann). One record from a museum skin.Both the above species were described from material collected from "gros rats" in Abyssinia. A subspecies of *T. nigricauda* occurs there.*liodon* group.

TATERA LIODON Thomas.

*†*Hoplopleura (Ctenopleura) cryptica* Ferris. Types from U.S.N.M. skin 165302; numerous records from wild hosts.*†*Polyplax subtaterae* Bedford. Numerous records from wild hosts.*afra* group.

TATERA BRANTSI (A. Smith).

†*Hoplopleura (Ctenopleura) biseriata* Ferris. Many records from wild hosts.†*Polyplax biseriata* Ferris. Many records from wild hosts.

TATERA LOBENGULAE (De Winton). (Lobengula's Gerbil.)

†*Hoplopleura (Ctenopleura) biseriata* Ferris. Many records from wild hosts.†*Polyplax biseriata* Ferris. Many records from wild hosts.A record of *Neohaematopinus faurei* on this host is erroneous and probably due to contamination.

TATERA JOANAE (Thomas).

†*Hoplopleura (Ctenopleura) biseriata* Ferris. Two records, different sources, one of hundreds of lice on a single wild host.

TATERA ANGOLAE Wroughton.

Hoplopleura (Ctenopleura) biseriata Ferris. One record of two females.The members of the *afra*-group replace one another geographically and it is probable that some of them are conspecific.

Subgenus *Gerbilliscus*.

TATERA BÖHMI (Noack).

Hoplopleura (Ctenopleura) veprecula* Ferris. One record of three specimens from U.S.N.M. skin 162250, another record without details.Polyplax biseriata* Ferris. One record of several specimens from the same skin.

Genus TATERILLUS.

TATERILLUS EMINI (Thomas).

Polyplax subtaterae Bedford. One record (my own), probably mislabelling.

Genus PACHYUROMYS.

PACHYUROMYS DUPRASI Lataste. (Fat-tailed Rat.)

**Polyplax weneri* (Glinkiewicz). Two records.

Genus MERIONES.

? MERIONES, sp.

Pediculus clavicornis Nitzsch, which is perhaps a *Hoplopleura*, was described from a single female obtained "auf einem schwarzbraunen *Meriones*, den Rüppel aus Afrika mitbrachte" (Giebel, 1874, p. 38). As *Meriones lacernatus* Rüppell "is probably based on an *Arvicanthus*" (Ellerman, 1941, p. 357) it seems altogether possible that the host of *clavicornis* was not a *Meriones*.

Subgenus *Meriones*.*meridianus* group.

MERIONES MERIDIANUS (Pallas).

Hoplopleura merionidis* Ferris. Three females from U.S.N.M. skin 172528.Polyplax chinensis* Ferris. Several males and females from U.S.N.M. skin 172573.

Family RHIZOMYIDAE.

Genus TACHYORYCTES.

TACHYORYCTES SPLENDENS (Rüppell). (Orange-toothed Mole-Rat.)

(*)*Polyplax eminentus* Fahrenholz. Described from the female only, perhaps a single specimen. The host is given as "*Paderoryctes gadat*", from East Africa. The only African mammal with a name remotely resembling this is *Tachyoryctes audax*, which is probably a subspecies of *splendens*.

Family MURIDAE.

Subfamily Murinae.

Genus MICROMYS.

MICROMYS MINUTUS (Pallas). (European Harvest-Mouse.)

*†*Hoplopleura longula* (Neumann) (synonym: *lineata*). Five records, different sources, including U.S.N.M. skin 85374.**Polyplax gracilis* Fahrenholz. One record, no details.

Genus APODEMUS.

sylvaticus group.

APODEMUS SYLVATICUS (Linn.). (European Wood-Mouse or Long-tailed Field-Mouse.)

Hoplopleura affinis (Burmeister). Two records, including U.S.N.M. skin 175174.

†*Polyplax serrata* (Burmeister). Many records, including U.S.N.M. skins 84718 and 120950 and Trento Mus. skin 107047.

Two records of *Polyplax spinulosa* (Burmeister) are probably erroneous. Fahrenholz contends that Burmeister's *Pediculus affinis* is the *Polyplax*, Ferris considers that it is the *Hoplopleura*.

APODEMUS FLAVICOLLIS (Melchior).

A record of three males and five females of *Trichodectes mustelae* must be due to mislabelling.

speciosus group.

APODEMUS SPECIOSUS (Temminck). (Japanese Long-tailed Field-Mouse.)

Polyplax serrata (Burmeister). One record from F.C.M. skin 19709.

agrarius group.

APODEMUS AGRARIUS (Pallas).

*†*Hoplopleura affinis* (Burmeister). Four records, including U.S.N.M. skins 120955 and 197805. See note below.

*†*Polyplax serrata paxi* Eichler. Three records, from skins, including U.S.N.M. no 197805 and F.C.M. no. 18929, and one from a wild host.

Hoplopleura affinis was described from specimens collected from *Mus agrarius* and *M. sylvaticus*. The first host mentioned by an author should always be regarded as the type host unless there are strong reasons to the contrary. A record of *Hoplopleura acanthopus* from a skin of this host is probably due to contamination.

Genus GRAMMOMYS.

GRAMMOMYS SURDASTER (Thomas and Wroughton).

Hoplopleura oenomydis Ferris. One record from F.C.M. skin 17133.

A single specimen of *Polyplax phthisica* found on F.C.M. skin 17097 was a contamination.

GRAMMOMYS DOLICHURUS (Smuts).

Polyplax spinulosa (Burmeister). One record, probably erroneous.

Genus OENOMYS.

OENOMYS HYPOXANTHUS (Pucheran). (Rusty-nosed Rat.)

*†*Hoplopleura oenomydis* Ferris. Types from F.C.M. skin 17090; several records from wild hosts.

A record of a single specimen of *Polyplax abyssinica* from this host is due to contamination.

Genus MYLOMYS.

MYLOMYS CUNINGHAMEI Thomas.

**Hoplopleura enormis mylomydis* Ferris. Two records, U.S.N.M. skin 183602 and F.C.M. skin 16842.

Genus DASYMYS.

DASYMYS INCOMTUS (Sundeval).

**Hoplopleura somereni* Waterson. One record, wild host.

**Polyplax cummingsi* Ferris. Two records, different sources, including U.S.N.M. skin 183151.

The single specimen of *Hoplopleura oenomydis* found by Ferris on a skin of this host was almost certainly a contamination.

Genus ARVICANTHIS.

ARVICANTHIS NILOTICUS (Desmarest). (Long-tailed Unstriped Grass-Rat.)

†*Polyplax abyssinica* Ferris. Many records from wild hosts.

ARVICANTHIS ABYSSINICUS (Rüppell). (Unstriped African Grass-Rat.)

*†*Polyplax abyssinica* Ferris. Very many records from wild hosts.

Genus PELOMYS.

Subgenus Pelomys.

PELOMYS FALLAX (Peters). (African Creek-Rat.)

**Hoplopleura enormis pelomydis* Ferris. Two records (U.S.N.M. skin 183667 and a wild host). It is very doubtful if *Pelomys* is the true host of this form (see *Lemniscomys striatus*) and I think the record from a wild host is probably a misdetermination.

Genus LEMNISCOMYS.

barbarus group.

LEMNISCOMYS BARBARUS (Linn.). (Solid-striped Grass-mouse.)

Hoplopleura e. enormis Kellogg and Ferris. One record of two females from U.S.N.M. skin 165195.

**Pediculus spiculifer* Gervais. One record; possibly an earlier name for the above. It is either a *Hoplopleura* or a *Polyplax*.

striatus group.

LEMNISCOMYS STRIATUS (Linn.). (Spot-striped Grass-Mouse.)

Hoplopleura enormis pelomydis Ferris. Three records, from U.S.N.M. skins 125426 and 163646, and from a wild host. The wild host was collected in Kampala, where *Pelomys* does not occur, and I suspect strongly that *L. striatus* is the true host of this louse.

griselda group.

LEMNISCOMYS GRISELDA (Thomas). (Single-striped Grass-Mouse.)

*†*Hoplopleura e. enormis* Kellogg and Ferris. Two records from wild hosts.

Genus RHABDOMYS.

RHABDOMYS PUMILIO (Sparrmann). (Four-striped Grass-Mouse.)

*†*Polyplax arvicantis* Bedford. Many records, wild hosts and U.S.N.M. skin 164194.

Genus HYBOMYS.

HYBOMYS UNIVITTATUS (Peters). (One-striped Grass-Mouse.)

**Hoplopleura laticeps* Ferris. One record of two females from U.S.N.M. skin 101514.

Genus EROPEPLUS.

EROPEPLUS CANUS Miller and Hollister.

**Polyplax eropepli* (Ewing). Two males and two females from U.S.N.M. skin 219711.

Genus AETHOMYS.

AETHOMYS CHRYSOPHILUS (De Winton). (African Bush-Rat.)

Polyplax cummingsi Ferris. Two records.

Genus THALLOMYS.

nigricauda group.

THALLOMYS NIGRICAUDA (Thomas). (Black-tailed Tree-Rat.)

Hoplopleura affinis (Burmeister). One record from U.S.N.M. skin 162539.

THALLOMYS MOGGI (Roberts). (Mogg's Tree-Rat.)

Hoplopleura affinis (Burmeister). One record.*Polyplax spinulosa* (Burmeister). One record.*namaquensis* group.

THALLOMYS NAMAQUENSIS (A. Smith).

*†*Polyplax praomydis* Bedford. One reliable record.

Genus RATTUS.

Subgenus Rattus.

rattus group.

RATTUS RATTUS (Linn.). (Black Rat.)

†*Hoplopleura pacifica* Ewing. Fifteen records, sometimes in great numbers.†*Polyplax spinulosa* (Burmeister). Very many records.

The records of *H. bidentata* and *Eulinognathus denticulatus* from this host are erroneous, and one of *P. otomydis* is practically certainly contamination. The specimens of *Hoplopleura pacifica* were all determined as *H. oenomydis*; as all are from the Malayo-Polynesian region, both geographical and host considerations suggest that they were *H. pacifica*. See note under *Rattus exulans*.

norvegicus group.

RATTUS NORVEGICUS (Berkenhout). (Brown Rat.)

*†*Polyplax spinulosa* (Burmeister). Very many records.

The record (Ferris, 1932) of *Hoplopleura oenomydis* from this host presumably refers to *H. pacifica* (see note under *Rattus exulans*), and is probably erroneous. The single specimen of "*Philundestia*" *fovi* Ewing from this host turns out to belong to the bird-infesting genus *Menacanthus*.

exulans group.

RATTUS EXULANS (Peale). (Pacific Rat.)

*†*Hoplopleura pacifica* Ewing. Many records, mostly from wild hosts but including U.S.N.M. skin 145778. See note below.*Polyplax spinulosa* (Burmeister). One record from U.S.N.M. skin 145778, probably a contamination.

H. pacifica is regarded by Ferris as being the same as *H. oenomydis* Ferris, but I consider this synonymy extremely improbable. The hosts of the two forms are neither very closely related nor geographically linked. Nor is *Oenomys* a house-rat, so that transfer through the agency of a cosmopolitan rat such as *R. rattus* is excessively improbable; the case is probably one of convergence. It is highly suggestive that *H. oenomydis* has not been recorded from *R. rattus* in Africa.

Following Ellerman (1941, p. 220), I have treated all forms of *Rattus concolor* as subspecies of *R. exulans*.

rajah group.

RATTUS SURIFER (Miller).

**Hoplopleura (Ctenura) pectinata* (Cummings). Two records, different sources, including U.S.N.M. skin 86750.*edwardsi-sabanus* group.

RATTUS SABANUS (Thomas).

Hoplopleura malaysiana* Ferris. One record from a skin.Polyplax insulsa* Ferris. One record from U.S.N.M. skin 104765.

RATTUS STRIDENS (Miller).

Polyplax spinulosa (Burmeister). One record from U.S.N.M. skin 104998. Probably a contamination.

tunneyi-villosissimus group.

RATTUS CULMORUM (Thomas and Dollman).

Polyplax spinulosa (Burmeister). One record.Subgenus *Praomys*.

RATTUS TULLBERGI (Thomas).

†*Hoplopleura intermedia* Kellogg and Ferris. Two records from skins (F.C.M. 17025 and U.S.N.M. 163353), and 18 records from wild hosts.†*Polyplax waterstoni* Bedford. One record from a skin (F.C.M. 17025), and 11 records from wild hosts.Subgenus *Mastomys*.

RATTUS COUCHA (A. Smith). (Multimammate Mouse.)

*†*Hoplopleura intermedia* Kellogg and Ferris. Numerous records from wild hosts.(*)†*Polyplax waterstoni* Bedford. Several records from wild hosts. Originally from undetermined rats, at least some of which were probably *coucha*.Records of *Polyplax praecisa*, *Neohaematopinus faurei*, and *Eulinognathus denticulatus* on this host are erroneous; a record of *Polyplax abyssinica* is due to mislabelling. In connection with the correspondence of their lice it is interesting to note that *Praomys* appears to be an arboreal modification of *Mastomys*.Subgenus *Limnomys*.

RATTUS MEARNSI (Hollister).

Hoplopleura oenomydis Ferris. One record, from U.S.N.M. skin 144621, probably refers to *H. pacifica* if this is separable.Subgenus *Tarsomys*.

RATTUS APOENSIS Mearns.

**Polyplax tarsomydis* Ewing. A single male from a skin.Genus *APOMYS*.

APOMYS INSIGNIS Mearns.

**Hoplopleura apomydis* Ferris. One record from U.S.N.M. skin 144592.Genus *ZELOTOMYS*.

ZELOTOMYS HILDEGARDEAE Thomas.

Hoplopleura intermedia Kellogg and Ferris. One record from F.C.M. skin 16955.Genus *MUS*.Subgenus *Mus*.

MUS MUSCULUS Linn. (European House Mouse.)

†*Hoplopleura acanthopus* (Burmeister). Seven records, different sources, including U.S.N.M. skins 105244 and 85056.†*Hoplopleura hesperomydis* (Osborn). Four records, different sources, including U.S.N.M. skins 155467 and 172503, F.C.M. skin 19073, and a wild host. Probably originally a straggler, but apparently established.*†*Polyplax serrata* (Burmeister). Numerous records from wild and tame hosts, including U.S.N.M. skin 152840.The supposed species *Haematopinus muris* Compton, described from this host, is probably a synonym of *Polyplax serrata*.*bufo-triton* group.

MUS TRITON (Thomas).

**Hoplopleura sukenyae* Ferris. A single female from F.C.M. skin 16769.

Genus LOPHUROMYS.

LOPHUROMYS AQUILUS (True).

*†*Polyplax phthisica* Ferris. From U.S.N.M. skin 162548 and F.C.M. skin 16866; several subsequent records from wild hosts.

LOPHUROMYS SIKAPUSI (Temminck).

†*Polyplax phthisica* Ferris. From U.S.N.M. skin 165210 and many wild hosts.

Genus ACOMYS.

cahirinus group (typical section).

ACOMYS CAHIRINUS (Desmarest). (Cairo Spiny Mouse.)

*†*Polyplax (Symoica) b. brachyrrhynchus* Cummings. One record of 360 specimens.*†*Polyplax oxyrrhynchus* Cummings. One record of 918 adults and many nymphs.

The above records must have been from many host-individuals.

ACOMYS PERCIVALI Dollman.

**Polyplax (Symoica) brachyrrhynchus minor* (Fahrenholz). One record from U.S.N.M. skin 182953.*Polyplax oxyrrhynchus* Cummings. One record of a single female from the same skin.

Not allocated to group.

ACOMYS HYSTRELLA Heller.

Polyplax (Symoica) brachyrrhynchus* Cummings. One record from U.S.N.M. skin 165216.Polyplax oxyrrhynchus hystrellae* Fahrenholz. One record of a pair from the same skin.

The host of *Polyplax miacantha* Speiser was "einer kleinem Ratte mit sehr dicken stachelartigen Haaren", from Salomona, Abyssinia. This description is certainly that of an *Acomys*, but it is to be noted that the host was in a jar with two other species of rats, so that the louse may have been derived from any of the three.

Genus BANDICOTA.

bengalensis group.

BANDICOTA BENGALENSIS (Gray and Hardwicke). (Indian "Mole-Rat.")

Polyplax spinulosa (Burmeister). One record, probably erroneous.

BANDICOTA MALABARICA Shaw.

†*Polyplax asiatica* Ferris. one record of 4 males and 12 females from a wild host.

Genus NESOKIA.

NESOKIA INDICA (Gray and Hardwické). (Short-tailed "Mole-Rat.")

(*)*Polyplax asiatica* Ferris. One record of several females from U.S.N.M. skin 200314. It is probable that this is the true host of the species and that its supposed occurrence on a shrew was erroneous (misidentification of host or mislabelling).

Genus SACOSTOMUS.

SACOSTOMUS CAMPESTRIS Peters. (South African Pouched Mouse.)

**Polyplax jonesi* Kellogg and Ferris. One record.

Genus CRICETOMYS.

Ellerman places all forms of *Cricetomys* as subspecies of *C. gambianus*. Although I have much sympathy with this view, the distribution of the orthopteran parasites of the genus *Hemimerus* suggests that there may be a number of species of their hosts, and I have preferred another arrangement. He also suggests (1941, p. 287) that the genus may not have had the same ancestors as the rest of the Murinae. This is to some extent supported by the *Polyplax*, which is very distinct.

CRICETOMYS GAMBIANUS Waterhouse. (Harsh-furred Giant Rat.)

*†*Polyplax (Symasodus) c. calva* Waterston. Many records from different subspecies, including U.S.N.M. skins 181806 and 183125 and F.C.M. skin 17043.

CRICETOMYS EMINI Wroughton. (Soft-furred Giant Rat.)

†*Polyplax (Symasodus) calva* Waterston. Numerous records from wild hosts.

CRICETOMYS COSENSI Hinton. (Zanzibar Giant Rat.)

**Polyplax (Symasodus) calva zanzibariensis* (Fahrenholz). One record (from *Cricetomys* sp., but there is no other *Cricetomys* in Zanzibar).

Subfamily *Dendromyinae*.

Genus DENDROMUS.

Subgenus Dendromus.

DENDROMUS INSIGNIS Thomas. (Chestnut Tree-Mouse.)

Hoplopleura intermedia Kellogg and Ferris. One record from U.S.N.M. skin 184091, probably a contamination.

Genus MALACOTHRIX.

MALACOTHRIX TYPICUS (A. Smith). (Mouse-"Gerbil.")

The single female from which *Hoplopleura biseriata* Ferris was described was certainly a straggler or (more probably) a contamination. The true hosts are gerbils of the *afra*-group (see p. 477).

Subfamily *Otomyinae*.

Genus OTOMYS. (Swamp or Vlei Rats.)

irroratus group.

OTOMYS ANGONIENSIS Wroughton.

Polyplax otomydis Cummings. One record from F.C.M. skin 16687.

OTOMYS IRRORATUS (Brants).

†*Polyplax otomydis* Cummings. Many records from wild hosts.

OTOMYS TROPICALIS Thomas.

*†*Polyplax otomydis* Cummings. Many records from wild hosts.

A record of *Polyplax arvicanthis* is due to contamination.

Genus PAROTOMYS.

PAROTOMYS BRANTSII (A. Smith). (Brants' Bush Otomys.)

Polyplax otomydis Cummings. One record.

Subfamily *Hydromyinae*.

Genus CHROTOMYS.

CHROTOMYS WHITEHEADI Thomas

**Hoplopleura chrotomydis* Ferris. One record from a skin.

Genus HYDROMYS.

HYDROMYS CHRYSOGASTER Geoffroy. (Australian Water-Rat.)

*†*Hoplopleura bidentata* Neumann. Host originally misidentified as *Rattus rattus*. Several records, from wild hosts and from U.S.N.M. skin 83708.

Superfamily GLIROIDEA.

Family GLIRIDAE. (Dormice.)

Subfamily Glirinae.

Genus MUSCARDINUS.

MUSCARDINUS AVELLANARIUS (Linn.). (Common Dormouse.)

Schizopthirus pleurophaeus (Burmeister). Three records from skins, including U.S.N.M. skin 112908.

Genus ELIOMYS.

ELIOMYS QUERCINUS (Linn.). (Garden Dormouse.)

†*Schizopthirus pleurophaeus* (Burmeister). Four records, one from U.S.N.M. skin 103031, once in numbers.

Genus DRYOMYS.

DRYOMYS NITEDULA (Pallas).

**Schizopthirus pleurophaeus* (Burmeister) (synonym: *leucophaeus*). One record, no details.

The host was recorded as *Myoxus nitela*, which seems to be a distortion of the above.

Subfamily Graphiurinae.

Genus GRAPHIURUS. (African Dormice.)

Subgenus Claviglis.

GRAPHIURUS MURINUS (Desmarest).

*†*Schizopthirus graphiuri* Ferris. (An., Hae.) Three records, U.S.N.M. skins 182834 and 164265, and a wild host.

GRAPHIURUS NANUS (de Winton).

Schizopthirus graphiuri Ferris. One record.

GRAPHIURUS ALTICOLA (Roberts).

Schizopthirus graphiuri Ferris. One record, no details.

Superfamily DIPODOIDEA.

Family ZAPODIDAE.

Subfamily Zapodinae.

Genus ZAPUS.

Professor Ferris kindly informs me that he has examined many specimens of this genus without finding any lice.

Family DIPODIDAE.

Subfamily Dipodinae.

Genus DIPUS.

DIPUS SAGITTA (Pallas). (Three-toed Oriental Jerboa.)

**Eulinognathus biuncatus* Ferris. Numerous males and females from U. S. N. M. skin 155092.

Genus *JACULUS*.

- JACULUS JACULUS* (Linn.). (North African Jerboa.)
 (*?)*Eulinognathus aculeatus* (Neumann). Described from 3 females collected from "*Dipus* sp.", Djerba, Tunis. This seems the most probable host.

Genus *ALLACTAGA*.

- ALLACTAGA SIBIRICA* (Forster). (Five-toed Oriental Jerboa.)
Eulinognathus ? aculeatus (Neumann). One record, U.S.N.M. skin 155188.

Suborder *HYSTRICOMORPHA*.Superfamily *ERETHIZONTOIDEA*.Family *ERETHIZONTIDAE*.Subfamily *Erethizontinae*.Genus *ERETHIZON*.

- ERETHIZON DORSATUM* (Linn.). (Urson or Canadian Porcupine.)
 *†*Eutrichophilus setosus* (Giebel). (Isc., Tric.) Many records from wild hosts.
ERETHIZON EPIXANTHUM Brandt. (Western Urson or Yellow-haired Porcupine.)
 †*Eutrichophilus setosus* (Giebel). Numerous records from wild hosts.

Genus *COENDOU*.Subgenus *Coendou*.

- COENDOU PREHENSILIS* (Linn.). (Prehensile-tailed Porcupine.)
 For records from this form see *C. villosus*.
COENDOU ROTHSCHILDI Thomas.
 **Eutrichophilus maximus* Bedford. Described from a single female.
COENDOU PLATYCENTROTUS (Brandt).
 A record of a single female of *Eutrichophilus cordiceps* is regarded by Werneck as a case of contamination.

Subgenus *Sphiggurus*.*mexicanum* group.

- COENDOU MEXICANUM* (Kerr).
 *†*Eutrichophilus mexicanus* (Rudow) (synonym: *coendu*). Many records, including A.M.N.H. skins 28485 and 29821.
COENDOU LAENATUM Thomas.
 A record of two male *Eutrichophilus setosus* from a skin is doubtless due to contamination.

paraguayensis group (typical section).

- COENDOU PARAGAYENSIS* (Oken).
Eutrichophilus cordiceps Mjöberg. One female from a skin.
Eutrichophilus minor Mjöberg. A single pair from a skin.
COENDOU SPINOSUS (Cuvier).
Eutrichophilus ? cordiceps Mjöberg. See note below.
Eutrichophilus minor Mjöberg. See note below.
 A single record of each of the above species (Maltbaek, 1937 c).

COENDOU VILLOSUS (Cuvier).

- (*)†*Eutrichophilus cercolabes* Mjöberg (synonym: *australis*). See note below.
 (*)†*Eutrichophilus cordiceps* Mjöberg. See note below.
 (*)†*Eutrichophilus minor* Mjöberg. See note below.

All the above were described from a "Quendu-Stachelschwein" which Mjöberg assumed to have been *C. prehensilis*. As all three forms have been taken many times in great numbers from specimens of *C. villosus* it seems almost certain that Mjöberg's assumption was incorrect.

paraguayensis group (*vestitus* section).

COENDOU PRUINOSUS Thomas.

- **Eutrichophilus lobatus* Ewing. Two males eight females and three nymphs from U.S.N.M. skin 172985.

Subfamily *Chaetomyinae*.

Genus CHAETOMYS.

CHAETOMYS SUBSPINOSUS (Kuhl).

- *†*Eutrichophilus moojeni* Werneck. Described from abundant material from wild hosts.

Superfamily CAVIOIDEA.

Family CAVIIDAE.

Subfamily *Caviinae*.

Genus CAVIA.

CAVIA APEREA Erxleben. (Restless Cavy.)

- *†*Trimenopon (Trimenopon) echinoderma* Cummings. Seven records from several different sources. A synonym of *T. hispidum*.
 †*Gyropus (Gyropus) ovalis* Burmeister. Five records, different sources, four from wild hosts.
 **Gliricola (Gliricola) brasiliensis* Werneck. One record, wild host (at first misidentified; see Werneck, 1942 *e.*, p. 311).
Gliricola (G.) porcelli (Schrank). Two records from wild hosts.
 **Gliricola (G.) spinosus* Werneck. One record of four males and some females. A synonym of *G. distinctus* Ewing.
 **Gliricola (G.) lindolphoi* Werneck. One record of a single male.

CAVIA PAMPARUM Thomas.

- Gyropus (Gyropus) ovalis* Burmeister. One male and one female from U.S.N.M. skin 236344, and one record from a wild host.

CAVIA TSCHUDII Fitzinger.

- Gyropus (Gyropus) ovalis* Burmeister. Several specimens from U.S.N.M. skin 221015 (formerly in Washington Zoo).
Gliricola (Gliricola) porcelli (Schrank). Several specimens from two skins, including U.S.N.M. no. 221015.

The type of *Gliricola quadrisetosus* (Ewing), a single female from U.S.N.M. skin 23758, was almost certainly a contamination. The true host is *Galea musteloides*.

CAVIA FULGIDA Wagler.

- †*Trimenopon (Trimenopon) hispidum* (Burmeister). See note below.
 †*Gyropus (Gyropus) ovalis* Burmeister. See note below.
 †*Gliricola (G.) porcelli* (Schrank). See note below.

The above are all recorded from a number of host-individuals, including wild hosts.

CAVIA ANOLAIMAE Allen.

Trimenopon (*T.*) *hispidum* (Burmeister). One record, apparently from a wild host.

**Gliricola* (*Gliricola*) *distinctus* Ewing. Two males and four females from U.S.N.M. skin 236907.

CAVIA PORCELLUS (Linn.). (Guineapig.)

(*†)*Trimenopon* (*Trimenopon*) *hispidum* (Burmeister) (synonyms: *jenningsi* and *rozeboomi*). Very many records, tame and wild hosts.

*†*Gyropus* (*Gyropus*) *ovalis* Burmeister (synonym: *mexicanus*). Many records, tame and wild hosts.

Gliricola lindolphi Werneck. One record.

*†*Gliricola* (*Gliricola*) *porcelli* (Schrank) (synonyms: *bicaudatus*, *bifurcatus*, *gracilis*, *perfoliatus*, *saviae* and probably *mexicanus*). Many records, tame and wild hosts.

Single records of many specimens of *Macrogyropus heteronychus* and *Gliricola quadrisetosus* from a wild host seem to have been from the same host-individual, which was probably misdetermined; a record of *Gliricola brasiliensis* is certainly due to this cause, the host being later redetermined as *Cavia uperea* (see Werneck, 1942e, p. 311). *Menopon extraneum* Piaget, supposed to be from a guineapig, proves to be a duck-parasite (information kindly supplied by Miss Clay). *Gliricola mexicanus* Zavaleta is indeterminate but is probably a synonym of *porcelli*.

Dr Kéler kindly informs me that he compared the type of "*Gyropus*" *hispidus* with *Trimenopon* from a guinea-pig and found it indistinguishable.

Genus KERODON.

KERODON RUPESTRIS (Wied). (Brazilian Rock-Cavy.)

*†*Gyropus* (*Tetragyropus*) *lineatus* Neumann. Many records from wild hosts.

Macrogyropus heteronychus (Ewing). One record from a wild host.

Mislabelling?

*†*Monothoracius penidoi* Werneck. At least five records from wild hosts.

The single record of *Gliricola perfoliatus* Neumann, described from this host, is probably due to mislabelling or to misdetermination of the host, the form being inseparable from *G. porcelli*.

Genus GALEA.

GALEA MUSTELOIDES Meyer.

†*Macrogyropus heteronychus* (Ewing). One female from a skin and specimens from more than 20 wild hosts, several sources.

(*†)*Gliricola* (*Paragliricola*) *quadrisetosus* (Ewing). One female from U.S.N.M. skin 236345; many records from wild hosts. In my opinion this should be regarded as the type-host, the type being a contamination on its supposed host (*Cavia tschudii*).

*†*Eulinognathus caviae* Werneck. Twenty records.

GALEA SPIXII (Wagler).

*†*Macrogyropus heteronychus* (Ewing). One female from U.S.N.M. skin 123391 and many records from wild hosts.

†*Gliricola* (*Paragliricola*) *quadrisetosus* (Ewing). One female from the same skin and many records from wild hosts.

Genus MICROCAVIA.

Subgenus Caviella.

MICROCAVIA AUSTRALIS (Geoffroy and D'Orbigny).

*†*Protygyropus normalis* Ewing. Described from five females from U.S.N.M. skins 23640 and 236337, since obtained from numerous wild hosts.

Gyropus (Tetragyropus) ? lineatus Neumann. A single nymph from U.S.N.M. skin 84177.

*†*Pterophthirus alatus* (Ferris). Described from specimens obtained from U.S.N.M. skin 84175, since collected in numbers from wild hosts.

A single record of a female and three nymphs of *Gliricola quadrisetosus* is probably due to contamination.

Family *HYDROCHOERIDAE*.

Subfamily *Hydrochoerinae*.

Genus *HYDROCHOERUS*.

HYDROCHOERUS HYDROCHAERIS (Linn.). (Capybara or Carpincho.)

Dr. Werneck informs me that he has searched many specimens without finding any lice.

Family *DASYPROCTIDAE*.

Subfamily *Cuniculinae*.

Genus *CUNICULUS*.

CUNICULUS PACA (Linn.). (Paca.)

*†*Macroglyropus amplexans costalimai* Werneck. (Amb., Gyr.) Many records from wild hosts.

Subfamily *Dasyproctinae*.

Genus *DASYPROCTA*

DASYPROCTA AGUTI (Linn.). (Golden Agouti or Cotia.)

*†*Macroglyropus a. amplexans* (Neumann) (synonym : *ratti*). Many specimens from wild hosts.

Burmeister's *Gliricola longicollis*, described from two specimens from a skin of this host, is unidentifiable and probably a contamination; the types were already lost in 1861. Dr. Werneck has examined very many individuals of the host and found no specimens of *Gliricola* on them.

DASYPROCTA FULIGINOSA Wagler. (Dark Grey Agouti.)

Macroglyropus a. amplexans (Neumann). One record of a male and two females.

DASYPROCTA AZARAE Lichtenstein.

†*Macroglyropus a. amplexans* (Neumann). Twelve records from wild hosts.

DASYPROCTA VARIEGATA Tschudi.

Macroglyropus a. amplexans (Neumann). One record, apparently wild host.

Genus *MYOPROCTA*.

MYOPROCTA ACOUCHY (Erxleben). (Acouchy or Cotiara.)

*†*Macroglyropus amplexans longisetis* Werneck. Three records from wild hosts.

*†*Monothoracius almeidai* Werneck. (Amb., Gyr.) Two single specimens from skins and many from a wild host.

Superfamily *CHINCHILLOIDEA*.

Family *CHINCHILLIDAE*.

Genus *LAGIDIUM*.

LAGIDIUM PERUANUM Meyen. (Vizcacha.)

†*Trimenopon (Philandesia) chinchillae* Werneck. Numerous records from wild hosts, and from U.S.N.M. skins 194467 and 194468.

†*Trimenopon* (*Philandesia*) *mazzai* Werneck. Many records from wild hosts, and a female from U.S.N.M. skin 194468.

*†*Trimenopon* (*Philandesia*) *townsendi* (Kellogg and Nakayama). Many records from wild hosts, different sources.

*†*Phtheiropoios lagotis* (Gervais) (synonym: *alpinus*). Many records from wild hosts and from U.S.N.M. skins 194468 and 194476.

**Eulinognathus parvus* (Kellogg and Ferris). Two records, different sources.

Genus CHINCHILLA.

CHINCHILLA LANIGER (Molina). (Chinchilla.)

*†*Trimenopon* (*Philandesia*) *chinchillae* Werneck. Many specimens from wild hosts.

*†*Trimenopon* (*Philandesia*) *mazzai* Werneck. Many specimens from wild hosts.

Trimenopon (*Philandesia*) *townsendi* (Kellogg and Nakayama). One record of a single female.

A record of a single male *Eutrichophilus minor* is a case of contamination.

Superfamily OCTODONTOIDEA.

Family CAPROMYIDAE.

Genus CAPROMYS.

CAPROMYS PILORIDES (Say).

*†*Gliricola capromydis capromydis* Werneck. Two records, one of many specimens from a wild host and the other of a male from U.S.N.M. skin 181232.

**Gliricola cubanus* Werneck. Described from 3 males and 1 female from U.S.N.M. skin 181232.

CAPROMYS PREHENSILIS Poeppig.

**Gliricola capromydis armatus* Werneck. Described from 2 males, 3 females and 2 nymphs from U.S.N.M. skin 103887.

**Gliricola ewingi* Werneck. Described from 3 males and 2 females from the same skin.

Subfamily Myocastorinae.

Genus MYOCASTOR.

MYOCASTOR COYPUS (Molina). (Nutria or Coypu.)

*†*Pitrusquenía coypus* Marelli. (Amb., Gyr.) Many records.

**Pitrusquenía mollis* Marelli. One record; probably a synonym of *P. coypus*.

Neumann's record of *Damalinia* (*Werneckiella*) *equi* from this host is obviously erroneous.

Family OCTODONTIDAE.

Genus OCTODON.

OCTODON DEGUS (Molina).

**Hoplopleura disgrega chilensis* Werneck. One record of many specimens.

Genus OCTODONTOMYS.

OCTODONTOMYS GLIROIDES (Gervais and D'Orbigny).

**Hoplopleura d. disgrega* Ferris. One record from U.S.N.M. skin 121167.

Family CTENOMYIDAE.

Genus CTENOMYS. (Tuco-tucos.)

magellanicus section.

CTENOMYS MAGELLANICUS Bennett.

Gyropus (Monogyropus) parvus (Ewing). A single male from a skin.

Phtheiropoios pollicaris Ewing (Amb., Gyr.) Two records, apparently from wild hosts.

CTENOMYS SERICEUS Allen.

Gyropus (Monogyropus) parvus (Ewing). A single male from U.S.N.M. skin 84192, and six pairs from U.S.N.M. skin 84194.

Eulinognathus americanus Ewing. A single female from U.S.N.M. skin 84194.

CTENOMYS TUCUMANUS Thomas.

Phtheiropoios forficulatus (Neumann). One record, no details. This species has no proper type-host, having been described from material collected from an unidentified *Ctenomys* at Tucuman, Argentina. It seems improbable that *tucumanus* is the true host as the only other records of the louse are from members of the *torquatus* section of *Ctenomys*.

CTENOMYS LATRO Thomas.

Phtheiropoios wetmorei (Ewing). Seven females and nine nymphs from U.S.N.M. skins 236335 and 236336.

Probably *magellanicus* section.

CTENOMYS COLBURNI Allen.

**Gyropus (Monogyropus) parvus* (Ewing). A single male from U.S.N.M. skin 238122.

**Phtheiropoios gracilipes* (Ewing). One male and four females from the same skin. A synonym of *P. latipollicaris* (Ewing).

CTENOMYS OSGOODI Allen.

*†*Phtheiropoios latipollicaris* (Ewing). Three records from wild skins (three pairs from U.S.N.M. skin 84160, two males from U.S.N.M. skin 84165, and five males and six females from U.S.N.M. skin 84141).

**Phtheiropoios pollicaris* (Ewing). A single specimen from a skin, probably a contamination.

torquatus section.

CTENOMYS SYLVANUS Thomas.

Phtheiropoios forficulatus (Neumann). One record of a single male from a wild skin.

†*Phtheiropoios wetmorei* (Ewing). One record from a wild skin, and one (of great numbers) from a wild host.

CTENOMYS BUDINI Thomas.

Phtheiropoios wetmorei (Ewing). One record from a wild skin.

CTENOMYS TORQUATUS Lichtenstein.

(*?)†*Phtheiropoios forficulatus* (Neumann). Many specimens from three wild skins.

**Eulinognathus americanus* Ewing. A single female from U.S.N.M. skin 3252, 1939 (*Ctenomys brasiliensis* Blainville, of which *torquatus* is regarded by Waterhouse as a synonym).

lewisii section.

CTENOMYS LEWISI Thomas.

*†*Phtheiropoios grypophallus* (Werneck). Many specimens from numerous wild hosts. A synonym of *P. ewingi* (Werneck).*opimus* section.

CTENOMYS OPIMUS Wagner.

**Phtheiropoios ewingi* (Werneck) (synonym: *forficulatus* Ewing *nec* Neumann). One male and two females from U.S.N.M. skin 121168. Possibly a synonym of *G. wetmorei* Ewing.*†*Phtheiropoios nematophallus* (Werneck). One record (of large numbers) from wild hosts and two from wild skins.

Not allocated to a section.

CTENOMYS ROBUSTUS Philippi.

Phtheiropoios latipollicaris (Ewing). Two males and three females from U.S.N.M. skin 84149.

CTENOMYS "SECULATUS", from La Rioja, Argentina.

Phtheiropoios forficulatus (Neumann). One record of five males and two females.There is no *Ctenomys* of this name or anything very similar. Presumably an error in transcription.

Family ABROCOMIDAE.

Genus ABROCOMA.

ABROCOMA BENNETTI Waterhouse.

*†*Gyropus* (*Monogyropus*) *longus* Neumann. Described from a single female from this host and two lots from undetermined hosts; since found in large numbers on this host.

ABROCOMA CINEREA Thomas.

Phtheiropoios pearsoni* Werneck. One record of a short series, apparently from a wild host.Neohaematopinus longus* Werneck. A single female, apparently from a wild host.

Family ECHIMYIDAE.

Subfamily Echimyinae.

Genus PROECHIMYS.

In this genus the parasite-records seem not to support Ellerman's provisional placing of most of the forms as subspecies of *cayennensis*. I have, therefore, followed the arrangement proposed by him (1940, p. 118) to be used in case this placing should prove incorrect. I have also thought it necessary to mention the subspecies from which each louse has been obtained, both here and in the case of the genus *Cercomys*.

Subgenus Proechimys.

cayennensis group.

PROECHIMYS CAYENNENSIS (Desmarest).

Harrisonia uncinata Ferris. (Amb., Trim.) Three males, four females and three nymphs from a skin of ssp. *calidior*.*Gyropus* (*Tetragyropus*) *setosus* Neumann. Two males and one female from a skin of ssp. *calidior*.**Gliricola* (*Paragliricola*) *echimydis* Werneck. One record of two males and nine females from ssp. *cayennensis*.

Gliricola decurtatus (Neumann). One record of a single male from ssp. *cayennensis*.

Pterophthirus audax (Ferris). (An., Hac.) One record of "a number of specimens" from a skin, and 4 specimens from a skin of ssp. *calidior*.

PROECHIMYS SEMISPINOSUS (Tomes).

Harrisonia uncinata Ferris. A single male from a skin of ssp. *semispinosus*, and a pair from a skin of ssp. *panamensis*.

(*) *Gliricola panamensis* Werneck. One record of 1 male, 12 females and two nymphs from U.S.N.M. skin 11669 (ssp. *panamensis*). I regard this as being more probably the true host than *Sigmodon hispidus* (p. 473) from which the types are supposed to have been obtained.

**Pterophthirus audax* (Ferris). From U.S.N.M. skin 113273 (ssp. *semispinosus*).

A record of 5 females of *Gyropus setifer* is very doubtful, the specimens having been collected from U.S.N.M. skin 113273, obtained at the same locality as a skin of *Hoplostomus gymnurus*.

PROECHIMYS MINCAE (Allen).

Harrisonia uncinata Ferris. A single male from a skin.

**Gliricola columbanus* Werneck. One male from U.S.N.M. skin 123486.

Pterophthirus audax (Ferris). One record from U.S.N.M. skin 113303.

A single female of *Gyropus lineatus* Neumann from U.S.N.M. 123490 was presumably a contamination.

PROECHIMYS SECURUS Thomas.

**Gyropus (Tetragyropus) setosus* Neumann. Two records, probably from wild hosts.

PROECHIMYS TRINITATIS (Allen and Chapman).

Harrisonia uncinata Ferris. One male from U.S.N.M. skin 85660.

PROECHIMYS BREVICAUDA (Günther).

Gyropus (Tetragyropus) parasetosus Werneck. One record of two pairs and six nymphs, apparently from a wild host.

**Gliricola aequatorialis* Werneck. One record of many specimens, apparently from a wild host.

PROECHIMYS ORIS Thomas.

†*Harrisonia uncinata* Ferris. Three females from two wild hosts (also from the same marmoset skin as *Gliricola pintoii*).

Gyropus (Tetragyropus) parasetosus Werneck. Two records of numerous specimens, apparently from wild hosts. It seems not unlikely that *P. oris* is the true host.

**Gliricola (Gliricola) calcaratus* Werneck. Two records of three males six females and two nymphs from a skin, and of one male without details.

(*)†*Gliricola pintoii* Werneck. Described from contaminations on a skin of a marmoset. Many records from *P. oris*, which Werneck regards as the true type-host.

†*Pterophthirus audax* (Ferris). One record of numerous specimens, wild host.

PROECHIMYS DIMIDIATUS (Günther).

Gyropus (Tetragyropus) martini martini Werneck. Many specimens from a wild host.

Gliricola (Paragliricola) echimydis Werneck. One record of two males from a wild host.

iheringi group.

PROECHIMYS IHERINGI Thomas.

*†*Gyropus martini iheringi* Werneck. Many specimens from two wild hosts.

*†*Gliricola (Gliricola) decurtatus maculatus* Werneck. Several records from wild hosts.

Subgenus Trinomys.

PROECHIMYS ALBISPINUS (Geoffroy).

**Gyropus (Tetragyropus) martini martini* Werneck. One record of three males and four females from ssp. *albispinus* (host possibly misdetermined; see Werneck 1948 : 63).

Gliricola (Paragliricola) echimydis Werneck. One record of many specimens from ssp. *albispinus* (a wild host).

PROECHIMYS SETOSUS (Geoffroy).

**Gyropus limai* Werneck. One record from a wild host.

Unplaced.

? PROECHIMYS sp.

**Gyropus martini matthaeensis* Werneck. From an undetermined wild rat, São Mateus, Espírito Santo, Brazil.

Genus HOPLOMYS.

HOPLOMYS GYMNURUS (Thomas).

**Harrisonia uncinata* Ferris. A single female from a skin.

**Gyropus (Tetragyropus) setifer* Ewing. A single female from U.S.N.M. skin 113270, and 3 pairs from U.S.N.M. skin 113268.

A record of a single female of *Gyropus ovalis* Burmeister may be a case of straggling, but is more probably contamination.

Genus EURYZYGOMATOMYS.

EURYZYGOMATOMYS SPINOSUS (Desmarest).

*†*Gyropus (Tetragyropus) cruzi* (Werneck). Large numbers from wild hosts.

**Gyropus (Tetragyropus) parasetosus* Werneck. Described from one male and four females from a skin. It seems possible that *Proechimys oris* may be the true host.

*†*Gliricola (Paragliricola) mesomydis* Werneck. Large numbers from wild hosts.

(*?)*Gliricola palladius* Kéler. Several records from undetermined rats in company with *G. mesomydis*.

A record of a single female of *Gyropus ovalis* Burmeister may be a case of straggling, but is more possibly contamination.

Genus CERCOMYS.

CERCOMYS CUNICULARIUS Cuvier.

**Gyropus cercomydis* Werneck. Two records, of 4 and 2 specimens respectively from wild hosts, ssp. *laurentius*.

*†*Gyropus freitasi* Werneck. Many records from wild hosts, subspecies *inermis* and *laurentius*.

*†*Gyropus scalaris* Werneck. Three records of numerous specimens from wild hosts of ssp. *laurentius* and *cunicularius*.

*†*Gyropus lenti lenti* Werneck. Numerous records from subspecies *laurentius* and *inermis*.

*†*Gyropus lenti distinctus* Werneck. Many specimens from a wild host and from U.S.N.M. skin 121408 (both ssp. *fosteri*).

*†*Ctenophthirus cercomydis* Ferris. (An., Hae.) Very many records from wild hosts and skins, subspecies *cunicularius*, *fosteri* (including U.S.N.M. skin 121408), *inermis* and *laurentius*.

Genus ISOTHRIX.

ISOTHRIX BISTRIATUS Wagner.

*†*Gyropus (Tetragyropus) thompsoni* Werneck. (Amb., Gyr.) Several records of large numbers from wild hosts.*†*Gliricola mirandai* Werneck. Two records from wild hosts.

ISOTHRIX PICTUS (Pictet).

**Gyropus travassosi* Werneck. Two records of many specimens from wild hosts.

Genus ECHIMYS.

dasythrix group.

ECHIMYS LAMARUM (Thomas).

(*)†*Gliricola decurtatus fonscai* Werneck. Two lots from wild hosts later determined as *Nelomys (=Echimys)* sp., and five later records from *E. lamarum*; the original hosts may well also have been of this species.*armatus* group.

ECHIMYS ARMATUS (Geoffroy).

*†*Gliricola decurtatus marajoensis* Werneck. Four records, from wild hosts, two sources.*grandis* group.

ECHIMYS GRANDIS (Wagner).

*†*Gliricola decurtatus paraensis* Werneck. Two records, of 4 males and 1 female and of many specimens, from wild hosts.Subfamily *Dactylomyiinae*.

Genus KANNABEOTOMYS.

KANNABEOTOMYS AMBLYONYX (Wagner).

*†*Gliricola (Gliricola) decurtatus decurtatus* Neumann. Many records from wild hosts.A single record of *Hoplopleura travassosi* Werneck (An., Hae.) from a wild host is probably erroneous, the other hosts being Muridae.Family *THRYONOMYIDAE*.

Genus THRYONOMYS.

THRYONOMYS GREGORIANUS (Thomas). (Lesser Cane-Rat.)

*†*Scipio aulacodi longiceps* Ewing. (An., Hae.) Described from material obtained from U.S.N.M. skins 184179, 184180; since obtained from several wild hosts. Perhaps inseparable from *S. aulacodi*.**Proenderleinellus africanus* Ewing. (Ann., Hae.) One record of a single male from U.S.N.M. skin no. 184180.

THRYONOMYS SWINDERIANUS (Temminck).

*†*Scipio a. aulacodi* (Neumann). Several records from wild hosts.*†*Scipio breviceps* Ferris. Described from *Thryonomys* sp., but there is no other *Thryonomys* in Zululand. Three records from wild hosts.Family *PETROMYIDAE*.

Genus PETROMUS.

PETROMUS TYPICUS Smith. (Nokey or Dassie Rat.)

*†*Scipio (Bedfordia) tripedatus* Ferris. Eleven records from wild hosts and wild skins, including T.M. 5683, 7942, 7944, 7952, 7961, 7974, 7978 and 9555.

? Suborder **HYSTRICOMORPHA.**Superfamily **BATHYERGOIDEA.**Family **BATHYERGIDAE.**Genus **BATHYERGUS.**

BATHYERGUS SUILLUS (Schreber). (Cape Dune Mole-Rat or Sand "Mole.")

*†*Bathyergicola laurensis* Bedford. (An., Hae.) Two records, different sources, at least one record reliable.

Genus **CRYPTOMYS.**

CRYPTOMYS HOTTENTOTUS (Lesson). (Hottentot Mole-Rat.)

**Bathyergicola hilli* Bedford. One probably reliable record of two males and two females.

Cohort **MUTICA.**Order **CETACEA.**

No lice are known from the whales and it is practically certain that none can occur. The entire lack of a hairy coat among whales means that lice would have no protection against the effects of long submergence under water and would certainly be drowned.

Cohort **FERUNGULATA.**Superorder **Ferae.**Order **CARNIVORA.**Suborder **FISSIPEDA.**Superfamily **CANOIDEA.**Family **CANIDAE.**Subfamily **Caninae.**Genus **CANIS.**Subgenus **Canis.**

CANIS LUPUS Linn. (Wolf.)

†*Trichodectes canis* (De Geer). (Isc., Tric.) Three records, two (Russia and Canada) apparently from wild hosts.

Linognathus setosus (von Olfers). (An., Hae.) One record, apparently wild host.

CANIS FAMILIARIS Linn. (Dog.)

*†*Heterodoxus spiniger* (Enderlein) (synonym: *armiferus*). (Amb., Bo.) Very many records.

*†*Trichodectes canis* (De Geer) (synonyms: *floridanus* and *latus*). Very many records, including three from *C. f. dingo* Blumenbach.

*†*Linognathus setosus* (von Olfers) (synonyms: *bicolor*, *flavidus*, *isopus* and *piliferus*). Very many records.

Records of *Haematopinus eurysternus*, *Linognathus vituli*, *Phthirus pubis* and *Pediculus humanus* are obviously due to contamination.

CANIS LATRANS Say. (Coyote.)

†*Heterodoxus spiniger* (Enderlein). Four records, apparently from wild hosts.

†*Trichodectes canis* (De Geer). One record from a captive, three (one in large numbers) from wild hosts.

Linognathus setosus (von Olfers). One record, no details.

Subgenus THOUS. (Jackals.)

CANIS AUREUS Linn. (Common Jackal.)

- †*Heterodoxus spiniger* (Enderlein). One reliable record and one probably reliable. Another (from "Jackal", Somaliland) may refer to this species.
Trichodectes canis (De Geer). One record from a captive.
Linognathus setosus (von Olfers). One record (Kolenati, 1846), apparently from a wild host.

CANIS ADUSTUS Sundevall. (Side-striped Jackal.)

I have dissolved two wild skins from Uganda without finding any lice. A third skin from Uganda produced a short series of *Heterodoxus spiniger*, but the record is doubtful because the skin was an old one that may well have been slept on by a dog (see p. 548, footnote).

CANIS MESOMELAS Schreber. (Black-backed Jackal.)

- †*Linognathus setosus* (von Olfers). Four reliable records, once as a very heavy infestation.

Genus ALOPEX.

ALOPEX LAGOPUS (Linn.). (Arctic Fox.)

- †*Linognathus setosus* (von Olfers). Numerous records from wild hosts, once in great numbers.

Genus VULPES.

VULPES VULPES (Linn.). (Common or Red Fox.)

- *†*Felicola (Suricatoecus) vulpis* (Denny). (Isr., Tric.) (synonyms: *micropus* and *abnormis*). Many records from wild hosts, also from U.S.N.M. skins 152620 and 173293 and skin 3296 of Mus. Vert. Zool. California Univ.
Linognathus setosus (von Olfers). One record from a captive.

Genus UROCYON.

UROCYON CINEREOARGENTEUS (Schreber). (North American Grey Fox.)

- *†*Felicola (Suricatoecus) quadriceps* (Chapman). Three records from apparently wild hosts, different sources. Inseparable from *vulpis*.

Genus NYCTEREUTES.

NYCTEREUTES PROCYONOIDES (Gray). (Long-haired "Raccoon"-Dog.)

A single record of *Trichodectes canis* from a captive in a zoo must be considered extremely doubtful.

Genus DUSICYON.

Subgenus Dusicyon.

DUSICYON CULPAEUS (Molina). (Colpeo Fox.)

- **Trichodectes canis riveti* Neumann. One record of more than 100 specimens, status of host not recorded. A synonym of *T. canis*.

DUSICYON FULVIPES (Martin).

- *†*Felicola (Suricatoecus) fahrenheitzi* (Werneck). One reliable record.
Trichodectes canis (De Geer). One record, apparently from a wild host.
Linognathus taeniotrichus Werneck. One record from a captive.

DUSICYON SECHURAE (Thomas).

- Felicola (Suricatoecus) fahrenheitzi* (Werneck). One female from U.S.N.M. skin no. 127171.

DUSICYON THOUS (Linn.).

- †*Trichodectes canis* (De Geer). Many records from wild hosts.
 *†*Linognathus taeniotrichus* Werneck. From several wild hosts.

Subfamily *Simocyoninae*.Genus *SPEOTHOS*.*SPEOTHOS VENATICUS* (Lund). (Bush Dog.)A record of many specimens of *Trichodectes barbarae* is probably due to mislabelling.Genus *CUON*.*CUON JAVANICUS* (Desmarest). (Indian Wild Dog or Dhole.)

The record (Paine, 1912 : 438) of four specimens of *Damalinea (Cervicola) forficula* from this host is perhaps an error in labelling, but possibly an indication that the dhole-pack had very recently killed and eaten a deer. A record of *Haematopinus curysternus*, from Calcutta, might be accepted as genuine straggling if Calcutta were a probable locality for a dhole other than a captive. I cannot accept the assumption (Eichler, 1947 : 21) that Mjöberg's "malajsk hund" was *Cuon javanicus* rather than a Malayan breed of *Canis familiaris*.

Genus *LYCAON*.*LYCAON PICTUS* (Temminck). (African Wild Dog or Hunting Dog.)I have dissolved six fresh skins of *L. pictus lupulinus* Thomas without finding any lice.Subfamily *Otocyoninae*.Genus *OTOCYON*.*OTOCYON MEGALOTIS* (Desmarest). (Big-eared Fox.)**Trichodectes (Suricatoecus) guinei* (Werneck). Two males, three females from U.S.N.M. skin 162124.Family *URSIDAE*. (Bears.)Genus *TREMARCTOS*.*TREMARCTOS ORNATUS* (F. Cuvier). (Spectacled Bear.)**Trichodectes (Werneckodectes) ferrisi* Werneck. One record (6 males, 12 females) from U.S.N.M. skin 170.656.Genus *SELENARCTOS*.*SELENARCTOS THIBETANUS* (G. Cuvier). (Himalayan Black Bear.)*Trichodectes (Ursodectes) pinguis* Burmeister. One record from a captive, probably a misdetermination.Genus *URSUS*.*URSUS ARCTOS* Linn. (European Brown Bear.)*†*Trichodectes (Ursodectes) pinguis* Burmeister. Two records, different sources.Family *PROCYONIDAE*.Subfamily *Procyoninae*.Genus *BASSARISCUS*.*BASSARISCUS ASTUTUS* (Lichtenstein). (Cacomistle or Ring-tail "Cat.")*†*Trichodectes (Neotrichodectes) thoracicus* Osborn. Several records, at least one from a wild host.Genus *PROCYON*. (Raccoons.)*PROCYON LOTOR* (Linn.). (Raccoon.)*†*Trichodectes octomaculatus* Paine (synonym : *procyonis*). Many records from wild hosts.*PROCYON CANCRIVOROUS* (G. Cuvier). (Crab-eating Raccoon.)*†*Trichodectes fallax* Werneck. Many records from wild hosts.

Genus *NASUA*. (Coatis or Coatimundi.)*NASUA NARICA* (Linn.). (White-nosed Coatimundi.)*†*Trichodectes* (*Neotrichodectes*) *pallidus* Piaget (synonym: *nasuati*). Numerous records, different sources.*NASUA RUF*A Desmarest. (Red Coatimundi.)†*Trichodectes* (*Neotrichodectes*) *pallidus* Piaget. Several records from different sources, louse in large numbers.*NASUA CANDACE* Thomas.*Trichodectes* (*Neotrichodectes*) *pallidus* Piaget. One record, apparently wild host.Genus *POTOS*.*POTOS FLAVUS* (Schreber). (Kinkajou.)*†*Trichodectes* (*Potusditi*) *potus* Werneck. At least four records, including wild hosts and Genoa Mus. skin CE. 1106.Family *MUSTELIDAE*.Subfamily *Mustelinae*.Genus *MUSTELA*.Subgenus *Mustela*.*MUSTELA NIVALIS* Linn. (Weasel.)*†*Trichodectes* (*Stachiella*) *mustelae* (Schrank) (synonyms: *dubius* and *pusillus*). Many reliable records.*MUSTELA ERMINEA* Linn. (Stoat or Ermine.)*†*Trichodectes* (*Stachiella*) *ermineae* (Hopkins). Several reliable records.A record of *Felicola subrostratus* is due to contamination or mislabelling, and one of *Trichodectes galictidis* is quite obviously erroneous.*MUSTELA CICOGNANI* Bonaparte.(*)*Trichodectes* (*Stachiella*) *kingi* McGregor. A pair, apparently from a wild host. The type-series was obtained from three individuals of "weasel, *Putorius* sp.", from Florence, Montana. Weasels from this locality could have been *M. cicognani*, *M. frenata* or *M. rixosa* (Bangs).*MUSTELA FRENATA* Lichtenstein. (Bridled Weasel.)*†*Trichodectes* (*Neotrichodectes*) *minutus* Paine. Several records, different sources.A single male of *T. (N.) mephitidis* was doubtless a contamination.*MUSTELA NIGRIPES* (Audubon and Backman). (Black-footed Weasel.)*Trichodectes* (*Neotrichodectes*) *minutus* Paine. One record, apparently from a wild host*MUSTELA STOLZMANNI* Taczanowski. (Peruvian Weasel.)*Trichodectes* (*Neotrichodectes*) *minutus* Paine. Two males and a female from two apparently wild hosts.Subgenus *Putorius*.*MUSTELA PUTORIUS* Linn. (Polecat and Ferret.)**Trichodectes* (*Stachiella*) *retusus jacobi* (Eichler). Described from a single female from a wild host; one other record from the wild form.Denny's record of *Linognathus setosus* from a ferret has been repeated so often that Ewing (1929, p. 139) includes the ferret without comment in a list of the hosts of this louse. It is certainly due to contamination. Records (Dudich, 1923) of *Phthirus pubis* and *Pediculus humanus* are even more meaningless.

Subgenus *Lutreola*.

MUSTELA VISON Schreber. (Mink.)

†*Trichodectes (Stachiella) ermineae* (Hopkins). One of the five records of *T. retusus* from this host definitely refers to this species, as also does one other record.

A single record of *Otilipeurus dissimilis* (Piaget) looks like genuine straggling from prey until one remembers that this is a bustard-parasite and that the range of *M. vison* nowhere coincides with that of any bustard.

Genus MARTES.

MARTES FOINA (Erxleben). (Beech-Marten or Stone-Marten.)

**Trichodectes (Stachiella) r. retusus* Burmeister. Two records, one probably from a wild host, the other (a pair) from a skin. Séguy's record of *mustelae* from this host also probably refers to *retusus*.

MARTES MARTES (Linn.). (Pine-Marten.)

**Trichodectes (Stachiella) retusus salfi* (Conci). Two records, one probably from a wild host, the other (one female) from a skin.

MARTES CAURINA Merriam.

(*?)*Trichodectes (Stachiella) retusus martis* (Werneck). Three males and two females from two specimens of "*Martes* sp." from Yosemite National Park, California.

Mr. Morrison-Scott tells me that a *Martes* from this locality would most probably be *M. caurina*.

Genus GALERA.

GALERA BARBARA (Linn.). (Tayta.)

*†*Trichodectes (Trigonodectes) barbarae* Neumann. Many records, different sources.

Genus GRISON.

GRISON CANASTER (Nelson).

Trichodectes (Galictobius) galictidis Werneck. One record, apparently from a wild host.

GRISON VITTATA (Schreber).

**Trichodectes (Stachiella) divaricatus* Harrison. A single female, apparently from a wild host.

Other records from this host (and perhaps this one also) probably refer to misdetermined specimens of *Grisonella furax*. See Werneck, 1946.

Genus GRISONELLA.

GRISONELLA FURAX (Thomas).

*†*Trichodectes (Galictobius) galictidis* Werneck (synonym: *paranensis*). Several records from wild hosts. Original host misdetermined. There has been much confusion between this host and *Grison vittata*.

Genus ICTONYX.

ICTONYX STRIATUS (Perry). (Greater African Skunk.)

*†*Trichodectes (Stachiella) ovalis* Bedford. Four records from wild hosts. Original host misdetermined (see Hopkins, 1941a, p. 284; 1942, p. 115).

As Simpson is doubtful if *Zorilla* really applies to this genus I have provisionally retained *Ictonyx*.

Genus POECILICTIS.

POECILICTIS LYBICA (Hemprich and Ehrenberg). (Zorilla.)

*†*Trichodectes (Stachiella) zorillae* Stobbe. Two records, from different subspecies.

Genus **POECILOGALE**.

POECILOGALE ALBINUCHA (Gray). (Lesser African Skunk.)

*†*Trichodectes (Stachiella) ugandensis* Bedford. Many reliable records.

Bedford's attribution of *T. ovalis* to this species was due to misidentification of the host.

Genus **GULO**.

GULO GULO (Linn.). (Glutton or Wolverine.)

Trichodectes retusus Burmeister. Two records: one probably a misidentification, the other (of a single female of ssp. *martis*) certainly due to contamination.

Subfamily **Mellivorinae**.Genus **MELLIVORA**.

MELLIVORA CAPENSIS (Schreber). (African Honey-Badger.)

*†*Trichodectes rosseleri* Stobbe. Three reliable records (South and East Africa). The original record was of specimens, without data, which Stobbe was informed were probably from a bush-pig. There is not the smallest doubt that this information was incorrect.

Subfamily **Melinae**.Genus **MELES**.

MELES MELES (Linn.). (European Badger.)

*†*Trichodectes melis* (J. C. Fabricius) (synonym *crassus*). Abundant.

Genus **TAXIDEA**.

TAXIDEA TAXUS (Schreber). (American Badger.)

*†*Trichodectes (Neotrichodectes) interrupto-fasciatus* Kellogg and Ferris. Two records, different sources, wild hosts.

A record of *T. mephitidis* from this host (Hall, 1912) is doubtless due to misdetermination of the above; a record of a single female was presumably a case of contamination.

Genus **HELICITIS**.

HELICITIS ORIENTALIS Horsfield. ("Ferret"-Badger.)

A single nymph (apparently from a skin) that was determined by Neumann as *Trichodectes mephitidis* ought never to have been recorded. The determination is a mere guess.

Subfamily **Mephitinae**.Genus **MEPHITIS**. (Striped Skunks.)

MEPHITIS MEPHITIS (Schreber). (Skunk.)

*†*Trichodectes (Neotrichodectes) mephitidis* (Packard) (synonym: *monticolus*). Very many records.

A single record of *Neohaematopinus pacificus* from *M. m. occidentalis* Baird is certainly not normal but may be due to true straggling from prey.

MEPHITIS MESOMELAS Lichtenstein. (Louisiana Skunk.)

†*Trichodectes (N.) mephitidis* (Packard). Several records from wild hosts.

Genus **SPILOGALE**. (Spotted Skunks.)

SPILOGALE ARIZONAE (Mearns). (Arizona Spotted Skunk.)

Trichodectes (Neotrichodectes) osborni (Kéler). A male, a female and six nymphs, apparently from a wild host.

SPILOGALE AMBARVALIS Bangs.

Trichodectes (*Neotrichodectes*) *osborni* (Kéler). One male, four females and eleven nymphs, apparently wild host.

SPILOGALE INTERRUPTA (Rafinesque). (Midwestern Spotted Skunk.)

**Trichodectes* (*N.*) *osborni* (Kéler). A single record, apparently from a wild host.

SPILOGALE PHENAX Merriam. (Pacific Coast Spotted Skunk.)

Trichodectes (*N.*) *osborni* (Kéler). One record, material formerly misidentified as *mephitidis*.

Dr. Hill told me he was inclined to consider most of the forms of *Spilogale* as subspecies of *S. putorius* (Linn.).

Genus CONEPATUS. (Hog-nosed Skunks.)

CONEPATUS MESOLEUCUS (Lichtenstein).

**Trichodectes* (*Neotrichodectes*) *arizonae* (Werneck). One record of three males, nine females and six nymphs, apparently wild host.

CONEPATUS CHINGA Molina.

**Trichodectes* (*Neotrichodectes*) *chilensis* (Werneck). Described from many specimens, apparently wild host.

**Trichodectes* (*Neotrichodectes*) *wolffhügeli* Werneck. Described from four males from the same host or hosts.

CONEPATUS HUMBOLTHI Gray.

Trichodectes (*N.*) *chilensis* (Werneck). One record of six males, seven females.

CONEPATUS AMAZONICUS (Lichtenstein).

Trichodectes (*N.*) *chilensis* (Werneck). Two records, apparently wild hosts.

The fact that the series from *Conepatus* sp., Choro, Bolivia, that Kellogg and Ferris misidentified as *mephitidis* includes a male of *T. wolffhügeli* as well as 4 males of *T. chilensis* tends to confirm the occurrence of the former louse on *Conepatus*.

Subfamily Lutrinae.

Genus LUTRA.

Subgenus Lutra.

LUTRA LUTRA (Linn.). (European Otter.)

*†*Trichodectes* (*Lutridia*) *exilis* Nitzsch. Numerous records from wild hosts.

Subgenus Hydriectis.

LUTRA MACULICOLLIS Lichtenstein.

**Trichodectes* (*Lutridia*) *matschiei* Stobbe. One probably reliable record (two females and a nymph, apparently from a wild host).

Genus PTERONURA.

PTERONURA BRASILIENSIS (Blumenbach). (Brazilian Otter.)

*†*Trichodectes* (*Lutridia*) *lutrae* Werneck. Three records, two reliable.

Genus PARAONYX.

PARAONYX PHILLIPSI Hinton. (Small-toothed Clawless Otter.)

†*Trichodectes* (*Lutridia*) *matschiei* Stobbe. One reliable record.

The host is probably a subspecies of *Paraonyx congica* (Lönnberg).

Superfamily FELOIDĒA.

Family VIVERRIDAE.

Subfamily Viverrinae.

Tribe VIVERRINI.

Genus GENETTA.

GENETTA GENETTA (Linn.). (Small-spotted Genet.)

(*?) *Felicola (Parafelicola) a. acuticeps* (Neumann) (synonym: *genetta*). Two records (Bedford's and Conci's, the latter of many specimens from a skin).

* *Felicola genetta* (Fresca). One record of a male and a nymph, apparently from a wild host.

Conci (1943, p. 20) suggests that *genettae* may be a synonym of *acuticeps*; if this is correct (which seems improbable) Fresca's figure must be grossly inaccurate.

GENETTA TIGRINA (Schreber). (Large-spotted Genet.)

† *Felicola (Parafelicola) a. acuticeps* (Neumann). Several reliable records, also from Genoa Mus. skins 4309, 4310 and 4361.

*† *Felicola (P.) acuticeps wernecki* Hopkins. Several records from wild hosts, also from C. M. M. skins 285 B/166 and 186 and U.S.N.M. skin 61701.

Felicola (P.) lenicornis (Werneck). A single male from a wild skin.

The distribution of the forms of *F. acuticeps* seems to be geographical rather than according to host. Specimens from *G. t. angolensis* from the Lower Congo (U.S.N.M. skin 61701) examined by Werneck, and those I have seen from *Genetta tigrina erlangeri* in Kenya and *G. t. stuhlmanni* in Uganda are all *a. wernecki*, but a male and nine females from a skin of the latter host-form from Tanganyika (Shinyanga), 16 males and 31 females from *G. t. ? mossambica* in Northern Rhodesia (Mwerowantipe, Kabwe) and a short series collected from *G. t. tigrina* in Natal (Bedford, 1932, p. 363) are all *a. acuticeps*. But genets are not very easy to identify, most of the host-determinations are my own, and it may yet prove that the distribution of the lice is governed by the host-form.

GENETTA VICTORIAE Thomas. (Giant Genet.)

* *Felicola (Parafelicola) lenicornis* Werneck. One male and five females from several wild skins.

Genus VIVERRICULA.

VIVERRICULA INDICA (Geoffroy). (Rasse.)

* *Felicola (Parafelicola) viverriculae* (Stobbe). One record, probably reliable.

Genus CIVETTICTIS.

CIVETTICTIS CIVETTA (Schreber). (African Civet.)

† *Felicola (Felicola) subrostratus* (Burmeister). A secondary infestation but definitely established. Five reliable records.

Tribe PRIONODONTINI.

Genus PRIONODON.

PRIONODON LINSANG (Hardwicke). (Linsang.)

* *Felicola (Neofelicola) aspidorhynchus* (Werneck). One male and three females from U.S.N.M. skin 144108.

* *Felicola (Neofelicola) sumatrensis* (Werneck). One male from the same skin.

Subfamily Paradoxurinae.

Tribe NANDINIINI.

Genus NANDINIA.

NANDINIA BINOTATA (Reinwardt). (African Tree-Genet or Palm-Civet.)

*† *Felicola (Suricatoecus) hopkinsi* Bedford. One reliable record.

A record of a single female of *Felicola acuticeps wernecki* from this host is definitely a case of contamination, the skin having been stored among skins of *Genetta tigrina stuhlmanni*.

Tribe PARADOXURINI.

Genus PARADOXURUS.

PARADOXURUS HERMAPHRODITUS (Schreber). (Common Palm-Civet.)

**Felicola* (*Neofelicola*) *bengalensis* (Werneck). Three females from U.S.N.M. skin 123979.

Genus PAGUMA.

PAGUMA LARVATA (Hamilton-Smith). (Masked Palm-Civet.)

*†*Felicola* (*F.*) *juccii* (Conci). From Genoa Museum skin CE 10423 and U.S.N.M. skins 254916, 254924 and 258351.

Tribe CYNOGALINI.

Genus CYNOGALE.

CYNOGALE BENNETTI Gray. (Otter "Civet.")

*†*Felicola* (*Suricatoecus*) *malaysianus* (Werneck). One reliable record from U.S.N.M. skin 144122.

Tribe EUPLERINI.

Genus EUPLERES.

EUPLERES GOUDOTII Doyère. (Small-toothed Mongoose.)

The record of *Trichodectes madagascariensis* Mjöberg, described from a single specimen supposed to be from this host, is a case of contamination, the name being a synonym of *Damalinea limbata* (a goat-parasite).

Subfamily Herpestinae.

Tribe SURICATINI.

Genus SURICATA.

SURICATA SURICATA (Erxleben). (Suricat or Slender-tailed Mierkat.)

*†*Felicola* (*Suricatoecus*) *cooleyi* (Bedford). One record from a wild host, and in numbers from eight skins, including T.M. 1700, 3502, 5326, 6531, 6532, and 9701.

Tribe HERPESTINI.

Genus HERPESTES.

Subgenus Herpestes.

HERPESTES ICHNEUMON (Linn.). (African Large Grey Mongoose.)

*†*Felicola* (*F.*) *inaequalis* (Piaget) (synonym: *rammei*). Many reliable records.

Stobbe stated that *rammei* was from *Herpestes galera* (= *Atilax paludinosus*) but this, unless due to contamination, must be a case of misdetermination of the host. The species does not occur on *Atilax* but has been found abundantly on wild specimens of at least three subspecies of *H. ichneumon*. I consider the single record of *F. rammei* from *Galerella brunneo-ochracea* (probably a form of *Myonax sanguineus*) as being due either to mislabelling or to misdetermination of the host.

HERPESTES VITICOLLIS Bennett. (Indian Stripe-necked Mongoose.)

**Felicola* (*F.*) *zeylonicus* Bedford. One record, of numerous specimens apparently from a wild host.

HERPESTES URVA (Hodgson). (Crab-eating Mongoose.)

Felicola (*F.*) *inaequalis* (Piaget). One record, no details, probably a misdetermination of the parasite.

Subgenus *Myonax*.

HERPESTES PULVERULENTUS Wagner. (South African Lesser Grey Mongoose.)

†*Felicola* (*F.*) *calogaleus* (Bedford). From a wild host and S.A.M. skin 18896.

HERPESTES CAUCI (A. Smith). (Slender Mongoose.)

**Felicola* (*F.*) *calogaleus* (Bedford). One record, probably reliable.

HERPESTES NIGRATUS (Thomas). (Black Slender Mongoose.)

Felicola (*F.*) *calogaleus* (Bedford). One record, probably reliable.

HERPESTES SANGUINEUS Rüppell.

†*Felicola* (*F.*) *calogaleus* (Bedford). Many reliable records, including C.M.M. skin 308 E/1645.

*†*Felicola* (*Suricatoecus*) *mungos* (Stobbe). Numerous reliable records.

Stobbe's material of *F. mungos* was supposed to have been collected in part from *Herpestes badius* in Zanzibar, but *badius* does not occur there and the Zanzibar host must have been *H. sanguineus rufescens*. All the forms of the subgenus *Myonax* that I have seen appear to me to be conspecific.

Genus *HELOGALE*.

HELOGALE PARVULA (Sundevall). (Pigmy Mongoose.)

*†*Felicola* (*Suricatoecus*) *helogale* Bedford. Two records, two males, seventeen females and fifteen nymphs from T.M. skin No. 5868, and six females and four nymphs from T.M. skin No. 5869. The numbers are sufficient to confirm the record.

Shortridge places all the South African forms of *Helogale* as subspecies of *parvula*; I have little doubt he is right, and have followed his arrangement instead of Allen's.

HELOGALE UNDULATA (Peters).

**Felicola* (*Suricatoecus*) *helogaloides* (Werneck). One record (three males, four females) from F.C.M. skin 1455.

ATILAX PALUDINOSUS (G. Cuvier). (Water Mongoose.)

*†*Felicola* (*F.*) *acutirostris* (Stobbe). Numerous reliable records, including T.M. skin 6191.

*†*Felicola* (*F.*) *macrurus* Werneck. Four records from wild skins.

*†*Felicola* (*F.*) *pygidialis* Werneck. One reliable record.

*†*Felicola* (*F.*) *minimus* Werneck. Five records from wild skins, including U.S.N.M. skin 19776:35252, and one from a wild host.

*†*Felicola* (*Suricatoecus*) *laticeps* (Werneck). Seven records from wild hosts and wild skins.

**Felicola* (*Suricatoecus*) *paralaticeps* (Werneck). One record from a wild host.

The distribution of the lice of *Atilax paludinosus* is most puzzling. Having collected *F. acutirostris* from several wild specimens of *Atilax p. robustus*, and *F. laticeps* from one of them, I regarded the presence of *F. pygidialis*, *F. minimus* and *F. paralaticeps* on a wild mongoose that I captured in Kampala on 12. ix. 1941 and determined as *Atilax paludinosus* ssp. as conclusive evidence that my determination was incorrect, but the skin and skull of this specimen were lost at sea by enemy action. Subsequently Dr. Werneck obtained *Felicola minimus* and *F. macrurus* from a skin determined by Dr. Remington Kellogg as that of an immature *A. paludinosus robustus* and I obtained the same two species from wild skins from the Kivu district that I sent, with the skulls, to Dr. J. E. Hill, who found that they, also, belonged to this subspecies. No two of the three species *Felicola pygidialis*, *F. macrurus* and *F. acutirostris* have yet been encountered in the same locality, but *pygidialis*, *minimus* and *paralaticeps* have occurred together on the same individual, and so have certain of the others. Much more evidence is needed, but there seems to be some possibility that the explanation of the puzzle may be geographical.

Stobbe's statement that the types of *Felicola rammei* were from this host is erroneous, possibly a case of contamination, but many of Stobbe's mongooses were certainly mis-determined. A single record of *Felicola subrostratus* doubtless refers to one of the species listed above.

Genus MUNGOS.

MUNGOS MUNGO (Gmelin). (Banded Mongoose.)

*†*Felicola (Suricataeocus) decipiens* Hopkins. Four reliable records. A record of a single male *Felicola setosus* is due to contamination.

Genus ICHNEUMIA.

ICHNEUMIA ALBIGAUDA (G. Cuvier). (White-tailed Mongoose.)

*†*Felicola (F.) rostratus* Bedford. Abundant. Apparently inseparable from *F. subrostratus*, from the domestic cat.

Genus BDEOGALE.

Subgenus Bdeogale.

BDEOGALE CRASSICAUDA Peters.

*†*Felicola (F.) bedfordi* Hopkins. Two records from different sources (six females and some nymphs from C.M.M. skin No. 290 A/1597, and seven males, eight females and three nymphs from T.M. skin 9195).

Subgenus Galeriscus.

BDEOGALE NIGRIPES Pucheran. (Black-footed Four-toed Mongoose.)

†*Felicola (F.) bedfordi* Hopkins. Three records from skins of ssp. *jacksoni* (a female from A.M.N.H. 36025, one male, three females from A.M.N.H. 36026 and one male, two females from A.M.N.H. 36029).

Genus RHYNCHOGALE.

RHYNCHOGALE MELLERI (Gray).

*†*Felicola (F.) robertsi* Hopkins. A good series from three skins including T.M. Nos. 8367 and 8368.

Genus CYNICTIS.

CYNICTIS PENICILLATA (G. Cuvier). (Yellow Mongoose.)

*†*Felicola (F.) cynictis* (Bedford). Many records, different sources, including T.M. skins 4959, 5323, 6525, 7561 and 7882.

Subgenus Paracynictis.

CYNICTIS SELOUSI De Winton. (Selous's Mongoose.)

*†*Felicola (F.) setosus* Bedford. Many specimens from T.M. skins 6082, 6201, 6239 and 6536.

Family HYAENIDAE.

Subfamily Protelinae.

Genus PROTELES.

PROTELES CRISTATUS (Sparrman). (Aardwolf.)

*†*Felicola (Protelicola) intermedius* (Bedford). Three records, one apparently from a wild host, one (three females) from T.M. skin 8902, and one from a Uganda wild skin.

Subfamily Hyaininae.

I have dissolved the hair of three wild specimens of the striped hyaena, *Hyaena hyaena* Linn., and seven of the spotted hyaena, *Crocuta crocuta* (Erxleben), and many scores of the latter species have been examined by searching, all without lice being found. It seems probable that the hyaenas are louse-free.

Family *FELIDAE*.Subfamily *Felinae*.Genus *FELIS*.Subgenus *Felis*.

FELIS SILVESTRIS Schreber. (European Wild Cat.)

†*Felicola (F.) subrostratus* (Burmeister). Two records from wild hosts and one from a wild skin.

FELIS CATUS Linn. (Domestic Cat.)

*†*Felicola (F.) subrostratus* (Burmeister). Very many records.

Records of *Pediculus humanus* from this host are obvious cases of contamination.

FELIS LYBICA Forster. (African Wild Cat.)

**Felicola (F.) caffra* (Bedford). Described from a single pair, apparently from a wild host; a second pair from T.M. skin 1811 (different localities in South Africa).

†*Felicola (F.) subrostratus* (Burmeister). Four records (once in huge numbers) from wild skins, Belgian Congo.

The Mallophaga of this host are discussed on p. 548.

Subgenus *Herpailurus*.

FELIS YAGUARONDI Desmarest. (Jaguarundi.)

†*Felicola (F.) felis* (Werneck). Two records from wild skins, different sources.

FELIS GEOFFROYI Gervais.

†*Felicola (F.) felis* (Werneck). One reliable record.

FELIS SALINARUM Thomas.

A single record of *Heterodoxus longitarsus* is probably due to contamination. Dr. Werneck kindly informs me that the host was captured very young and was already infested when brought to Dr. Mazza. The infestation persisted throughout the life of the host (a year), so that, though contamination prior to Dr. Mazza's receipt of the animal is extremely probable, the occurrence is of considerable biological interest. The host is probably a subspecies of *F. geoffroyi*.

Subgenus *Dendrailurus*.

FELIS PAJEROS Desmarest. (Pampas Cat.)

Felicola (F.) felis (Werneck). One record of two males and a female from a skin.

Subgenus *Panthera*.

FELIS LEO Linn. (Lion.)

I have dissolved the hair of the head and shoulders of one East African wild skin. No lice were found.

FELIS TIGRIS Linn. (Tiger.)

**Trichodectes tigris* Ponton. One record, almost certainly from a captive and perhaps a contamination.

The description of *T. tigris* is so excessively bad that almost the only evidence that it is a trichodectid is that Denny saw specimens and referred it to that family. The description, such as it is, does not suggest a *Felicola*, which suggests that the louse was probably a contamination. The types cannot be traced.

FELIS PARDUS Linn. (Leopard or Panther.)

I have dissolved the hair of two East African skins and brushed several more. No lice were found.

Subgenus *Leopardus*.

FELIS PARDALIS Linn. (Ocelot.)

**Felicola (F.) felis* (Werneck). One record of four males, six females and some nymphs, probably reliable.

Subgenus *Puma*.

FELIS CONCOLOR Linn. (Puma.)

Felicola (F.) felis (Werneck). One record of a single male collected immediately after the death of the host in a forest.

Subgenus *Leptailurus*.

FELIS SERVAL Schreber. (Large-spotted Serval Cat.)

Three wild skins (Busoga and Kigezi in Uganda, and Kivu area, Belgian Congo) dissolved; no lice found.

Subgenus *Lynx*.

FELIS RUFUS Schreber. (American Lynx or Bobcat.)

†*Felicola (F.) felis* (Werneck). Two records both of which seem reliable.

†*Felicola (F.) subrostratus* (Burmeister). Many records from wild skins and wild hosts.

Suborder *PINNIPEDIA*.Family *OTARIIDAE*. (Eared Seals.)Genus *ARCTOCEPHALUS*.

ARCTOCEPHALUS AUSTRALIS (Zimmermann). (Southern Fur Seal.)

Antarctophthirus sp. (An., Hae.) One fragmentary specimen from U.S.N.M. skin 16463 ("16413" of Ferris).

Genus *CALLORHINUS*.

CALLORHINUS ALASCANUS Jordan and Clark. (Northern Fur Seal.)

(*)†*Proechinophthirus fluctus* (Ferris). (An., Hae.) Four records, different sources. See note below.

*†*Antarctophthirus (Achimella) callorhini* (Osborn) (synonym: *monachus*). Two records, different sources.

The host from which the original specimens of *P. fluctus* were obtained was determined as *Eumetopias jubata* but was probably a specimen of the present species (see Ferris, 1920-1935, p. 481).

Genus *ZALOPHUS*.

ZALOPHUS CALIFORNIANUS (Lesson). (Californian Sea-Lion.)

Antarctophthirus microchir californianus Fahrenholz. Two records.

Genus *EUMETOPIAS*.

EUMETOPIAS JUBATA (Schreber). (Northern or Steller's Sea-Lion.)

**Antarctophthirus microchir californianus* Fahrenholz. Two records.

I regard the skin of a seal-pup from which Ferris obtained the type-series of *Proechinophthirus fluctus* as a misdetermined specimen of *Callorhinus alascanus*.

Genus *OTARIA*.Subgenus *Phocarcos*.

OTARIA HOOKERI Gray. (Hooker's Sea-Lion.)

**Antarctophthirus m. microchir* (Trouessart and Neumann). One record of many specimens, very probably reliable.

Family *ODOBENIDAE*.Genus *ODOBENUS*.

ODOBENUS ROSMAREUS (Linn.). (Walrus.)

*†*Antarctophthirus trichechi* (Bohemann). Many records from both subspecies.

Family *PHOCIDAE*. (True Seals.)Subfamily *Phocinae*.Genus *PHOCA*.

PHOCA GROENLANDICA Erxleben. (Greenland Seal or Harp Seal.)

*†*Echinophthirus horridus groenlandicus* Becher (synonyms: *sericans*, *setosus*). (An., Hae.) Many records. Ferris considers this inseparable from *horridus*.

PHOCA HISPIDA Schreber. (Ringed Seal or Jar Seal.)

†*Echinophthirus horridus* (von Olfers). Many records. *E. annulatus* (Schilling) is not available for this form if distinct, because it is a *nomen nudum*.

PHOCA SIBIRICA Gmelin. (Lake Baikal Seal.)

*†*Echinophthirus horridus baicalensis* Ass. Description not seen but the record is reliable because there is only one species of seal in Lake Baikal.

PHOCA VITULINA Linn. (Common Seal.)

*†*Echinophthirus h. horridus* (von Olfers) (synonym: *phocae*). Very many records. Stated (Jancke, 1938) to occur only on the head of the host.

Lucas gives only "phoque" as host of *phocae*, but later authors state definitely that it was *P. vitulina*.

PHOCA RICHARDII (Gray). (Pacific Harbour Seal.)

Doetschman's record of *Antarctophthirus microchir* is probably due to contamination. This host may be a subspecies of *P. vitulina*.

Genus *HALICHOERUS*.

HALICHOERUS GRYPHUS (Fabricius). (Grey Seal.)

†*Echinophthirus horridus* (von Olfers). Several records.

Genus *ERIGNATHUS*.

ERIGNATHUS BARBATUS (Erxleben). (Bearded Seal.)

Echinophthirus horridus (von Olfers). One record, probably reliable.

Subfamily *Lobodontinae*.Genus *LOBODON*.

LOBODON CARCINOPHAGUS (Jacquinot and Pucheran). (Crab-eating Seal.)

*†*Antarctophthirus lobodontis* Enderlein. Two reliable records.

Genus *OMMATOPHOCA*.

OMMATOPHOCA ROSSI Gray. (Ross Seal.)

**Antarctophthirus mawsoni* Harrison. A single female from a wild host.

Genus *HYDRURGA*.

HYDRURGA LEPTONYX (Blainville). (Sea-Leopard.)

*†*Antarctophthirus ognorhini* (Enderlein). Several records from wild hosts and skins.

Genus **LEPTONYCHOTES**.**LEPTONYCHOTES WEDDELLI** (Lesson). (Weddell Seal.)†*Antarctophthirus* ? *ogmorhini* (Enderlein). Two records from wild hosts, fifteen nymphs and four males, thirty-one females one nymph respectively.Subfamily **Cystophorinae**.Genus **CYSTOPHORA**.**CYSTOPHORA CRISTATA** (Erxleben). (Hooded or Bladder-nosed Seal.)*Echinophthirus horridus* (von Olfers). One record.Genus **MIROUNGA**.**MIROUNGA LEONINA** (Linn.). (Southern Elephant-Seal.)*†*Lepidophthirus macrorhini* Enderlein. (An., Hae.) Several records from wild hosts.Superorder **Protungulata**.Order **TUBULIDENTATA**.Family **ORYCTEROPODIDAE**.Genus **ORYCTEROPUS**.**ORYCTEROPUS AFER** (Pallas). (Aardvark or African Ant-Bear.)*†*Hybophthirus notophallus* (Neumann) (synonym : *orycteropodi*). (An., Hae.) Several records from wild hosts.Superorder **Paenungulata**.Order **PROBOSCIDEA**.Suborder **ELEPHANTOIDEA**.Family **ELEPHANTIDAE**.Subfamily **Elephantinae**.Genus **LOXODONTA**.**LOXODONTA AFRICANA** (Blumenbach). (African Elephant.)*†*Haematomyzus e. elephantis* Piaget (synonyms : *longirostris*, *paradoxus* and *proboscideus*). (Rhyn.) Many records, at least two from wild hosts.Genus **ELEPHAS**.**ELEPHAS MAXIMUS** Linn. (Indian Elephant.)*†*Haematomyzus elephantis sumatranus* Fahrenholz. Many records, some apparently from wild hosts. Fahrenholz (1939, p. 42) agrees with Ferris that this form is inseparable from *elephantis*.Order **HYRACOIDEA**.Family **PROCAVIIDAE**.Genus **DENDROHYRAX**.**DENDROHYRAX ARBOREUS ARBOREUS** (A. Smith).*Dasyonyx (D.) v. validus* Bedford. (Is., Tric.) One record from a probably fresh specimen (Port Alfred, Cape Province).*Procaviphilus granulatus* (Ferris) or *P. dubius* Werneck. (Is., Tric.) Recorded (three females) from T.M. skins 1144 and 1164. Females of these two species are not separable with certainty.†*Procavicola (P.) cichleri* Werneck. (Is., Tric.) Obtained from the Port Alfred specimen and from T.M. 1144 and 1164.*†*Procavicola (Condylcephalus) b. bedfordi* Werneck. Many specimens from the Port Alfred specimen and from T.M. 1164.

DENDROHYRAX ARBOREUS SCHEELEI Matschie.

- Dasyonyx (D.) v. validus* Bedford. One record from B.M. skin 11.4.23.2.
Procaviphilus granulatus (Ferris). One record from B.M. skin 11.4.23.2.
Procavicola (P.) eichleri Werneck. One male and two females from B.M. skin 11.4.23.2.
Procavicola (C.) bedfordi dissimilis Werneck. A few specimens from B.M. skin 11.4.23.2.
Procavicola (C.) hopkinsi Werneck. One male from B.M. skin 11.4.23.2.

DENDROHYRAX ARBOREUS STUHLMANNI (Matschie).

- Procaviphilus granulatus* (Ferris). One record from B.M. skin 4.2.6.33.
Procavicola (P.) eichleri Werneck. One male and one female from B.M. skin 4.2.6.33.
Procavicola (Meganarionoides) congoensis (Ferris). One record from B.M. skin 4.2.6.33.
Procavicola (C.) bedfordi dissimilis Werneck. Two males from B.M. skin 4.2.6.32.
Procavicola (C.) hopkinsi Werneck. One female from B.M. skin 4.2.6.32.

DENDROHYRAX ARBOREUS ADOLFI-FRIEDERICI (Brauer).

- (*)†*Eurytrichodectes paradoxus* Stobbe. (Isc., Tric.) Types from *Dendrohyrax* sp., without further particulars. Later collected from ten specimens of the present host, from four different localities. It is not at all improbable that *adolphi-friederici* was the host from which the original material was obtained.
- *†*Dasyonyx (D.) v. validus* Bedford. Large numbers from numerous fresh specimens and skins, from five different localities, including A.M.N.H. skin 82439.
- *†*Procaviphilus dubius* Werneck. Described from numerous males obtained from several fresh specimens. Also obtained from A.M.N.H. skins 82439 and 82441.
- *†*Procaviphilus granulatus* (Ferris). Described from a single female; subsequently found in considerable numbers on many fresh specimens and on A.M.N.H. skins 82439 and 82441.
- *†*Procavicola (P.) eichleri* Werneck. Abundant on numerous individuals, including B.M. 28.1.30.29. and A.M.N.H. 82439.
- *†*Procavicola (M.) congoensis* (Ferris). Many specimens from five different individuals from several localities, including B.M. skin 30.8.1.54 and A.M.N.H. 82441.
- *†*Procavicola (C.) bedfordi dissimilis* Werneck. Many, from numerous individuals from several localities, including B.M. 30.8.1.54 and A.M.N.H. 82439 and 82441.
- *†*Procavicola (C.) hopkinsi* Werneck. Many, from numerous individuals from several different sources, including A.M.N.H. 82441.

DENDROHYRAX ARBOREUS BETTONI (Thomas and Schwann).

- Dasyonyx (D.) v. validus* Bedford. Nine males and two females from A.M.N.H. skin 82434, one female from C.M.M. skin 612 B/3117.
- †*Procaviphilus dubius* Werneck. Many males from three fresh individuals (Molo and Kikuyu), three males and one female from A.M.N.H. skin 82434, two males, six females from C.M.M. skin 612/106.
- †*Procaviphilus granulatus* (Ferris). Many males and females from two fresh individuals (Molo and Kikuyu, Kenya), two males and three females from A.M.N.H. 82434, one male from C.C.M. skin 612/106.
- †*Procavicola (P.) eichleri* Werneck. Ten males and fourteen females from A.M.N.H. skins 82434 and 82435, many specimens from C.M.M. skin 612 B/3117, four males, two females from C.M.M. skin 612/106.

- ‡*Procavicola* (*C.*) *bedfordi dissimilis* Werneck. One male and two females from a skin (Kenya, Feb. 1936), three males one female from A.M.N.H. skin 82434, eleven males, four females from C.M.M. skin 612/106.
- ‡*Procavicola* (*C.*) *hopkinsi* Werneck. Many specimens from a recently-collected skin (Molo, Kenya, June 1939), one female from A.M.N.H. skin 82434.

DENDROHYRAX ARBOREUS CRAWSHAYI (Thomas).

- Dasyonyx* (*D.*) *v. validus* Bedford. One male from A.M.N.H. skin 55878.
- Procaviphilus dubius* Werneck. One male, one female from A.M.N.H. skin 36002.
- ‡*Procaviphilus granulatus* (Ferris). One record from B.M. skin 11.4.7.161, one male from C.M.M. skin 612B/1155, one male four females from A.M.N.H. skin 36003, one male from A.M.N.H. skin 55878.
- ‡*Procavicola* (*P.*) *cichleri* Werneck. Recorded by Bedford (as *neumanni*) from B.M. skins 3.4.4.4. and 3.4.4.6, one male and four females from C.M.M. skin 612B/1155, four males, nine females from A.M.N.H. skins 36003 and 55878.
- ‡*Procavicola* (*C.*) *bedfordi dissimilis* Werneck. Two records from B.M. skins 3.4.4.4. and 3.4.4.6, one male, two females from A.M.N.H. skins 36002 and 36003, one male, two females from A.M.N.H. skin 55878, many specimens from C.M.M. skin 612B/1155. C.M.M. skin No. 612B/1155 (from 6000 feet on Mount Kenya) is perhaps *D. a. bettoni*.

DENDROHYRAX VALIDUS TERRICOLA Mollison.

- ‡*Dasyonyx* (*D.*) *dendrohyracis* (Ferris). Ten males, seventeen females from a fresh specimen (now A.M.N.H. skin 118552), six males, four females from A.M.N.H. skins 55401 and 55410.
- *‡*Procaviphilus harrisi* Werneck. A very long series (about thirty of each sex) from the fresh specimen, two males and one female from A.M.N.H. skins 55408 and 55410.
- ‡*Procavicola* (*M.*) *neumanni baculatus* (Ferris). Thirty-one males and seventy females from the fresh specimen, twenty males and thirty females from A.M.N.H. skins 55401, 55408 and 55410.

The fresh specimen was collected specially by Mr. W. V. Harris and had no opportunity of becoming contaminated from others. All the specimens examined are *schusteri* Brauer, if this form is separable from *terricola*.

DENDROHYRAX VALIDUS VALIDUS True.

- *‡*Dasyonyx* (*D.*) *dendrohyracis* (Ferris). Described from three males and three females, subsequently obtained in a short series from B.M. skin 85.1.17.8.
- *‡*Procavicola* (*M.*) *neumanni baculatus* (Ferris). Described from four males and two females, later obtained in a short series from B.M. skin No. 85.1.17.8.

Ferris recorded the females of *P. baculatus* as *P. congoensis*; the two species greatly resemble each other in this sex, but *congoensis* is not known from this host. A single record of *Dasyonyx* (*D.*) *v. validus* (Bedford) is probably a misidentification or perhaps contamination.

Procavicola (*Meganarionoides*) *colobi* (Kellogg), supposedly from *Colobus polykomos*, is almost certainly really from *Dendrohyrax validus* ssp. (see Werneck, 1946 a).

DENDROHYRAX VALIDUS NEUMANNI (Matschie).

- Dasyonyx* (*D.*) *dendrohyracis* (Ferris). One record of two males, four females.
- *‡*Procavicola* (*M.*) *neumanni neumanni* (Stobbe). Described from a long series probably from a fresh specimen; a short series obtained from B.M. skin 13.10.28.5.
- Procavicola* (*C.*) *bedfordi dissimilis* Werneck. A single female from B.M. skin 13.10.28.5.

DENDROHYRAX DORSALIS NIGRICANS (Peters).

Dasyonyx (*D.*) *hopkinsi* Werneck. Two females from A.M.N.H. skin 90064.

Procavicola (*M.*) *africanus* Werneck. Four females from the same skin.

Procavicola (*C.*) *bedfordi dissimilis* Werneck. Two males from the same skin.

Procavicola (*C.*) ? *univirgatus* (Neumann). One male, two females from the same skin. Determination queried because I have not seen authentic material.

A.M.N.H. skin 90064 may be *D. d. adametzi* (Brauer), which Allen regards as a synonym of *nigricans*.

DENDROHYRAX DORSALIS SYLVESTRIS (Temminck).

**Dasyonyx* (*D.*) *guineensis* Werneck. Described from a single pair obtained from *Dendrohyrax dorsalis* at Kumasi, Gold Coast.

A form of *Dendrohyrax dorsalis* from the Gold Coast could hardly be *D. dorsalis dorsalis* and must almost certainly have been *D. d. sylvestris*.

DENDROHYRAX DORSALIS EMINI Thomas.

Procavicola (*P.*) *ugandensis* Werneck. One male from A.M.N.H. skin 53819.

**Procavicola* (*M.*) *africanus* Werneck. Three males and nine females from a skin.

Procavicola (*A.*) *scutifer* Werneck. One male from a skin.

DENDROHYRAX DORSALIS MARMOTA Thomas.

*†*Dasyonyx* (*D.*) *hopkinsi* Werneck. A large number of specimens from one fresh individual.

*†*Procavicola* (*P.*) *ugandensis* Werneck. A series from the same individual.

*†*Procavicola* (*M.*) *scutifer* Werneck. Two males and three females from the same individual.

†*Procavicola* (*C.*) *bedfordi dissimilis* Werneck. A few specimens from the same individual.

The above records, though all from one individual, are entirely reliable. The host (a toptype) was never in contact with any other hyrax, alive or dead, between its capture and the collection of the parasites, and was determined at the British Museum.

DENDROHYRAX BOCAGEI (Gray).

*†*Procavicola* (*M.*) *angolensis* Bedford. Described from a very long series from two fresh specimens.

*†*Procavicola* (*M.*) *jordani* Bedford. Described from a short series from one fresh specimen; a single male later identified from the other.

†*Procavicola* (*C.*) *b. bedfordi* Werneck. A number of specimens on both host-individuals.

With regard to the host recorded by Bedford as *Dendrohyrax angolensis*, see Hopkins, 1944 b, p. 410. I have referred *bocagei* to *Dendrohyrax* (not *Heterohyrax*, as is done by Allen) because its louse-fauna is absolutely typical of *Dendrohyrax*.

DENDROHYRAX sp.

**Dasyonyx* (*D.*) *bedfordi* Werneck. Described from a single male.

**Procavicola* (*C.*) *univirgatus* (Neumann). Stated to have been described from about twenty specimens, but it is not certain that more than a single pair were this species, and is established that some were not even congeneric.

Procavicola (*M.*) sp. One female from the original host.

The only available particulars about the host of the above species is that the specimens came from "un Daman (*Hyrax* sp.) du Congo" and were collected by A. Mocquerys. From the presence of a *Procavicola* of the subgenus *Condylcephalus* it seems nearly certain that the host was a *Dendrohyrax*.

Genus HETEROHYRAX.

HETEROHYRAX WELWITSCHII OTJIWARONGENSIS Roberts.

**Dasyonyx* (*Neodasyonyx*) *waterbergensis* Bedford. Described from a short series from T.M. skin 5335. I subsequently obtained a further two males and four females from the same skin.

†*Prolinognathus leptocephalus* (Ehrenberg). Many specimens from T.M. skin 5335.

T.M. skin 5335 is the Type of *otjiwarongensis*; Bedford's recording of it as *waterbergensis* was probably due to the fact that the Transvaal Museum contains two skins with the number 5335. In Allen's Checklist *welwitschii* is placed as a form of *Procavia capensis*, while Dr. Roberts considers it to be certainly a distinct species and refers it to *Heterohyrax*; I have followed Dr. Roberts on the principle that the man on the spot is usually right.

HETEROHYRAX WELWITSCHII WELWITSCHII (Gray).

†*Dasyonyx* (*N.*) *waterbergensis* Bedford. From T.M. skins 8319 (3♂), 8321 (1♀), 8324 (1♀) and 8325 (1♂, 1♀).

†*Prolinognathus leptocephalus* (Ehrenberg). Many specimens from T.M. skins 8317, 8318, 8319, 8320, 8321, 8323, 8324, 8325, 8326 and 9622.

HETEROHYRAX SYRIACUS GRANTI (Wroughton).

*†*Procaviphilus sclerotis* Bedford. Obtained in numbers from T.M. skins 3044, 3573, 3574, 3983, 4490, 4774 and 4775.

*†*Procavicola* (*P.*) *heterohyracis* Bedford. Obtained from T.M. skins 3044, 3573, 3574 and 4490.

†*Procavicola* (*C.*) *lindfieldi* (Hill). From T.M. skins 3573 (4♂, 1♀), 3983 (3♀), 4490 (1♂, 1♀) and 4775 (1♂, 2♀).

A single female of *Dasyonyx* (*N.*) *transvaalensis* from T.M. skin 4490 was almost certainly a contamination.

HETEROHYRAX SYRIACUS RUDDI (Wroughton).

**Dasyonyx* (*D.*) *oculatus* (Bedford). Only known from the holotype.

*†*Procaviphilus robertsi* (Bedford). Described from a single male; later obtained from T.M. skins 5885 (8♂, 10♀), 6215 (1♂, 1♀) and 6216 (1♂, 1♀).

*†*Procavicola* (*P.*) *emarginatus* (Bedford). Described from a single male; later obtained from T.M. skins 6215 (2♂, 2♀) and 6216 (1♂).

†*Procavicola* (*C.*) *lindfieldi* (Hill). Numerous specimens from T.M. skins 5885, 5886, 6215 and 6216.

Prolinognathus leptocephalus (Ehrenberg). One record from T.M. skin 6215.

The types of *D. oculatus*, *Procaviphilus robertsi* and *Procavicola emarginatus* were all obtained from one individual host, apparently a fresh specimen (but see p. 435).

HETEROHYRAX SYRIACUS HINDEI (Wroughton).

**Procaviphilus ferrisi hindei* Werneck. A series from C.M.M. skin 617/128.

Procavicola (*P.*) *emarginatus* (Bedford). A series from the same skin.

HETEROHYRAX SYRIACUS RUDOLFI (Thomas).

*†*Procaviphilus f. ferrisi* Bedford. Recorded by Ferris (1930, p. 1028 as *serraticus*) from possibly fresh wild hosts. Many specimens from C.M.M. skins 617D/3122 and 617D/3124.

*†*Prolinognathus ferrisi* Fahrenholz. Three records, that of Ferris and from C.M.M. skins 617D/3122 and 617D/3124.

HETEROHYRAX SYRIACUS BAKERI (Gray).

*†*Dasyonyx* (*D.*) *validus ugandae* Werneck. Described from abundant material from fresh wild hosts at Umi Rocks, East Madi, Uganda. Later obtained in numbers from two fresh wild hosts (now A.M.N.H. nos. 118669 and 118750) in Acholi District, Uganda.

*†*Procaviphilus ferrisi granuloides* Bedford (synonym: *serraticus*, Ferris *neq* Hill). Described from a long series obtained from the wild hosts at Umi Rocks. One record by Ferris (1930, p. 1028).

*†*Procavicola* (*P.*) *brucei* Werneck. Described from a long series from the Umi Rocks hosts and obtained in quantity from the hosts which are now A.M.N.H. skins 118669 and 118750.

Some of the hosts from Umi Rocks were determined at the British Museum as *H. s. brucei*, but this was described from an unspecified locality in Abyssinia and the determination is geographically and oecologically almost impossible. It is exceedingly probable that they were *bakeri*, since Umi is only about 50 miles from the type-locality of this form, on the same bank of the Nile (see Moreau, Hopkins and Hayman, 1946, p. 431) and in oecologically similar country, while the specimens from Acholi District were practically topotypes of *bakeri*. The host from which Ferris obtained material was from Nimule, about 20 miles downstream from Umi and on the same bank of the Nile, and was determined as *bakeri*.

HETEROHYRAX SYRIACUS SYRIACUS (Schreber).

**Dasyonyx* (*N.*) *diacanthus* (Ehrenberg). Only known from one male and two female cotypes, but record probably reliable.

*†*Prolinognathus leptcephalus* (Ehrenberg). Five records, including three from uncontaminated wild skins.

Genus PROCAVIA.

PROCAVIA C. CAPENSIS (Pallas).

†*Procaviphilus serraticus* (Hill). Twenty-two males and twenty-seven females from S.A.M. skins 19448, 19449 and 19450.

*†*Procavicola* (*P.*) *vicinus* Werneck. Ten males and many females from S.A.M. skins 18899, 19448 and 19449.

†*Procavicola* (*Condylcephalus*) *lindfieldi* (Hill). Many specimens from five skins, including S.A.M. nos. 18899, 19448, 19449 and 19450.

*†*Prolinognathus caviae-capensis* (Pallas). Three records, including from S.A.M. skins 18899 and 19449.

†*Prolinognathus leptcephalus* (Ehrenberg). Many specimens from S.A.M. skins 18899 and 19449.

The skins mentioned above are all topotypes of *P. c. capensis*. Three of them were originally recorded under their field-numbers, F.M. 116, 117 and 118.

PROCAVIA CAPENSIS MARLOTHI Brauer.

Procaviphilus serraticus (Hill). From T.M. skin 2148.

**Procavicola* (*P.*) *parvus* Bedford. Described from "males and females" from T.M. skin 2148.

Prolinognathus caviae-capensis (Pallas). Fourteen specimens from T.M. skin 2144, and one from 2147.

Prolinognathus leptcephalus (Ehrenberg). From T.M. skins 2144 (twenty-eight specimens) and 2148.

A single male *Procavicola* (*P.*) *subparvus* Bedford from T.M. skin 2147 was probably a contamination.

PROCAVIA CAPENSIS KLAVERENSIS Roberts.

†*Procaviphilus serraticus* (Hill). From T.M. skins 2145, 2149 and 2150.

Procavicola (*P.*) *subparvus* Bedford. Three males from T.M. skin 2150.

Procavicola (*C.*) *lindfieldi* (Hill). A pair from T.M. skin 2145, 3♂, 2♀ from 2150.

Prolinognathus caviae-capensis (Pallas). Two specimens from T.M. skin 2149, three from 2150.

†*Prolinognathus leptcephalus* (Ehrenberg). Twenty-one specimens from T.M. skin 2145, eleven from 2146 and three from 2149.

T.M. skin 2145 is the holotype of *klaverensis*.

PROCAVIA CAPENSIS VANDERHORSTI Roberts.

Procaviphilus serraticus (Hill). Three males from T.M. skins 7795 and 7797.

PROCAVIA CAPENSIS CHIVERSI Roberts.

Procaviphilus serraticus (Hill). 2♂, 1♀ from apparently wild host.

**Procavicola* (*P.*) *subparvus* Bedford. Described from "males and females" from T.M. skin 4861.

T.M. skin 4861 is the holotype of *P. capensis chiversi*.

PROCAVIA CAPENSIS GRIQUAE Roberts.

Procavicola (*P.*) *subparvus* Bedford. 4♂, 2♀ from T.M. skin 9607.

Prolinognathus caviae-capensis (Pallas). From T.M. skin 9331.

Prolinognathus leptocephalus (Ehrenberg). 3♂, 4♀ from T.M. skin 9331.

PROCAVIA CAPENSIS ALBANIENSIS Roberts.

†*Procaviphilus serraticus* (Hill). A long series from T.M. skins 6749, 6752, 6755, 6756, 6757, 6758 and 6759.

†*Procavicola* (*P.*) *natalensis* Bedford. From T.M. skins 6749, 6752, 6757, 6758 and 6759.

†*Procavicola* (*C.*) *lindfieldi* (Hill). From T.M. skins 6755 (2♂, 1♀), 6758 (2♂, 2♀) and 6759 (1♂, 2♀).

Prolinognathus caviae-capensis (Pallas). Two specimens each from T.M. skins 6756 and 6757.

†*Prolinognathus leptocephalus* (Ehrenberg). From T.M. skins 6749, 6757 and 6759.

PROCAVIA CAPENSIS NATALENSIS Roberts.

†*Procaviphilus serraticus* (Hill). From T.M. skins 1168, 2005, 2006, 9326 and 9330.

*†*Procavicola* (*P.*) *natalensis* Bedford. Described from "males and females" from T.M. skins 1168, 2005, 2006, and from a fresh individual. Later obtained from T.M. skin 2919.

†*Procavicola* (*C.*) *lindfieldi* (Hill). In numbers from T.M. skins 1168 and 2005 and from the fresh specimen.

Prolinognathus caviae-capensis (Pallas). Six specimens from T.M. skin 9326.

Prolinognathus leptocephalus (Ehrenberg). From T.M. skins 2005 and 9326.

T.M. skin 2005 is the holotype of *P. c. natalensis*.

PROCAVIA CAPENSIS ORANGIAE Roberts.

**Dasyonyx* (*D.*) *minor* Bedford. Described from two females found on T.M. skin 4324.

**Procavicola* (*P.*) *furca* Bedford. Described from two males from T.M. skin 4324.

T.M. skin 4324 (accidentally recorded by Bedford as 1324) is determined by Dr. Roberts as *P. capensis* ssp. near *orangiae*.

PROCAVIA CAPENSIS ssp. (from Mtabamhlopi, Estcourt district, Natal).

**Procaviphilus serraticus* (Hill). Described from "several males and females" found on a hyrax collected at Mtabamhlopi (see note below).

**Procavicola* (*C.*) *lindfieldi* (Hill). "Numerous males and females" from the Mtabamhlopi hyrax must have included *sternatus*, which Hill did not distinguish.

**Procavicola* (*P.*) *sternatus* (Bedford). Described from "females and males" from the same hyrax.

Prolinognathus leptocephalus (Ehrenberg). From the same hyrax.

The hyrax from which all the above were obtained was a fresh specimen and was determined at the time as *Procavia capensis* [s.l.]. Apparently the skin and skull were not preserved. Bedford (1928, p. 845) suggested that it was *P. c. natalensis*, probably because of the locality, but later (1932, p. 718) considered (as I do) that the presence on it of *Procavicola sternatus*, which has not been obtained again, indicates that it belonged to an undescribed form of *Procavia capensis*.

PROCAVIA CAPENSIS COOMBSI Roberts.

†*Dasyonyx* (*Neodasyonyx*) *transvaalensis* Bedford. Many specimens from T.M. skins 3489, 3506, 4344 and 7575.

Procaviphilus sclerotis Bedford. A female and a male from T.M. skins 4344 and 7575 respectively.

*†*Procavicola* (*P.*) *pretoriensis* Bedford. Described from "males and females" from what appears to have been a fresh specimen (Onderstepoort, near Pretoria). Obtained from T.M. skins 3507 (3♂, 1♀), 4344 (11♂, 16♀) and 7575 (13♂, 8♀).

†*Prolinognathus leptcephalus* (Ehrenberg). From the Onderstepoort hyrax and T.M. skins 3489 and 4344.

T.M. skin 3489 is the holotype of *P. c. coombi*, 4344 is a topotype. Specimens from the Rustenberg and Zoutpansberg areas of the Transvaal, determined by Dr. Roberts as *P. c. coombi*, are kept separate because they have a different louse-fauna.

I am convinced that *Dasyonyx* (*D.*) *ovalis* Bedford is a contamination, and believe it to be an earlier name for *D. (D.) windhuki*. It was described from "males and females" from T.M. skin 3506, but only one male, one female and a nymph in the type series are *ovalis*, the rest being *D. (N.) transvaalensis*.

PROCAVIA CAPENSIS "COOMBSI Roberts." (Rustenburg and Zoutpansberg areas.)

*†*Dasyonyx* (*N.*) *transvaalensis* Bedford. Described from a single female from Rooikrans, Rustenberg (probably from a skin). Later obtained from T.M. skins 1545 (1♀), 1548 (2♂, 3♀), 1805 (1♀), 3569 (3♂, 9♀) and 3570 (2♀).

†*Procaviphilus sclerotis* Bedford. Obtained from T.M. skins 1545 (1♂), 1548 (3♂), 3569 (2♂) and 3570 (1♂). See first note below.

†*Procavicola* (*P.*) *mokeetsi* Bedford. Obtained from T.M. skins 1547 (1♂), 1548 (3♂, 4♀), 1805 (6♂, 5♀), 3568 (3♂, 1♀) and 3569 (9♂, 4♀). See second note below.

†*Procavicola* (*C.*) *lindfieldi* (Hill). From T.M. skins 1548 (3♂, 3♀), 1804 (1♂, 3♀) and 3569 (3♂, 2♀).

†*Prolinognathus caviae-capensis* (Pallas). From T.M. skins 1548 (thirty-five specimens) and 1805, 3568 and 3569 (one each).

†*Prolinognathus leptcephalus* (Ehrenberg). From T.M. skins 1546, 1548 (twenty specimens), 1805, 3568 and 3569.

The males of *Procaviphilus sclerotis* were accompanied by numerous females of which (using the character by which Bedford separated these forms) some were referable to *sclerotis* and some to *P. serraticus* (Hill). Dr. Werneck and I both consider that this means either that there had been gross contamination or that the character by which Bedford separated the females of *sclerotis* and *serraticus* (the degree of development of the sclerotic sternal bar) is unreliable. In view of the fact that the females showed all degrees of transition between the form of sternal bar characteristic of *serraticus* and that found in *sclerotis*, I think it nearly certain that the form of this bar is governed by the degree of sclerotization of the specimen and is quite unreliable as a specific character. Only a single male obtained from these skins was *serraticus*, and this can certainly be regarded as a contamination.

The extraordinary anomaly whereby *Procavicola pretoriensis*, characteristic of *Procavia capensis coombi*, is replaced on specimens from the Rustenburg and Zoutpansberg areas which Dr. Roberts considers to be *coombi* by *Procavicola mokeetsi*, characteristic of *P. c. letabae*, is discussed on p. 421.

PROCAVIA CAPENSIS LETABAE Roberts.

†*Dasyonyx* (*N.*) *transvaalensis* Bedford. From T.M. skins 3043 (1♀), 3276 (1♀), 3981 (2♂, 8♀), 4488 (1♂, 2♀), and 5883 (1♀).

Procaviphilus sclerotis Bedford. Three males from T.M. skin 4488 (records of females ignored for reasons given under last host-form).

*†*Procavicola* (*P.*) *mokeetsi* Bedford. Described from 2♂, 2♀ from T.M. skin 3275; also obtained from T.M. skins 3981 (7♂, 3♀), 4488 (2♂, 7♀), 5881 (3♂, 6♀), 5882 (2♂, 2♀) and 5883 (2♂, 5♀).

Procavicola (*C.*) *lindfieldi* (Hill). A male and a female from T.M. skins 4484 and 4489 respectively.

Prolinognathus caviae-capensis (Pallas). Two specimens from T.M. skin 5881.

Prolinognathus leptocephalus (Ehrenberg). Obtained from T.M. skin 5882. T.M. skin 3043 is the holotype of *letabac*, 3275 and 3276 are paratypes.

PROCAVIA CAPENSIS ? SCHULTZEI Brauer.

Dasyonyx (*D.*) *windhuki* Bedford. A single female from T.M. skin 8338.

*†*Procavicola* (*P.*) *affinis* Werneck. Two males and three females from T.M. skin 8339.

Prolinognathus caviae-capensis (Pallas). Four specimens from T.M. skin 8338.

Dr. Roberts queries the determination of both these skins.

PROCAVIA CAPENSIS WINDHUKI Brauer.

*†*Dasyonyx* (*D.*) *windhuki* Bedford. Described from a long series from a wild host (later determined at the British Museum); obtained in numbers from T.M. skins 9610, 9613, 9614, 9617 and 9618.

†*Procaviphilus serraticus* (Hill). From T.M. skins 9611, 9613, 9614, 9615, 9616, 9617, 9618 and 9619.

Prolinognathus caviae-capensis (Pallas). From T.M. skins 9610, 9613, and 9615 (two, one and three specimens respectively).

Prolinognathus leptocephalus (Ehrenberg). From T.M. skins 9614, 9617 and 9619 (one, two and one specimens).

PROCAVIA CAPENSIS ? REUNINGI Brauer.

†*Dasyonyx* (*D.*) *windhuki* Bedford. From T.M. skins 8335 (4♂, 8♀), 8336 (2♂, 5♀) and 9620 (5♀).

†*Procaviphilus serraticus* (Hill). From T.M. skins 8335 (1♂), 8336 (6♂, 9♀), 9620 (2♂, 4♀) and 9621 (2♂, 4♀).

Prolinognathus caviae-capensis (Pallas). Eleven specimens from T.M. skin 8336 and one each from 9620 and 9621.

Prolinognathus leptocephalus (Ehrenberg). Twenty-two specimens from T.M. skin 8336.

The determination of all these skins is given with a query by Dr. Roberts.

PROCAVIA CAPENSIS WATERBERGENSIS Brauer.

†*Dasyonyx* (*D.*) *windhuki* Bedford. From T.M. skins 8333 (17♂, 12♀), 8334 (1♂, 1♀) and 8335 A (3♂, 2♀).

†*Procaviphilus serraticus* (Hill). From T.M. skins 8333 (2♂, 1♀), 8334 (1♂, 8♀) and 8335 A (1♂, 1♀).

†*Prolinognathus caviae-capensis* (Pallas). In numbers from T.M. skins 8333, 8334 and 8335 A.

†*Prolinognathus leptocephalus* (Ehrenberg). Numerous on the same three skins.

Bedford's statement (1932 *b*, p. 724) that the type series of *Dasyonyx* (*N.*) *waterbergensis* was obtained from this form is erroneous, for Dr. Roberts informs me that the skin from which the lice were obtained (T.M. 5335) is *Heterohyrax welwitschii otjivarongensis*. A single male of *D. waterbergensis* obtained from T.M. skin 8334 represents a contamination.

PROCAVIA JOHNSTONI JOHNSTONI Thomas.

†*Dasyonyx* (*N.*) *nairobiensis* Bedford. Fourteen males and thirty females from T.M. skins 9294 and 9295. Perhaps subspecifically distinct.

†*Procavicola* (*P.*) *thorntoni* Hopkins. Twenty-six males and thirty females from the same two skins.

Prolinognathus caviae-capensis (Pallas). Three specimens from T.M. skin 9294.

†*Prolinognathus leptocephalus* (Ehrenberg). Many specimens from both skins.

PROCAVIA JOHNSTONI MATSCHIEI Neumann.

†*Dasyonyx (N.) nairobiensis* Bedford. Three males and six females from the skin of a freshly-collected topotype.

*†*Procavicola (P.) thornstoni* Hopkins. Seven males and twenty-four females from the same skin.

†*Prolinognathus leptcephalus* (Ehrenberg). Many specimens from the same skin.

The above records are wholly reliable, the skin never having been in contact with any other hyrax-skins after the animal was killed. The skull of this specimen is now A.M.N.M. No. 118748.

PROCAVIA JOHNSTONI MACKINDERI Thomas.

†*Dasyonyx (N.) nairobiensis* Bedford. A large number from one individual from Mount Kenya (specimens sent to Dr. Werneck by Miss Clay). Two males and three females from C.M.M. skin 621A/133.

Prolinognathus leptcephalus (Ehrenberg). A few specimens from C.M.M. skin 621A/133.

PROCAVIA JOHNSTONI LOPESI Thomas and Wroughton.

†*Dasyonyx (N.) nairobiensis* Bedford. Large numbers from several fresh specimens.

*†*Procavicola (P.) lopesi* Bedford. Very large numbers from several fresh specimens.

†*Prolinognathus leptcephalus* (Ehrenberg). Large numbers from several fresh specimens.

The specimens from which the above parasites were obtained were collected at Umi Rocks, East Madi, Uganda, and were determined at the British Museum.

PROCAVIA HABESSINICA ZELOTES Osgood.

*†*Dasyonyx (N.) nairobiensis* Bedford. Described from a long series from a fresh specimen. Two males and two females later obtained from another host-individual, and ten males and six females from another fresh specimen (now A.M.N.H. skin 118749).

†*Procavicola (P.) lopesi* Bedford. Fifteen males and nineteen females from a fresh specimen (now A.M.N.H. skin 118749).

†*Prolinognathus leptcephalus* (Ehrenberg). Many specimens on the host which is now A.M.N.H. 118749.

The specimen which later became A.M.N.H. 118749 was collected by myself and the possibility of contamination was excluded.

PROCAVIA HABESSINICA SCIONA (Giglioli).

**Procaviphilus sclerotis major* Maltbaek. The number of specimens in the type-series is not recorded.

**Procavicola (P.) shoanus* Maltbaek. Described from "one male and several females."

**Prolinognathus aethiopicus* Fahrenholz. One record.

**Prolinognathus arcuatus* Fahrenholz. One record.

The host of all the above was a "*Hyrax shoana* from Abyssinia, that had once been held in the Zoo of Kobenhavn." A host-record of this nature very badly needs confirmation, but Fahrenholz's doubts because of two species of *Prolinognathus* being recorded from the same host are unfounded; the occurrence of two species of this genus on the same host-individual in nature is well-established.

PROCAVIA RUFICEPS BOUNHIOLI Kollmann.

**Prolinognathus foleyi* Fahrenholz. One record, apparently from a wild host.

Order SIRENIA. (Dugongs and Manatees.)

No lice are known from the members of this order, nor is it probable that any could survive on almost hairless aquatic hosts. Dr. Werneck informs me that he has examined several manatees but has found no lice on them.

Superorder **Mesaxonia.**
 Order PERISSODACTYLA.
 Suborder HIPPOMORPHA.
 Superfamily EQUOIDEA.
 Family EQUIDAE.
 Subfamily Equinae.
 Genus EQUUS.
 Subgenus ASINUS.

EQUUS ASINUS Linn. (Ass or Donkey.)

†*Damalinea (Werneckiella) equi* (Denny) (Isch., Tric.) Many records.

*†*Haematopinus a. asini* (Linn.) (synonym: *coloratus*). (An., Hae.) Many records.

(*)†*Ratemia squamulata* (Neumann). (An., Hae.) Described from three females obtained at Dire-Dawa, Ethiopia, "sans indication d'hôte." Obtained in great numbers from a donkey in Uganda.

Single records of *Damalinea bovis* and *Holakartikos pilosus* (Piaget) (= *H. crassipes*) from this host are certainly erroneous, and Piaget's mention of *Equus caballus* in connection with *pilosus* is a quotation from Giebel, whose *pilosus* Piaget thought he was redescribing.

Subgenus Hippotigris.

EQUUS BURCHELLI (Gray). (Common Zebra.)

*†*Damalinea (Werneckiella) ocellata* (Piaget). Original record from a captive; five African records, of which at least three are reliable. Not a synonym of *equi* as has been supposed.

*†*Damalinea (Werneckiella) sp. nov.* One reliable record.

*†*Haematopinus asini minor* Fahrenholz. Several reliable records. Not a synonym of *a. asini*.

*†*Haematopinus acuticeps* Ferris. Two records, at least one reliable.

†*Haematopinus burchelli* Webb.‡ Several reliable records.

†*Ratemia squamulata* (Neumann). Four reliable records.

‡ It seems to me that the difference in head-shape of this form is sufficient to suggest that it should be regarded as a species rather than a subspecies.

Ferris (1920-1935, p. 468) considered it improbable that two distinct species of *Haematopinus* occur on zebras. The occurrence of three perfectly distinct forms is now established, but I have not had *acuticeps* and *burchelli* from the same locality. The two species of *Damalinea* are also not found together.

Subgenus Equus.

EQUUS CABALLUS Linn. (Horse.)

*†*Damalinea (Werneckiella) equi* (Denny) (synonyms: *parumpilosus*, *pilosus* Giebel, *pubescens*, *tarsatus* and *vestitus*). Abundant.

*†*Haematopinus asini macrocephalus* (Burmeister) (synonyms: *equi* and *elegans*). Innumerable records. Ferris considers this a synonym of *asini*.

Records of *Pediculus humanus* on this host are meaningless cases of contamination.

Suborder CERATOMORPHA.

Superfamily TAPIROIDEA.

Family TAPIRIDAE. (Tapirs.)

Dr. Werneck tells me he has unsuccessfully examined a fairly large number of tapirs for lice. As, however, some tapirs are well-clothed with hair and the Eocene forms were very closely related to the contemporary members of the Equoidea, I expect both Mallophaga and Anoplura to be found on tapirs. If the group is really louse-free it is a definite case of secondary absence.

Superfamily RHINOCEROTOIDEA.

There are no reliable records of lice from the rhinoceroses, a single record of *Haematomyzus elephantis* from an Indian rhinoceros (*Rhinoceros unicornis* Linn.) in an Austrian zoo being certainly due to contamination. The almost hairless condition and thick skin of these animals would render survival of lice difficult, though obviously not impossible since the elephants are infested. In this connection, examination of the hair of ice-preserved specimens of the extinct woolly rhinoceros would be of immense interest.

Superorder **Paraxonia**.

Order ARTIODACTYLA.

Suborder SUIFORMES.

Infraorder Suina.

Superfamily SUOIDEA.

Family SUIDAE. (Pigs, Hogs or Swine.)

Subfamily Suinae.

Genus POTAMOCHOERUS.

POTAMOCHOERUS PORCUS (Linn.). (Red River-Hog or Bush-Pig.)

*†*Haematopinus latus* Neumann (synonyms: *incisus* and *latissimus*). (An., Hae.) Many reliable records.

Stobbe's belief that his *Trichodectes vosseleri* came from this host was due to his having been misinformed; the true host is *Mellivora capensis*.

Genus PHACOCHOERUS.

PHACOCHOERUS AETHIOPICUS (Pallas). (Wart-Hog.)

*†*Haematopinus phacochoeri* Enderlein (synonym: *peristictus*). Many reliable records.

Genus HYLOCHOERUS.

HYLOCHOERUS MEINERTZHAGENI Thomas. (Giant Forest-Hog.)

†*Haematopinus* sp. nov. near *latus* and *phacochoeri*. Two reliable records.

Genus SUS.

For the synonymy of lice found on this genus see p. 438.

SUS SCROFA Linn. (European Wild Boar.)

*†*Haematopinus suis apri* Goureaux (synonym: *aperis*). Numerous records from wild hosts. Fahrenholz considers that this form must have been the louse of domestic pigs in Europe during the eighteenth century and therefore calls it *H. s. suis* (Linn.).

Single records of *Linognathus vituli* and *Haematopinus tuberculatus* from this host are probably due to mislabelling but possibly to contamination.

SUS sp. or spp. (European Domestic Pigs.)

*†*Haematopinus suis suis* (Linn.) (synonyms: *chinensis*, *germanicus*, *germanus*, *irritans*, *sardiniensis* and *urius*). Innumerable records.

Records of *Pediculus humanus* from domestic pigs are obvious cases of contamination. Various authors have stated that modern domestic pigs in Europe and America have a large infusion of the blood of *Sus leucomystax*, but this species is the Japanese pig, and I am informed that modern European and American pigs derive their oriental strain from the Chinese pig, which is a subspecies of *S. scrofa*. In the circumstances I can only record the facts and state my belief that much more work is necessary (especially much more collecting of material from wild swine) before we can explain the apparent anomaly of the occurrence of very different forms of *Haematopinus* on wild and tame swine in Europe,

SUS CRISTATA Wagner. (Indian Wild Boar.)

†*Haematopinus suis suis* (Linn.). Four records, different sources, at least one of which appears to be from a wild host.

SUS VITTATUS Müller and Schlegel. (Malayan Banded Pig.)

**Haematopinus suis adventicius* Neumann. One record.

Family TAYASSUIDAE.

Subfamily Tayassuinae.

Genus TAYASSU. (Peccaries.)

TAYASSU PECARI (Fischer). (White-lipped Peccary.)

†*Macrogyropus dicotylis* (Macalister). (Amb. Gyr.) Several reliable records.

TAYASSU TAJACU (Linn.). (Collared Peccary.)

*†*Macrogyropus dicotylis* (Macalister) (synonym: *dentatus*). Several records from wild hosts, different sources.

*†*Peccarococcus javalii* Babcock and Ewing. (An., Hae.) One reliable record.

Infraorder Ancodonta.

Superfamily ANTHRACOTHERIOIDEA.

Family HIPPOPOTAMIDAE.

I have searched two specimens of the common hippopotamus, *Hippopotamus amphibius* Linn., without result and consider it very improbable that this animal, almost hairless and spending a great part of its life in water, has any lice. Lice can tolerate aquatic habits in a well-clothed host or hairlessness in a terrestrial one, but the combination of the two factors is probably fatal to them. Occurrence of lice on the much more terrestrial pigmy hippopotamus, *Choeropsis liberiensis* (Morton) would not be very surprising.

Suborder TYLOPODA.

Family CAMELIDAE.

Subfamily Camelinae.

Genus LAMA.

LAMA HUANACA (Linn.). (Guanaco, Llama and Alpaca.)

*†*Lepikentron breviceps* (Rudow). (Isc., Tric.) (synonyms: *auchenialamae* and *inaequalemaculatus*). Many records, from all three forms.

*†*Microthoracius praelongiceps* (Neumann). (An., Hae.) Many records, from all three forms.

*†*Microthoracius mazzui* Werneck. Many records, from all three forms.

**Microthoracius minor* Werneck. Two records, a pair from an alpaca and a female from a llama.

Genus CAMELUS.

CAMELUS DROMEDARIUS Linn. (One-humped Camel.)

*†*Microthoracius cameli* (Linn.). One record in 1668, another (of abundant material) in 1934!

Haematopinus tuberculatus (Burmeister). Four records from different sources. Certainly contamination in domestication but louse perhaps established.

A single record of *Haematopinus suis* (Linn.) is almost certainly a case of mislabelling.

CAMELUS BACTRIANUS Linn. (Two-humped Camel.)

Torre (1908) gives a record of *Microthoracius cameli* from this host, but appears to have misquoted Gervais (1844), who merely says "chameau".

Suborder *RUMINANTIA*.

Infraorder Tragulina.

Superfamily TRAGULOIDEA.

Family *TRAGULIDAE*. (Chevrotains or Mouse-Deer)Genus *TRAGULUS*.

TRAGULUS KANCHIL (Raffles). (Smaller Mouse-Deer.)

**Damalinia (Tricholiperus)* sp. nov. No. 1. (Isc., Tric.)

TRAGULUS JAVANICUS (Osbeck). (Larger Mouse-Deer.)

**Damalinia (Tricholiperus)* sp. nov. No. 2.

Infraorder Pecora.

Superfamily CERVOIDEA.

Family *CERVIDAE*. (Deer.)Subfamily *Muntiacinae*.Genus *MUNTIACUS*.

MUNTIACUS MUNTJAK (Zimmermann). (Muntjak, Barking Deer or Jungle "Sheep.")

*†*Damalinia (Cervicola)* sp. nov. No. 3. Two records, one reliable.

*†*Solenopotes muntiacus* Thompson. (An., Hae.) Two records from wild hosts.

Subfamily *Cervinae*.Genus *MEGALOCEROS*.

MEGALOCEROS GIGANTEUS (Blumenbach). (Giant Fallow-Deer or Irish "Elk.")

Ferris (1920-1935, p. 397) states that he is inclined to the view that *Solenopotes capillatus* "was originally a deer-infesting form which has transferred to cattle and that it will eventually be found upon some Cervid." Not only do I share this view, but I suggest the probability that if *S. capillatus* is not eventually found upon *Alce alces* (the only existing European deer of which the *Solenopotes* remains unknown) it will be because its original host was *M. giganteus*, now extinct but very common in parts of Europe as late as the Bronze Age. Use of the same rubbing-tree is a possible method for transfer of this louse from deer to domestic cattle.

Genus *DAMA*.

DAMA DAMA (Linn.). (Fallow Deer.)

*†*Damalinia (Cervicola) tibialis* (Piaget) (synonym: *punctum*). Several reliable records.

Genus *AXIS*.Subgenus *Axis*.

AXIS AXIS (Erxleben). (Spotted Deer or Chital.)

†*Damalinia (Cervicola) forficula* (Piaget). Several records, at least one from a wild host.

Subgenus *Hyelaphus*

AXIS PORCINUS (Zimmermann). (Hog-Deer.)

**Damalinia (Cervicola) forficula* (Piaget). One record from a captive.

Genus CERVUS.

Subgenus Rusa.

CERVUS UNICOLOR Kerr. (Sambar.)

**Haemalopinus longus* Neumann. A single record (of two males and fourteen females) which badly needs confirmation but is probably correct, the louse being very unlike any other species of its genus.

Subgenus Rucervus.

CERVUS ELDI Guthrie. (Thamin or Eld's Deer.)

Damalinea (Cervicola) tibialis (Piaget). One record from a captive, doubtless a misdetermination.

Subgenus Sika.

CERVUS NIPPON Temminck. (Sika or Japanese Park Deer.)

Solenopotes sp. near *burmeisteri* (Fahrenheit). One record of many specimens from a captive.

Subgenus Cervus.

CERVUS ELAPHUS Linn. (European Red Deer.)

*†*Damalinea (Rhabdopedilon) longicornis* (Nitzsch) (synonym: *similis*). Many records from wild hosts.

*†*Solenopotes burmeisteri* (Fahrenheit). Six records, several different sources.

CERVUS CANADENSIS Erxleben. (Wapiti.)

*†*Damalinea (Rhabdopedilon) americanus* (Jellison). Many records from wild hosts. Possibly a synonym of *longicornis*.

This host should probably be regarded as a subspecies of *elaphus*.

Subfamily Odocoileinae.

Tribe ODOCOLEINI.

Genus ODOCOILEUS.

ODOCOILEUS VIRGINIANUS (Boddaert). (White-tailed Deer.)

*†*Damalinea (Cervicola) lipeuroides* (Mégnin) (synonyms: *mazama*, *mexicanus*, *virginianus*). Very many records, various sources, including hosts often referred to a different species (*couesi*).

(*)†*Damalinea (Cervicola) parallelus* (Osborn). Original record from unidentified deer believed to be *virginianus*. Two subsequent records from wild hosts and one (Kellogg and Ferris, 1916 *b*, p. 59) from "red deer" in Michigan, which probably means this host.

ODOCOILEUS HEMIONUS Rafinesque. (Mule-Deer and Black-tailed Deer.)

†*Damalinea (Cervicola) lipeuroides* (Mégnin). Three records from wild hosts.

†*Damalinea (Cervicola) parallelus* (Osborn). Eleven records, at least six of them from wild hosts.

*†*Solenopotes ferrisi* (Fahrenheit). Four records, at least two from wild hosts. All the lice are known from both the mule-deer and the black-tail.

ODOCOILEUS CHIRIQUENSIS Allen. (Panama White-tailed Deer.)

**Solenopotes panamensis* (Ewing). One record of a few females from U.S.N.M. skin 240843. Ferris considers this the same as *binipilosus* but I think they should be kept separate, at least until the male of *panamensis* is discovered.

Genus MAZAMA.

MAZAMA AMERICANA (Erxleben). (Red Brocket.)

*†*Damalinia (Cervicola) albimarginata* (Werneck). Four records, at least two reliable.*Solenopotes binipilosus* (Fahrenheit). One record from a wild host.

MAZAMA SIMPLICICORNIS (Illiger). (Grey Brocket.)

†*Damalinia (C.) albimarginata* (Werneck). Two records, at least one reliable.(*?)†*Solenopotes binipilosus* (Fahrenheit). Three records, two from wild hosts; original record from "Mazama Hirsch (*Reducina* spec.)"; original record of *coassus* (which Ferris considers a synonym) from "*Coassus* spec."

MAZAMA SARTORII (Saussure).

Damalinia (C.) albimarginata (Werneck). Two records.

MAZAMA RONDONI Riberio.

†*Damalinia (C.) albimarginata* (Werneck). Four records, at least two reliable.*Solenopotes binipilosus* (Fahrenheit). One record, wild host.

Genus BLASTOCERUS.

BLASTOCERUS BEZOARTICUS (Linn.). (Pampas Deer.)

**Damalinia (Cervicola) dorcelaphi* (Werneck). One record, probably reliable.Simpson places this species in *Ozotoceras* but admits to much misgiving. I consider such changes should not be made on doubtful grounds.

Tribe ALCINI.

Genus ALCE.

ALCE ALCES (Linn.). (Elk or Moose.)

Olsen and Fenstermacher (1942) summarize the results of examinations for parasites of a large number of specimens of the European elk and its American subspecies, the moose (*Alce alces americanus*). No lice have been recorded from either form, but many of the searches were primarily for internal parasites and it is most improbable that the apparent absence of lice is genuine. The elk is one of the two possible original hosts of *Solenopotes capillatus*, now known only from domestic cattle.

Tribe RANGIFERINI.

Genus RANGIFER.

RANGIFER TARANDUS (Linn.). (Reindeer and Caribou.)

*†*Damalinia (Rhabdopedilon) tarandi* (Mjöberg). Four records, three different sources, two from each host-form.*†*Solenopotes tarandi* (Mjöberg). Two probably reliable records.

Tribe CAPREOLINI.

Genus CAPREOLUS.

CAPREOLUS CAPREOLUS (Linn.). (Roe Deer.)

†*Damalinia (Cervicola) meyeri* (Taschenberg). Many records, almost all under the misdetermination *tibialis* Piaget.

Superfamily GIRAFFOIDEA.

Family GIRAFFIDAE.

Subfamily *Palaeotraginae*.

Genus OKAPIA.

OKAPIA JOHNSTONI (P. L. Sclater). (Okapi.)

I have unsuccessfully dissolved the hair of small portions of one wild skin.

Subfamily *Giraffinae*.

Genus GIRAFFA.

GIRAFFA CAMELOPARDALIS (Linn.) (Common Giraffe.)

*†*Linognathus brevicornis* (Giebel). (An., Hae.) Two records from captives in Europe, one (in enormous numbers) from a recently-captured host in Kenya, and two from wild skins in Tanganyika.

Superfamily BOVOIDEA.

Family BOVIDAE.

Subfamily Bovinae.

Tribe STREPSICEROTINI.

Genus STREPSICEROS.

Subgenus *Strepsiceros*.

STREPSICEROS STREPSICEROS (Pallas). (Greater Kudu.)

Damalinia (D.), sp. nov. No. 4. One probably reliable record.

Haematopinus taurotragi Cummings. One record.

Linognathus sp. One reliable record.

Subgenus *Tragelaphus*.

STREPSICEROS ANGASII (Gray). (Nyala.)

Damalinia (D.), sp. nov. No. 5. One record from a wild skin.

Linognathus sp. Two records from wild skins.

STREPSICEROS SCRIPTUS (Pallas). (Bushbuck.)

*†*Damalinia* (D.) *annectens* Hopkins. Many reliable records.

*†*Linognathus fractus* Ferris. Many reliable records.

†*Linognathus limnotragi* Cummings. Many reliable records.

STREPSICEROS SPEKII (P. L. Selater). (Situtunga.)

†*Damalinia* (D.) *annectens* Hopkins. One reliable record.

†*Linognathus fractus* Ferris. Two reliable records.

*†*Linognathus limnotragi* Cummings. Three reliable records.

The bushbuck and situtunga are often placed in different genera and Simpsen retains *Limnotragus* as a subgenus, but I believe them to be very closely related and certainly not even subgenerically distinct. The situtunga on Nkosi Island in Lake Victoria, on which there is little papyrus-swamp, have reverted to a bushbuck mode of life and their hoofs have become like those of bushbuck. Furthermore, a doe of a bushbuck-situtunga cross, bred at Entebbe, was mated with a situtunga ram, and on dissection after accidental death was found to be pregnant. This latter observation suggests the two forms being conspecific, since hybrids (unlike mongrels) are usually sterile, but the differences are rather too great for this suggestion to be probable.

Genus TAUROTRAGUS.

Subgenus *Taurotragus*.

TAUROTRAGUS ORYX (Pallas). (Eland.)

*†*Damalinia* (D.) *hopkinsi* Bedford. One reliable record.

*†*Haematopinus taurotragi* Cummings. Five records, some from wild hosts.

*†*Linognathus taurotragus* Bedford. Five records from wild hosts.

TAUROTRAGUS DERBIANUS (Gray). (Giant Eland.)

Linognathus, sp. nov. near *taurotragus*. A long series from a captive in Khartoum zoo.

Tribe BOVINI.

Genus BUBALUS.

BUBALUS BUBALIS (Linn.). (Indian Buffalo.)

*†*Haematopinus tuberculatus* (Burmeister). Numerous records. It seems nearly certain that *H. bufali-europaei* (Latreille) is an earlier name for this species.

A single record of *Haematopinus s. suis* is probably an instance of mislabelling, but the habit of both buffalos and pigs of using mud-wallows makes natural straggling a possible explanation.

Genus Bos.

Subgenus Bos.

BOS TAURUS Linn. (Domestic Ox.)

*†*Damalinia (Bovicola) bovis* (Linn.) (synonyms : *scalaris* and *tauri*). Very many records.

*†*Haematopinus eurysternus* Nitzsch. Abundant.

*†*Linognathus vituli* (Linn.) (synonyms : *oxyrrhynchus* and *tenuirostris*). Very many records.

*†*Solenopotes capillatus* Enderlein. Many records. Doubtless once a deer-parasite (see p. 523), but now definitely established.

BOS INDICUS Linn. (Zebu or Humped Cattle.)

Haematopinus eurysternus Nitzsch. Two apparently reliable records.

Piaget described *Haematopinus penicillatus* from this host, but the record is due to contamination in Rotterdam zoo. Ferris (1920-1935, p. 428) considers the name a synonym of *Haematopinus suis*, but Ewing (1934 b) states that Piaget's description and figure represent a form of *Haematopinus tuberculatus*. Possibly the specimens seen by Ferris were not the types.

Fahrenholz's two supposed species, *Haematopinus quadripertusus* (from *Bos*, sp.) and *H. parviprocursus* (assumed to be from *Bos*, sp.) are the sexes of one species which Ferris finds inseparable from *H. eurysternus*. As they are from Africa the host must have been either *Bos indicus* or *Bos taurus*, probably the former.

Subgenus Poëphagus.

BOS GRUNNIENS Linn. (Yak.)

**Haematopinus punctatus* Rudow. A single record, probably due to contamination in a zoo. Ferris saw the types and found them inseparable from *H. tuberculatus*.

Genus SYNCERUS.

SYNCERUS CAFFER (Sparrman). (African Buffalo.)

*†*Haematopinus bufali* (De Geer) (synonyms : *bufali-capensis*, *neumannii* and *phthiriopsis*). Numerous reliable records.

A single record of *Haematopinus phacochoeri* is possibly due to natural straggling via a mud-wallow, more probably mislabelling or contamination. A record of *H. tuberculatus* from a captive is certainly due to contamination.

Genus BISON.

BISON BISON (Linn.). (American Bison or "Buffalo.")

A single record of *Haematopinus tuberculatus* is probably a case of contamination in a zoo. Cameron (1923) records examination of 250 individuals without any lice being found, but this is by no means conclusive since only the searching technique was employed.

BISON BONASUS (Linn.). (European Bison or Wisent.)

**Damalinia (Bovicola) sedecimdecembrii* (Eichler). One almost certainly reliable record.

Subfamily *Cephalophinae*.

Tribe CEPHALOPHINI.

Genus CEPHALOPHUS.

- CEPHALOPHUS SYLVICULTOR (Afzelius). (Yellow-backed Duiker.)
Linognathus, sp. nov. A few females from a wild skin (C.M.M. No. 657 A/3422).
- CEPHALOPHUS NATALENSIS A. Smith. (South African Red Duiker.)
Linognathus gazella Mjöberg. One record of many specimens, apparently from a wild host. This louse has no proper type-host, the original record being "von einer Gazelle." It seems certain that the host was a duiker and not a gazelle.
- CEPHALOPHUS NIGRIFRONS Gray. (Black-fronted Duiker.)
 *†*Damalinia (Tricholipeurus) hendrickxi* Hopkins. Two reliable records.
 *†*Linognathus unguatus* (Piaget) (synonym: *anguatus*). Two records, one of them reliable.
- CEPHALOPHUS HARVEYI Thomas. (Harvey's Red Duiker.)
Linognathus sp. near *gazella*. One record of three males and two females from a wild skin.
- CEPHALOPHUS ADERSI Thomas. (Zanzibar Red Duiker.)
 *†*Damalinia (Tricholipeurus) pakenhami* (Werneck). One reliable record
 †*Linognathus* sp. near *gazella*. One reliable record.

Genus PHILANTOMBA.

- PHILANTOMBA MAXWELLI (Hamilton-Smith). (Maxwell's Duiker.)
 **Linognathus breviceps* (Piaget). One record, no details.
- PHILANTOMBA CAERULEA (Hamilton-Smith). (Blue Duiker.)
 **Damalinia (Tricholipeurus) bedfordi* (Hill). One record from a wild host.
 †*Damalinia (Tricholipeurus) pakenhami* (Werneck). Numerous records from wild hosts.
 †*Linognathus gazella* Mjöberg. Many records from wild hosts.

Genus SYLVICAPRA.

- SYLVICAPRA GRIMMI (Linn.). (Common or Brown Duiker.)
 **Damalinia (Tricholipeurus) lerouxi* (Bedford). Two records from wild hosts.
 †*Damalinia (Tricholipeurus) pakenhami* (Werneck). Several records from wild hosts.
 †*Linognathus gazella* Mjöberg. Many records from wild hosts.

Subfamily *Hippotraginae*.

Tribe REDUNCINI.

Genus KOBUS.

- KOBUS ELLIPSIPRYMNUS (Ogilby). (Waterbuck.)
 *†*Damalinia (Bovicola) hilli* (Bedford). Many reliable records.
K. ellipsiprymnus and *K. defassu* (Rüppell) are usually considered distinct species, but their ranges are purely geographical and in Kenya, where they meet, they interbreed and form intermediate herds. The louse occurs on both forms.

Genus ADENOTA.

ADENOTA KOB (Erxleben). (Kob.)

*†*Damalinea (Bovicola) adenota* (Bedford). Many reliable records.

ADENOTA VARDONII (Livingstone). (Puku or Puku Kob.)

†*Damalinea (Bovicola) adenota* (Bedford). One reliable record.There does not seem to be any obvious reason why *A. vardonii* should be considered specifically distinct from *A. kob*.

Genus ONOTRAGUS.

ONOTRAGUS LECHE (Gray). (Lechwe.)

**Damalinea (Bovicola) martinaglia* (Bedford). One record from a captive.

Genus REDUNCA.

REDUNCA ARUNDINUM (Boddaert). (Reedbuck.)

*†*Damalinea (Tricholipeurus) reduncae* (Bedford). Three records, different sources, at least one reliable.*†*Linognathus fahrenheitzi* Paine (synonym: *forficula* Kellogg and Paine). Three records, different sources, at least one reliable.

REDUNCA REDUNCA (Pallas). (Bohor Reedbuck.)

†*Damalinea (T.) reduncae* ssp. Many reliable records.†*Linognathus fahrenheitzi* Paine. Many reliable records.

REDUNCA FULVORUFULA (Afzelius). (Mountain Reedbuck.)

*†*Damalinea (Tricholipeurus) trabeculae* (Bedford). Two records, at least one reliable.†*Linognathus fahrenheitzi* Paine. Two records, one (or both) reliable.

Genus PELEA.

PELEA CAPREOLUS (Bechstein). (Vaal Rhebok.)

*†*Damalinea (Bovicola) pelea* (Bedford). One reliable record.*†*Linognathus pelcus* Bedford. One reliable record.

Tribe HIPPOTRAGINI.

Genus HIPPOTRAGUS.

HIPPOTRAGUS NIGER (Harris). (Sable Antelope.)

**Linognathus hippotrangi* Ferris. One record from a captive.

HIPPOTRAGUS EQUINUS (Desmarest). (Roan Antelope.)

Linognathus, sp. nov. near *hippotrangi*. Three pairs from a wild skin.Neumann (1913, p. 626) recorded as *Trichodectes cornutus* some over-cleared specimens of *Damalinea* which he stated were from "Blaubock (*Hippotragus equinus*)", from the Hyslop collection. As the blaauwbok, *Hippotragus leucophaeus* (Pallas), became extinct about 1799, it seems certain that the roan antelope was the species meant. In any case the record is almost certainly a misdetermination, many different species of Trichodectidae from antelopes having been miscalled *cornutus* by authors.

Tribe ALCELAPHINI.

Genus DAMALISCUS.

DAMALISCUS PYGARGUS (Pallas). (Bontebok and Blesbok.)

*†*Damalinea (D.) crenelata* (Piaget). Five records, different sources.*†*Linognathus damaliscus* Bedford. Three records, different sources.

The bontebok and blesbok had ranges separated by the Orange River and in semi-captivity they interbreed freely, producing fertile and intermediate offspring; they are obviously geographical forms of one species. Both the lice were described from the blesbok but occur on both forms of the host.

DAMALISCUS KORRIGUM (Ogilby). (Topi, Korrigum or Tiang.)

- *†*Damalinea (D.) baxi* Hopkins. Three records, at least one reliable.
Linognathus damaliscus ssp. Three males from one wild skin.

Genus ALCELAPHUS.

ALCELAPHUS BUSELAPHUS (Pallas). (Bubal Hartebeest or Kongoni.)

- *†*Damalinea (Bovicola) chorleyi* (Hopkins). Several reliable records.

Allen places the *cokii* and *lehwel* groups as forms of one species, but as this is not universally accepted it may be as well to mention that all the records are from a *lehwel* form.

ALCELAPHUS CAAMA (G. Cuvier). (Cape Hartebeest.)

The original record of *Linognathus antennatus* (Piaget) was from "*Antilope*, sp." in Rotterdam zoo, but Ferris states that the types are labelled as being from *Antilope caama*. Ferris considers *antennatus* inseparable from *tibialis*, in which case the record must be due to either mislabelling or contamination.

ALCELAPHUS LICHTENSTEINI (Peters). (Lichenstein's Hartebeest.)

One wild skin examined by the dissolving technique but no lice found.

Genus CONNOCHAETES.

CONNOCHAETES GNOU (Zimmermann). (Black Wildebeest or White-tailed Gnu.)

- *†*Damalinea (Bovicola) harrisoni* (Cummings). Three records, different sources.
 **Linognathus gnu* Bedford. One record of two females, apparently from a wild host.

Genus GORGON.

GORGON TAURINUS (Burchell). (Blue Wildebeest or Brindled Gnu.)

- *†*Damalinea (D.) theileri* Bedford. Two records, different sources.
Haematopinus sp. near *taurotragi*. Two females from a wild skin.
 *†*Linognathus gorgonus* Bedford (synonym: *ferrisi* Bedford). Three records, different sources.
 **Linognathus hologastrus* Werneck. One record of two pairs, apparently from a wild host.
 *†*Linognathus spicatus* Ferris. Two records, different sources.

The occurrence of three species of one louse-genus on one host-species is unusual and needs confirmation, but several parallel cases are well-established.

Subfamily *Antilopinae*.

Tribe NEOTRAGINI.

Genus OREOTRAGUS.

OREOTRAGUS OREOTRAGUS (Zimmermann). (Klipspringer.)

- *†*Damalinea connectens* Hopkins. Two reliable records.
 A single record of *Linognathus oviformis* (Rudow) is probably due to contamination.

Genus OUREBIA.

OUREBIA OUREBI (Zimmermann). (Common Oribi.)

- *†*Damalinea (Tricholipeurus) ourebiae* Hopkins. Numerous records from wild hosts.
 †*Linognathus* sp. near *gazella*. Several reliable records.

Genus RAPHICERUS.

RAPHICERUS CAMPESTRIS (Thunberg). (Common Steinbok.)

- *†*Damalinea (Tricholipeurus) lineata* (Bedford). Three records, wild hosts
 †*Linognathus* sp. near *gazella*. One reliable record.
 ▲ record of *D. bedfordi* is almost certainly due to mislabelling.

RAPHICERUS SHARPEI Thomas. (Sharpe's Steinbok.)

†*Damalinia (T.) lineata* (Bedford). Very large numbers from one wild skin.

Genus NEOTRAGUS.

NEOTRAGUS PYGMAEUS (Linn.). (Royal Antelope.)

**Damalinia (Tricholipeurus) clayi* (Werneck). Two records, one apparently from a wild host.

Genus RHYNCHOTRAGUS.

RHYNCHOTRAGUS KIRKII (Günther). (Kirk's Long-snouted Dik-dik.)

*†*Damalinia (Tricholipeurus) victoriae* Hopkins. Five reliable records.

†*Linognathus* sp., probably new. Several reliable records.

The chief character used for the separation of *R. kirkii* and *R. guentheri* intergrades completely. Both lice occur on both forms.

Tribe ANTILOPINI.

Genus ANTILOPE.

ANTILOPE CERVICAPRA Linn. (Blackbuck.)

*†*Damalinia (Tricholipeurus) balanica* (Werneck). Three records, two different sources.

*†*Linognathus cervicaprae* (Lucas). Two records, different sources.

*†*Linognathus pithodes* Cummings. Four records, three different sources.

Genus AEPYCEROS.

AEPYCEROS MELAMPUS (Lichtenstein). (Mpala.)

*†*Damalinia (Tricholipeurus) elongata* (Bedford). Several reliable records.

**Damalinia (T.) aepyceros* (Bedford). One record, wild host.

*†*Linognathus aepycerus* Bedford. Four records from wild hosts.

There is some doubt about the host of *D. aepyceros*. Bedford first stated it was *Aepyceros melampus*, but on discovering *D. elongata* he considered that the host of *D. aepyceros* must have been *A. petersi*; the latter, however, is only a subspecies of *A. melampus*. The occurrence of two species of *Damalinia* on one host-species is uncommon, but cf. *Capra hircus* and *Odocoileus hemionus*.

Genus LITOCRANIUS.

LITOCRANIUS WALLERI (Brooke). (Gerenuk.)

Damalinia (Tricholipeurus), sp. nov. No. 6. One female from a wild skin.

Linognathus sp. A short series from the same skin.

Genus GAZELLA.

GAZELLA ARABICA Lichtenstein. (Arabian Gazelle.)

**Damalinia (Tricholipeurus) longiceps* (Rudow). One record, probably from a captive.

A record of *D. appendiculata* from a captive in London zoo is probably due to contamination.

GAZELLA DORCAS (Linn.). (Dorcas Gazelle.)

*†*Damalinia (Tricholipeurus) cornuta* (Gervais). Three records from captives, different sources.

Linognathus stenopsis (Burmeister). One record from a captive, probably misdetermination.

GAZELLA SUBGUTTUROSA Guldenstadt. (Persian Gazelle.)

*†*Damalinia (Tricholipeurus) appendiculata* (Piaget). Several records, different sources.

**Linognathus tibialis appendiculatus* (Piaget). One record from a captive. Ferris considers this inseparable from *tibialis*.

GAZELLA GRANTI Brooke. (Grant's Gazelle).

- *†*Damalinia (Tricholipeurus) spinifer* Hopkins. Many reliable records.
 †*Linognathus* sp. near *tibialis*. Many reliable records.

GAZELLA DAMA (Pallas). (Nanger, Dama, Mhorr or Addra Gazelle.)

Piaget (1880, p. 646) described *Linognathus tibialis* from specimens obtained from "Antilope maori" in Rotterdam zoo. There is apparently no antelope with this specific or subspecific name and I suggest the probability that the animal may have been *Antilope mhorr*, now known as *Gazella dama mhorr* (Bennett).

GAZELLA THOMSONI Günther. (Thomson's Gazelle.)

- *†*Damalinia (Tricholipeurus) parkeri* (Hopkins). Five reliable records.
 *†*Linognathus lewisi* Bedford. Three records from wild hosts.
 †*Linognathus*, sp. nov. near *tibialis*. Several records from wild hosts.

Genus ANTIDORCAS.

ANTIDORCAS MARSUPIALIS (Zimmermann). (Springbok.)

- *†*Damalinia (Tricholipeurus) antidorcas* (Bedford). Three records, different sources.
 **Linognathus bedfordi* Ferris. One record.
 *†*Linognathus tibialis euhore* Waterston. Several records from different sources. Ferris considers this inseparable from *tibialis*.

Subfamily Caprinae.

Tribe SAIGINI.

Genus SAIGA.

SAIGA TATARICA (Linn.). (Saiga Antelope.)

- Damalinia (Tricholipeurus) cornuta* (Gervais). One record from a captive, doubtless a misdetermination.

Tribe RUPICAPRINI.

Genus NAEMORHEDUS.

NAEMORHEDUS GORAL (Hardwicke). (Grey Goral.)

- (?*)*Damalinia (Bovicola) dimorpha* (Bedford). Two records from "wild goat", Hangchow, China.

It seems most improbable, from the distinctive characters of *Damalinia dimorpha*, that the host was a true goat. Serow and grey goral occur in the Hangchow neighbourhood, and I suggest the probability that the host was the latter species.

Genus CAPRICORNIS.

CAPRICORNIS SUMATRAENSIS (Bechstein). (Serow.)

- **Damalinia (Bovicola) thompsoni* (Bedford). One record, apparently from a wild host.

Genus RUPICAPRA.

RUPICAPRA RUPICAPRA (Linn.). (Chamois.)

- *†*Damalinia (Bovicola) alpina* (Kéler) (synonym: *rupicaprae*). Three records, different sources, one in great numbers.
 **Linognathus schistopygus* (Nitzsch) (synonym: *rupicaprae*). Two records, different sources. Ferris considered this a synonym of *stenopsis* but had not seen males.

A single record (without details) of *Damalinia (B.) caprae* from this host may be due to contamination or to misdetermination of *D. alpina*.

Tribe CAPRINI.

Genus HEMITRAGUS.

HEMITRAGUS JEMLAICUS (Hamilton-Smith). (Tahr.)

**Damalinea (Bovicola) hemitragi* (Cummings). One record of 13 females from a captive.

Genus CAPRA.

CAPRA IBEX Linn. (European Ibex.)

**Linognathus stenopsis forficulus* (Rudow). One record. Ferris considers this inseparable from *stenopsis*.

CAPRA HIRCUS Linn. (Domestic Goat.)

*†*Damalinea (Bovicola) caprae* (Gurlt) (synonyms: *climacium*, *climax*, *mambriacus* and *solidus*). Very many records.

*†*Damalinea (Bovicola) limbata* (Gervais) (synonyms: *madagascariensis*, *major*, *sachtlebeni* and *wernecki*). Very many records.

*†*Holakartikos crassipes* (Rudow) (synonyms: *hermsi*, *penicillatus* and *pilosus* Piaget). Many records.

*†*Linognathus oviformis* (Rudow). Many records.

*†*Linognathus stenopsis* (Burmeister). Many records.

Schömmmer's *Trichodectes baculus* was described from material stated to have been obtained from several goats in Upper Bavaria, but I do not believe it to be a goat-parasite. It appears to be either a tricholipeuroid *Damalinea* or a member of the subgenus *Cervicola*.

The distribution of the goat-parasites is very peculiar. *Damalinea caprae* appears to be normally confined to common goats and to be found on Angora goats (*C. hircus angorensis* Shaw) only when these have been in contact with the common form; the same applies inversely to *D. limbata* (described from the Angora form), while *Holakartikos crassipes* is only known from Angora goats. These facts could be explained either by a polyphyletic origin of our tame goats (the common and Angora forms having separate wild ancestors) or by the difference in coat-texture having favoured the survival on each strain of different members of a multiple infestation, but mammalogists whom I have consulted are not inclined to accept the former suggestion. A similar phenomenon occurs in the case of the two species of *Linognathus*: the only species recorded in Europe is *L. stenopsis*, but the only species I have encountered on native goats in Kenya and Uganda is *L. africanus* Kellogg and Paine, which I therefore assume to be a synonym of *L. oviformis* (Rudow), which was described from material obtained from a West African goat. I have not been able to discover whether common and Angora goats have different species of *Linognathus*. "Merino" goat (Kellogg and Nakayama, 1915) is an obvious slip for Angora goat.

The "Bouc d'Égypte", in a zoo, from which Gervais described *Linognathus saccatus*, has been mistranslated as "*Capra aegyptiaca*", but there is not the slightest warrant for assuming the host to have been a goat, and the host of *saccatus* will always remain unknown unless the types are still in existence.

Genus AMMOTRAGUS.

AMMOTRAGUS LERVIA (Pallas). (Barbary Sheep, Arui or Udad.)

*†*Damalinea (Werneckiella) neglecta* Kéler. Three records, different sources.

A single record of *D. ovis* from a captive specimen of this host may have been a zoo-contamination or perhaps a misidentification of *D. neglecta*.

Genus OVIS.

OVIS MUSIMON Linn. (Mouflon.)

Damalinea (Bovicola) ovis (Schränk.) Two records, at least one from a captive.

OVIS ARLES Linn. (Domestic Sheep.)

*†*Damalinea (Bovicola) ovis* (Schränk) (synonym: *sphaerocephalus*). Abundant.

Holakartikos crassipes (Rudow). Two records, one of a heavy infestation. Doubtless secondary but possibly established.

*†*Linognathus ovillus* (Neumann). Many records. Occurs mainly on the head and body, though also on the legs.

*†*Linognathus pedalis* (Osborn) (synonym: *microcephalus*). Many records. Apparently occurs exclusively on the legs of the host.

*†*Linognathus africanus* Kellogg and Paine. Six records (all from Africa), which ought perhaps to be transferred to the next host.

A single record of very many specimens of *Microthoracius praelongiceps* (Neumann), presumably from many host-individuals, may mean that this louse, whose true host is *Lama glama*, has established itself on sheep running in mixed flocks with llamas or alpacas, but the possibility of mislabelling cannot be excluded. A single record of *L. stenopsis* (Burmeister) is very probably erroneous.

The case of *Linognathus africanus*, which I consider to be a synonym of *L. ociformis* (Rudow), is a peculiar one. Finding it abundantly on goats in Uganda, and in view of the difficulty of distinguishing certain breeds of sheep and goats, I believed it to have been originally a goat-parasite which had perhaps become established on sheep after contamination in the distant past, but Fahrenholz's discovery that it occurs freely on *Ovis longipes* makes this belief less tenable. The opportunities for contamination (and subsequent establishment) among parasites of two common domestic animals which are closely related and often kept in mixed flocks are obvious, but the question will perhaps be cleared up by careful collecting from wild sheep and goats.

OVIS LONGIPES Shaw. (Long-legged Sheep.)

†*Linognathus africanus* Kellogg and Paine. Several records, wild and tame hosts.

Fahrenholz (1939*a*, p. 36) regards the occurrence of this louse on the present host (which is regarded by some authors as a subspecies of *Ovis aries*) as indicating that records from goats are erroneous. He may be right in his belief that sheep were the original hosts of *L. africanus*, but I have collected the species in numbers on several occasions from undoubted goats in Uganda, as well as from sheep.

UNDETERMINED BOVIDAE.

Haematopinus breviculus Fahrenholz was described from a single female without record of either host or locality; its form suggests that it is probably a parasite of the Bovidae rather than of the Equidae or Suidae.

IV. LICE AND THE PHYLOGENY OF THEIR HOSTS.

Jordan (1942, p. 27) wrote, with special reference to fleas, "the parasites adapted to a host are a part of the host and, as a rule, being more conservative in their morphology than their host, may sometimes be a better guide to the study of the ancestral history of the host than fur or feathers." This statement applies still more strongly to the case of the lice because of the extremely specific nature of their host-associations and the great rarity of anomalies in these associations. In my opinion (and I know of no modern writer on lice who opposes this view) the facts set out on pages 419-423 admit of only one explanation: that, in the vast majority of instances, lice were present on the original ancestors of the groups of mammals and birds on which we find them today, and that the lice have diverged as their hosts have diverged, though usually more slowly. I have pointed out elsewhere (Hopkins, 1942*a*), as have many other authors before me (see Metcalf, 1929), the value of this relative slowness of the evolution of the parasites in enabling us to draw useful deductions as to the relationships and phylogeny of their hosts.

The existence of secondary absence entails the use of very great caution in making phylogenetic deductions from the distribution of lice, because we dare not argue much from the fact that the lice occurring on the hosts under consideration may not be closely related. Nor must we forget the occasional cases of secondary infestation, in spite of their great rarity, and we must cease building theories on records which are doubtful or even certainly erroneous. Notwithstanding these difficulties, however, much useful information about host-relationships may be deduced from the lice: the occurrence of very closely related lice on two hosts is an excellent, though not infallible, indication that the hosts are

themselves related, and multiplication of the instances of correspondence between the lice of two hosts very greatly increases the significance of the evidence. From the very close relationship between their lice, coupled with the difference of these lice from other species of the same group of *Felicola*, I had deduced that *Suricata* and *Mungos* are more closely related to one another than to the other genera of mongooses from which similar lice are known before I was aware that Roberts (1923, p. 192) had placed them close together on completely different grounds, and it is permissible to state that the obviously close relationship between the lice of these two genera and that of *Proteles* suggests (but no more) that they may be nearer to the hyaena-stock than are the other mongooses. In this instance the evidence is weak because only one species of louse on each host is involved, but in a second example the evidence is immensely stronger. The bushbuck and situtunga, often placed in different genera, are both infested, normally and in nature, by precisely the same three species of lice: this seems to me to be conclusive proof that these two antelopes are exceedingly closely related—far more closely than, for instance, the different species of *Gazella*. Here, again, there is independent evidence in favour of the suggested close relationship (p. 526).

But, since the possession by different hosts of closely related lice indicates a very strong probability that the hosts themselves are related, it follows that the common stock from which both hosts diverged must also in most cases have been infested with similar lice. Since the approximate age of many of the host-groups is known from the evidence of fossils, we can use this argument to deduce the antiquity of any given group of lice, and this will be done in a later section of this paper.

V. DISCUSSION OF THE HOST-LIST.

(1). GENERAL.

The class Mammalia is apparently descended from the Ictidosaurian reptiles, which lived during the later part of the Triassic period and which were themselves derived from the Bauriamorpha of the earlier part of the Triassic. The most ancient known mammalian fossils are from the Upper Triassic and are regarded by Simpson as not to be placed with confidence in any subclass. Their only importance to our present theme is that they prove that mammals were in existence during the period. Similarly, the Multituberculata (known from the Jurassic period and possibly earlier but now wholly extinct) are of little interest to us because they “probably represent one or more lines derived from the Reptilia independently of other known mammals, but nevertheless derived from the same limited reptilian stock” (Simpson, p. 169) and because they do not seem to have given rise to any of the extant groups of mammals. The Pantotheria, on the other hand, whose most ancient known remains are from Jurassic strata, are believed to be very close to the common stock which gave rise to modern marsupials and placentals.

All living mammals fall into the two subclasses Prototheria and Theria, of which the former contains the Monotremata or egg-laying mammals and the latter the Metatheria or marsupials and the Eutheria or placentals. The Monotremata are of very obscure origin; they may have “evolved independently . . . from a very early period of mammalian history, perhaps even from the reptilian ancestry” (Simpson, p. 168) or they may be derived from very early marsupials.

The marsupials and placentals are apparently both derived from the Pantotheria and are not far apart either in origin or in time of appearance, the marsupials and first placentals seeming to have diverged from one another early in the Cretaceous period, while about the middle of the same period the first placentals split up into the main branches which later re-divided to form the modern orders of mammals. Early in the following period (the Eocene) the

placentals were already dominant and all the larger orders of living placental mammals were already extant; the smaller orders were doubtless also in existence, though a few are not known as fossils from the Eocene strata. Further details will be mentioned under the headings of the various orders.

(2). MONOTREMATA.

Practically nothing is known as to the origin of the Monotremata, all the fossils referable with certainty to this subclass being of quite recent date (Pleistocene). In view of our lack of knowledge as to the origin of the monotremes and as to whether they are louse-infested, the group will not be discussed further.

(3). MARSUPIALIA.

Here, again, our knowledge is rather meagre, but marsupial remains are found in the Upper Cretaceous, and during the Eocene and Oligocene periods most of the marsupials were already referable to existing families. No remains definitely referable to the Marsupialia are known from formations earlier than the Cretaceous, and it seems possible that they arose from the Pantotheria very early in that period. Recent work suggests that marsupials may have arrived in Australia during the Cretaceous period.

From the list on pages 439-442 it would seem at first sight that our knowledge of the louse-fauna of the marsupials is rather good, but actually this is not the case. We know very little about the forms found on American marsupials, and (as pointed out by Werneck and Thompson) a very high proportion of the known material from Australian forms has been collected from animals in captivity and therefore exposed to contamination, so that confirmation of most of the records is much needed. Furthermore, Werneck (1941a, p. 54) has pointed out that under the name *Heterodoxus longitarsus* (Piaget) are comprised a number of species which he considers should not be named until more reliable material is available.

At the same time, the list is sufficient to give us a fairly clear picture of the louse-fauna of the group as a whole. No sucking lice are known from the marsupials and their Mallophaga all belong to the more primitive suborder, Amblycera. The distribution on marsupials of the latter group of lice is peculiar and interesting, the Boopidae occurring only on Australian marsupials, whereas the Trimenoponidae occur on South American marsupials and also on certain South American rodents. To the statement just made there is one curious exception: *Heterodoxus spiniger* (Enderlein), very closely related to the kangaroo-parasite *H. longitarsus* (Piaget) (with which it was long confused), has at some time transferred to the dog (perhaps through the intervention of the dingo), and has been carried to many parts of the world with its new host; that the transfer is no affair of recent date is indicated by the fact that the parasite has become specifically distinct. The very ancient nature of the occurrence of Boopidae on the Australian marsupials is proved by the fact that they have differentiated into seven genera, comprised in two subfamilies.

The case of the Trimenoponinae* is puzzling and of such importance that it must be considered at some length. Since it seems improbable (though not impossible) that the infestation of Marsupialia and Rodentia by this subfamily dates back to a common ancestor of these two host-groups, it must be assumed that the infestation of one of the groups is secondary. Ewing (1929, p. 94) boldly puts forward as fact the assumption that the American marsupials derived their Trimenoponinae from rodents, but I am in no way inclined to accept this view without conclusive proof, and in my opinion such proof is

* This group has usually been regarded as a family but Werneck (1948) does not consider it deserving of this rank. I have no particular views on this point, but the three genera referred to the group are apparently more closely related to each other than to other Amblycera and I am calling them the Trimenoponinae merely to have a group-name for them

altogether wanting. The two tests which we can apply are the sporadic or general occurrence of the parasites on the orders concerned and the relationships of the parasites themselves.

Of the three known genera of the Trimenoponinae, *Cummingsia* occurs on all three genera of South American marsupials from which any records are available (Dr. Werneck tells me that the larger species apparently have no lice and that lice are very rare on the small species). *Trimenopon* has a distinctly sporadic distribution: it occurs on the rodent families Chinchillidae and Caviidae, but (in the latter case, at least) apparently only on a very small proportion of the species, though on these there is no doubt that it is established*. It is certainly not significant that Werneck (1936*b*, p. 477) records finding *Trimenopon hispidum* in large numbers on a marsupial, *Metachirus opossum*, because this louse was in company with other guineapig parasites and the host was a captive. The remaining genus, *Harrisonia*, is monotypical and was described from three single specimens collected from museum-skins of two genera (*Hoplomys* and *Proechimys*) of echimyid rodents; Werneck (1936*b*, p. 488) obtained three adults and a nymph from a museum-skin of a marmoset and correctly regarded the occurrence as being due to contamination, and it is now practically certain that members of the genus *Proechimys* are the true hosts of *Harrisonia*, for Mr. O'Mahony has obtained several more specimens from dry skins of this genus of rodents (Hopkins, 1948, p. 100).

Coming to the relationships of the Trimenoponinae with other families of lice, it may be stated at once that they show no evidence of any very close relationship with the only other group of Amblycera (the family Gyropidae) found on rodents, although this family is also confined to South America and reaches its greatest development on the rodent families Caviidae and Echimyidae together with other rather closely related families of rodents. But are the Trimenoponinae related to the Boopidae? Harrison (1915, p. 124) thought these groups to be both very isolated among the Amblycera. He did not explicitly state that he considered them to be related, but placed them next to one another in his list and noted that they have in common the possession of a posterior commissure in the tracheal system, a feature which he did not find in any other Mallophagan genera examined by him but which he noted as characteristic of the Anoplura (which suggests that it may be an ancient character). He stated that *Trimenopon* "shows a superficial resemblance to the Boopidae, but is without the accessory sac in the ♂ genitalia and the special sensory organs of the first abdominal segments which characterize that family. In addition, it exhibits a fusion of prothorax and metathorax [*i. e.* pterothorax], a condition not seen elsewhere in the Mallophaga." He also mentions the fact that *Trimenopon* possesses spiracles on abdominal segments 3-7, whereas in the Boopidae they occur on segments 2-7, but that this latter point is of little importance is shown by the presence of exactly similar differences between the two subfamilies of the Gyropidae. It is interesting to note that he prophesied (1916*b*, p. 257) that Mallophaga would be found on American marsupials, and would prove to be very closely related to the Boopidae; he was able to describe such a form later (1922) and considered it to approach the Boopidae. In a still later paper (1926, p. 1585) he thought the Boopidae to be most closely related to the Gyropidae, and suggested the possibility that the discovery of further forms might cause these two families and the Trimenoponidae to be united into one group. Subsequent discoveries have, however, not markedly narrowed the gap between the Gyropidae and the other two groups.

My own belief is that the two groups are quite closely related, that the differences between them can be accounted for by evolution during the very great length of time which has elapsed since the Australian and South American

* One supposed member of this genus, *Philandesia foxi* Ewing, is based on two single specimens which Dr. Werneck has examined and which he finds to belong to the bird-infesting genus *Menacanthus* (*s.l.*). They are very obvious contaminations.

marsupials separated off from their common stock, and that their infestation of marsupials is probably primary, and Harrison (1922, p. 155; 1928 *a*, p. xxvii) was also of this opinion. If this belief is erroneous, then the Trimenoponinae may be of secondary occurrence on marsupials, but this does not seriously affect the position of the Boopidae. The latter are of such widespread distribution on widely-differing groups of marsupials (both flesh-eaters and herbivores) that I cannot regard their occurrence on marsupials as other than primary.

(4). INSECTIVORA.

Fossils certainly belonging to this order are found as early as the Cretaceous period and remains from the Oligocene rocks are referable to existing families and sometimes perhaps even to existing genera. The Insectivora probably split off from the main stem of the earliest placental mammals before the middle of the Cretaceous period. Simpson (p. 175) states "The insectivores are . . . of extremely ancient origin and differentiation. The characters that unite them are in great part primitive for all placental mammals, and in this sense the common view that the insectivores are the most primitive of placentals and stand near the origin of all other groups is apparently true." There is no clear-cut division between the Insectivora and the Primates, and the Tupaiidae (here placed, following Simpson, in the Primates) are often referred to the Insectivora and placed near the Macroscelidae.

No Mallophaga are known from the Insectivora, but Anoplura of the family Haematopinidae occur on Talpidae and Soricidae, and *Neolinognathus*, for which Fahrenholz has erected the family Neolinognathidae, on the Macroscelidae. *Neolinognathus* seems to be very isolated and therefore must be tentatively assumed to represent a primary infestation. *Haematopinoides*, found on Talpidae, is regarded by Ferris (1920-1935, p. 150) as being "quite closely related" to *Schizophthirus*, a genus found on rodents (dormice). Waterston (1929, p. 161) and Ferris (1920-1935, p. 308) are in agreement that *Ancistroplax*, recorded from a shrew of the genus *Crocidura*, is closely related to *Schizophthirus* and *Haematopinoides*, of which "to a certain extent it combines the characters" (Ferris, *l. c.*); Webb (1926, p. 66) finds the spiracle-structure to be very similar in *Schizophthirus* and *Ancistroplax*. *Polyplax*, occurring on Soricidae, has a very wide distribution on rodents and it seems probable that its occurrence on Soricidae is secondary, though it must be noted that the occurrence, on shrews from Europe, Southern Asia and Central Africa, of forms which are so closely related that they have mostly been considered to belong to one species is very strong evidence that if the infestation is indeed secondary the transfer must have taken place at a rather remote date, before the Ethiopian, Palaearctic and Oriental regions became separated and before the divergence of the genera *Sorex*, *Crocidura* and *Scutisorex* from a common stock. Too much stress must not be laid on *Ancistroplax* when considering the primary or secondary nature of the louse-infestation of Insectivora, because we have only a single unconfirmed record which may be erroneous, but it is worth noting that Webb finds that *Ancistroplax* and *Haematopinoides* (together with *Docophthirus*, from a tupaiid) have very similar spiracle-structure and that he states (1946, p. 62) that "It is of particular interest that the three genera of sucking-lice occurring on three distinct families of the Insectivora*, the most primitive placental mammals, should agree in possessing spiracles of the simplest and presumably most primitive type yet found in the Suborder." The occurrence of *Ancistroplax* and *Haematopinoides* on Insectivora may well be primary and that of *Neolinognathus* must be assumed to be primary; the fact that Webb (1946, p. 116) finds that its spiracle-structure suggests the probability of a relationship to *Pedicinus* (from Primates) is most interesting and probably significant, for the Primates are almost certainly derived from Insectivora. It is conceivable

* Webb retains the Tupaiidae in the Insectivora.

that *Polyplax* occurred on a common ancestor of rodents and insectivores; as we know nothing of the origin of the rodents this suggestion cannot be wholly ruled out, but I regard it as very improbable, because the resemblances between the species of *Polyplax* found on shrews and those which occur on rodents seem to me to be far too close to admit of a likelihood that the infestation of the former could be as remote in time as it would have to be if it were to date back to a common ancestor of the two groups of hosts. The repeated cropping up in the lice of Insectivora of resemblances to the lice of rodents is striking and perhaps indicates that the latter are derived from the ancestral stock of the former.

(5). DERMOPTERA.

The Cynocephalidae or colugos are among the most interesting of mammals because they represent the survival of an extremely generalized type, possessing characters which have caused them to be placed by different authors among the lemurs, the bats and the Insectivora. They are now considered to be derived from the same branch of the primitive insectivore stock from which the bats are descended. Fossils attributable to this order are known from Paleocene strata.

The unique systematic position of the colugos gives very special interest to the relationships of their anopluran parasite, *Hamophthirus galeopitheci* Mjöberg (Haematopinidae), and it is extremely unfortunate that this louse seems to have been encountered only once and has never been adequately described. Sufficient is known of the insect, however, to show that it is "possibly more or less related to *Docophthirus* although in certain respects . . . it suggests *Lemurphthirus*" (Ferris, 1920-1935, p. 306). But *Docophthirus* parasitises an Asiatic tree-shrew of the family Tupaiidae, and *Lemurphthirus* an African lemur, so that if we accept the belief that the colugos, lemurs and tree-shrews are fairly closely related (Simpson places them in the same cohort), the relationships of *Hamophthirus* give strong support to the view that its infestation of the Cynocephalidae is primary. A further piece of evidence which points in the same direction is that the colugos are herbivorous and therefore could not acquire a louse secondarily in devouring prey—by far the most likely way in which a secondary infestation could be acquired.

(6). CHIROPTERA.

Fossil bats are known as far back as the Eocene period, and are all fairly closely related to existing forms, so it seems certain that the order must have been in existence not later than the earliest Eocene.

A very considerable number of parasitic mites and insects are known from the bats, and it seems highly improbable that lice could have escaped notice if they were present. I have suggested (see p. 432) that this abundance of other parasites and absence of lice are cause and effect, and it only remains to add that, if my belief that the presence of a louse on the Cynocephalidae is primary and the suggestion that this group is very close to the original stock of the bats are both well founded, the absence of lice on the bats must necessarily be secondary.

(7). PRIMATES.

The Primates seem to be quite definitely derived from Insectivora and the relationship is so close that there is still no agreement among mammalogists as to whether the Tupaiidae are "the most primate-like insectivores or the most insectivore-like primates" (Simpson, p. 183). The same author notes (*l. c.*) that the only unquestionable tupaoid fossil (early Oligocene in date) is in some respects even more lemur-like than the living forms. Lemuroidea (the Plesiadapidae) are known from the Paleocene strata. The oldest known remains of members of the Anthroipoidea (monkeys, apes and man) are from

Lower Oligocene rocks, both Cercopithecoidea and Hominoidea being then extant. The Ceboidea, as known fossils, only date back to the Miocene period, but are doubtless much earlier. Simpson (p. 185) considers it probable that they have been confined to South America almost throughout their history. It is likely that the Ceboidea, Cercopithecoidea and Hominoidea diverged from each other early in the Eocene period and that man had already diverged from the main stock of hominoids in the early Miocene.

The Primates are infested by Amblycera, Ischnocera and Anoplura. Amblycerous Mallophaga are represented only by the family Gyropidae, of which one species occurs on a couple of species of ceboid monkeys. Though certainly not very recent (the species differs much from other members of the genus *Gyropus*), this infestation is probably secondary.

The same might be written of the Ischnocera (Trichodectidae) found on Primates but for the very interesting fact that *Lorisicola*, which occurs on an Asiatic lemur, and *Cebidicola*, which is found on several American members of the family Cebidae, are obviously closely related. It seems highly significant both that the Lemuroidea and Ceboidea are the two most primitive groups of the Primates after the Tupaiidae, and that those Cebidae on which *Cebidicola* occurs are precisely those which appear not to be normally infested with Anoplura. I am convinced that *Lorisicola* and *Cebidicola* are the remnants of a once very wide-spread primary infestation of the Primates with Trichodectidae, but the supposed occurrence of *Procaricola colobi* on a monkey is not evidence in this connection because it is almost certainly erroneous and if correct is obviously secondary.

Our information about the distribution of *Trichophilopterus* (Ischnocera, Philopteridae) is tantalisingly meagre. Stobbe gives no indication whether the specimen of *Indri indri* from which he obtained his original pair was wild-killed, a museum-skin, or an animal which had been in captivity, and Mjöberg's supposed new species has never been described. Ferris obtained eleven adults from an apparently wild skin in a museum, this number being certainly sufficient to suggest that *Lemur mongoz* is a genuine host of the parasite. The belief that *Trichophilopterus* is a genuine parasite of lemurs seems to be well founded, but the question of whether it has a wide distribution on Madagascan lemurs remains open: in this connection the habit of captive lemurs of huddling together for warmth must not be forgotten. The relationships of the insect are obscure; it is perhaps a transitional stage in the evolution of the Trichodectidae from a philopteroid form, but may be a comparatively recent acquisition by the lemurs from birds. Ferris (1933*b*, p. 471) considers that the similarities to the Trichodectidae may be misleading and due to convergence, though he does not exclude the possibility that the genus may be an annectant form between the Philopteridae and the Trichodectidae; Eichler (1941*b*, p. 356) refers it to the Trichodectiformia. Unfortunately we know very little about the mallophagan fauna of lemurs; intensive collecting of their lice would probably produce results of exceptional interest.

Turning to the Anoplura, three genera of Haematopinidae, *Docophthirus*, *Lemurphthirus* and *Phthirpediculus* are recorded from Tupaiidae and from African and Madagascan lemurs respectively. *Docophthirus* is of very special interest because "the absence of the prothoracic pleural apodeme and the prothoracic pleural ridge seems to connect this genus with *Phthirpediculus*" (Ferris, 1920-1935, p. 303), which supports both the placing of the Tupaiidae among the lemuri-form primates and a belief that the occurrence of Anoplura on the lemuri-forms is primary. *Phthirpediculus* "is apparently related in general to the rodent-infesting Anoplura" (Ferris, *l.c.*, p. 296). *Lemurphthirus* does not seem to be closely related to the other two genera under discussion, Ferris being of the opinion (1920-1935, p. 300) that it is more closely connected with *Neohaematopinus* (found on squirrels and other rodents) than with any other group, while Webb (1946, p. 72) comes to the same conclusion on different grounds. It

therefore seems likely that *Lemurphthirus* may represent a secondary infestation, but it must be noted that absence of close relationship between two louse-genera found on one group of hosts is not necessarily evidence that one of the infestations is secondary, because both genera may represent primary infestations and one genus may have died out on one section of the hosts and the other genus on the other group, as in the case of *Neohaematopinus* and *Enderleinellus* on different species of *Xerus* (see p. 428). A further line of examination is as to the relationships of the lice found on Lemuriformes with the lice of the Anthropeida, but we get little help from this examination, for there does not appear to be any close relationship. Ewing (1923, p. 149) considered *Phthirpediculus* to be very close to the lice of the Anthropeida, but Ferris (1920-1935, p. 295) states that this belief is erroneous. In any case the absence of eyes in all three genera from Lemuriformes places them off the direct line of descent of the genera found on the Anthropeida, all of which have eyes. The evidence is insufficient to enable us to decide whether the infestation of the Lemuriformes with sucking lice is primary or secondary, but the apparently rather close relationship between *Docophthirus* (on Asiatic tree-shrews), *Hamophthirus* (on a member of the Dermoptera) and *Lemurphthirus* (on African lemurs) suggests the strong probability that the infestation may not only be primary but may go back beyond the order Primates to the cohort Unguiculata.

There is no doubt whatever that the sucking lice of the family Pediculidae which are found on the Anthropeida represent a mainly primary infestation. *Pedicinus*, known from a great variety of cercopithecoïd monkeys, is undoubtedly very closely related to *Pediculus*, which replaces it on man and some of the other great apes; *Phthirus*, abundant on man and possibly occurring also on the gorilla and chimpanzee (see p. 451) is also evidently nearer related to these two genera than to any others.

The occurrence of lice on man's nearest living relatives is a subject which requires further investigation. The fact that a *Pediculus* occurs on the chimpanzee is established, but we have no conclusive evidence with regard to the status of *Phthirus* on the chimpanzee and gorilla, and no knowledge whatever as to whether the orang-outang is infested with lice. Fahrenholz's two supposed species of *Pediculus* on gibbons are almost certainly mere contaminations with *Pediculus humanus*, for the gibbons are much further removed from man in a phylogenetic sense than is the chimpanzee, yet the lice described by Fahrenholz appear not to differ from *P. humanus* while the *Pediculus* of the chimpanzee is very distinct. If the gibbons are really louse-free the case must be one of secondary absence, for they ought to possess either a *Pediculus* showing characters somewhat annectant to *Pedicinus* or (much less probably) a *Pedicinus* with characters approaching those of *Pediculus*.

The question of the forms of *Pediculus* on the South American spider-monkeys is one of extreme interest and considerable difficulty. There is no difficulty about the relationships of the form (or forms): it is exceedingly closely related to the *Pediculus* of man, much more closely related to the latter than is the *Pediculus* found on man's near relative, the chimpanzee. Furthermore, *P. humanus* varies in a way which brings certain forms of it very near to the lice of *Ateles*, and there is an apparently authentic record of one of the forms of *Ateles*-lice on man. Until a few years ago all records of *Pediculus* from *Ateles* (except for certain eggs obtained by Ewing from wild skins) were from captive hosts, and "Mr. L. H. Dunn . . . states that the examination of more than a hundred monkeys killed in the wild has revealed no lice. All of his specimens came from hosts which had been in captivity for some time" (Ferris, 1920-1935, p. 598). Werneck, however (1937*d*, pp. 161-163), while confirming the frequent occurrence of this group of lice on captive *Ateles* and the extreme rarity of infestations of wild hosts, put the natural occurrence of *Pediculus* on spider-monkeys beyond doubt by finding a heavy infestation on a wild *Ateles paniscus* killed in virgin forest in Brazil. The host distribution of the *Pediculus* of

spider-monkeys is also moderately clear : accepting Ewing's contention that he is able to determine eggs of *Pediculus*, there are a number of authentic records from wild-killed specimens of several forms of *Ateles*, whereas all the records from other groups of South American monkeys are from captive animals and very probably due to contamination.

The host-distribution of *Pediculus* is, therefore, wholly at variance with any theory that the forms found on *Ateles* represent a primary infestation, since they are far more closely related to man's *Pediculus* than is the corresponding form (*Pediculus schäffi*) on man's much nearer relative, the chimpanzee. Wigglesworth (1929, p. 830) makes a most interesting observation in this connection : " It has been shown by Friedenthal that both the blood and the hair of the spider-monkey present characters which approximate more closely to those of the anthropoid apes and man than is generally the case with the lower monkeys, and it appears probable that—perhaps in virtue of this fact—*Pediculus* crossed over from an anthropoid host to the ancestor of the modern *Ateles*." Ewing (1924*d* ; 1926, p. 25 ; 1938, pp. 31–33) had independently put forward the same hypothesis, but substituting the American Indian for Wigglesworth's " anthropoid host." I believe that this hypothesis, in the form given to it by Ewing, represents as close an approximation to the truth as we can hope to obtain without actual experiment. I suggest that *Ateles* had, at some period probably much later than the time when the ceboid group diverged from the rest of the anthropoids, become free from sucking lice, but that at a date not much later than the historically remote but geologically very recent period when man entered South America, captive *Ateles* acquired from man a stock of his characteristic louse. It is known that the Indians were in the habit of keeping *Ateles* as pets before white men entered the country, and there is very strong evidence that captivity favours in some way the multiplication of lice on *Ateles*. From time to time a captive *Ateles* escaped and rejoined his brethren, to whom he passed on the undesired gift that man had bestowed on him. It is not necessary to assume, as is done by Ewing (1926, p. 28), that all this took place before the divergence of the various species of *Ateles*, for the captives would naturally not all be of one form and they would (if possible) rejoin their own kind and not another species. On its new host *Pediculus humanus* (an exceptionally labile species) began to alter and in some ways to revert to a form showing more resemblance to the lice of man's Old World relatives : it seems entirely possible that the degrees of difference between the various " species " recognized by Ewing are an indication of the lengths of time which have elapsed since a captive member of any particular species of *Ateles* succeeded in infesting its wild relatives, and that all the members of the *lobatus*-group would be best regarded as subspecies of *Pediculus humanus*. Obviously our knowledge of the status of these forms cannot be much advanced without the aid of much more material from unquestionably wild hosts, and especially without experiment. It would be of immense interest if an investigator were to transfer *Pediculus humanus* of a known human strain to louse-free specimens of *Ateles* and were to examine the characteristics of the resultant louse-population at intervals over as long a period as possible. In any case, the *Pediculus lobatus* group must be dismissed from consideration in any examination of the primary or secondary nature of the louse-infestation of the Primates ; the group is a relatively recent secondary acquisition from another branch of the primate stock.

(8). EDENTATA.

Simpson (p. 191), considers that the evidence " strongly suggests that the edentates arose from proto-Insectivora, along with several other archaic orders, about the beginning of the Paleocene." The living members of the order include Myrmecophagidae (ant-eaters), Bradypodidae (sloths), and Dasypodidae (armadillos).

No lice are recorded from the ant-eaters or from the armadillos. The armoured dorsal surface and thinly-haired underside of the armadillos would not provide very favourable conditions for lice and it would not be surprising if this family of mammals is louse-free, but the ant-eaters are well-clothed with hair and may be expected to have lice. The single member of the Amblycera recorded from a sloth is certainly a mere contamination, but the two records of Trichodectidae of the genus *Lymecoon*, though insufficiently confirmed, are perhaps correct, the strongest point in their favour being that both are from the Neotropical Region. There is certainly no obvious reason why the sloths should not be infested with Trichodectidae, but it seems to me that the supposed occurrence should be left out of consideration until more confirmation is forthcoming. The uncomfortably close resemblance between *Lymecoon* and *Procavicola* is (if the occurrence of the former genus on sloths is confirmed) possibly accounted for by the stock which gave rise to the Edentata and that which was ancestral to the Procaviidae having originated from the proto-Insectivora close together. We do not know enough about the origin of the Edentata to be able to say whether this suggestion is probable.

(9). PHOLIDOTA.

The Manidae or pangolins were formerly included in the Edentata, but it is now considered that any common ancestry " must have been exceedingly remote (probably before the edentates were differentiated clearly from the proto-insectivores)" (Simpson, p. 195).

It would not be surprising if the pangolins should be found to be louse-free, for the same reason that makes absence of lice probable in the case of the armadillos.

(10). LAGOMORPHA.

The Lagomorpha were formerly placed in the Rodentia as the suborder Duplicidentata, and their separation as a distinct order is still not universally accepted, one view being that the two groups diverged from a common stock before all the typical rodent characters had been acquired, while the opponents of this view point out that a rodent-like type of dentition has certainly been acquired independently in several different groups (in the aye-aye among the Primates, for example) and that no fossils intermediate between the Lagomorpha and Rodentia have been found. Simpson places the two groups as orders of the same cohort, though admitting that this is rather because of the absence of evidence against this course than because of the existence of evidence in its favour. Lagomorpha from the Eocene rocks were apparently already differentiated into the two existing families, and nothing is known about the earlier history of the group.

Each of the two families which constitute this order is infested by one genus of sucking lice, but the genera concerned are not particularly closely related. *Hoplopleura* (occurring on the Ochotonidae) is very widely distributed among the rodents, while *Haemodipsus* (from Leporidae) seems to be closely related to *Eulinognathus*, which has a wide distribution on other rodent-families. There seems to be little doubt that *Haemodipsus*, at least, represents a primary infestation, for it occurs on Leporidae in at least the Holarctic and Ethiopian regions. Another point of interest about *Haemodipsus* is that at least one of the species seems to be very rare and possibly in danger of becoming extinct. The louse-evidence is definitely in favour of Lagomorpha and Rodentia having had a common origin.

The rather numerous records of *Linognathus setosus* from Leporidae are almost certainly due to contamination from dogs employed in hunting these animals.

(II). RODENTIA.

Remains of a rodent occur in Paleocene strata, and many of the modern families are known to have become differentiated by the time the Oligocene period was reached; the earliest of these rodents seem to have belonged to the Sciuromorpha, though the Myomorpha and Hystricomorpha were well established in the Oligocene and therefore must surely have made their first appearance not later than the Eocene. This fact is of some significance, for it suggests that the Muroidea, which now completely dominate the order, were of later origin than the other main groups. This, in turn, will be of great importance in considering which of the genera of rodent-lice are to be considered the more primitive, because among such a group as the lice simplicity may well mean simplification from a more complex type.

Rodents are infested by Amblycera of two families, by one family (Trichodectidae) of Ischnocera, and by very numerous Anoplura.

The amblycerous subfamily Trimenoponinae has already been discussed (p. 536) in connection with its occurrence on marsupials; it is confined to South America and occurs on the rodent-families Echimyidae, Chinchillidae and Caviidae, all belonging to the Hystricomorpha. Gyropidae are also confined to South America, where they are abundant on the hystricomorph families Echimyidae, Dasyproctidae, Chinchillidae and Caviidae; the occurrence of one member of the Gyropidae on the genus *Scapteromys* of the mureoid family Cricetidae is confirmed but seems obviously secondary. Outside the order Rodentia the Gyropidae occur on one genus of the Primates and on the family Tayassuidae (peccaries) of the Suina, both these infestations being in all probability secondary. I think it almost certain that the infestation of the Hystricomorpha with Gyropidae is primary and very probable that the family once had a wide distribution on the early rodents but has died out on those groups on which Ischnocera or Anoplura have become abundant. It seems highly significant in this connection that on those groups of rodents which are heavily infested with Gyropidae the Ischnocera and Anoplura are absent or very rare, and *vice-versa*.

Ischnocera are only known to occur on two families of rodents, the Erethizontidae and Geomyidae, which belong to the Hystricomorpha and Sciuromorpha respectively. The two genera of Trichodectidae concerned, *Eutrichophilus* and *Geomydoecus*, do not appear to be at all closely related to one another, but are both somewhat isolated from the other members of the family; I have very little doubt that they are relics of a once universal infestation of the rodents with a wide variety of Trichodectidae, and I consider it significant that Anoplura are absent or very rare on these two families of rodents. Jellison (1942, p. 249) has endeavoured to interpret the anomalies in the distribution of the different groups of lice on New World rodents in terms of geography, but these anomalies seem much more readily explicable in terms of phylegeny, modified by competition and other factors conducing to secondary absence.

There is no possible doubt about the status of the infestation of the rodents with Anoplura of the family Haematopinidae; it is undoubtedly primary. Sucking lice occur on all rodents which have been adequately examined (including members of nearly all the families) except some of those which are heavily infested with Mallophaga; on some of these latter sucking lice appear to be absent and on others they are very rare. The distribution of the genera of lice is of considerable interest, but we know too little about their relationships for a discussion of them to be very profitable at this time. It must suffice to note that all the genera are rather closely related (to the extent that some of them are difficult to define) and that parallelism seems to have played almost as large a part in their evolution as it has in that of their hosts. Very commonly a given family of rodents is infested by only one genus of Anoplura, but two

genera are normal in many cases ; four genera are known from the Sciuridae, but of these *Microphthirus* is clearly a modification of *Enderleinellus*, which it replaces, and *Hoplopleura* is probably a secondary acquisition from Muroidea.

The relationships of the Haematopinidae of rodents with those of other groups of mammals are very obscure. We have seen that there are suggestive resemblances between certain lice of the Insectivora (*Haematopinoides* and *Ancistroplox*) and the rodent-infesting genus *Schizophthirus*, while the genus *Polyplax* is common to the two orders of mammals but is almost certainly a secondary (though far from recent) acquisition as far as the Insectivora are concerned. The genus *Lemurphthirus*, found on a few of the lower Primates, is believed to be fairly close to *Neohaematopinus*, found on rodents, and *Phthirpediculus*, another lemur-infesting genus, is stated to be "related in general to the rodent-infesting Anoplura" (Ferris, 1920-1935, p. 296). It is not surprising that the lice of Lagomorpha are closely related to those of the rodents, because specialists on mammals are not completely agreed as to whether these two groups ought to constitute separate orders. Ferris has pointed out the apparent close relationship of *Hybophthirus*, on *Orycteropus* (the sole living representative of the Tubulidentata) with *Scipio*, occurring on rodents, but has omitted to mention one resemblance in this connection which I find rather significant—that in both these genera, as also in the rodent-infesting genus *Neohaematopinus* (especially *N. faurei*), there are indications of that production of the head behind the antenna which is so characteristic a feature of the genus *Haematopinus* (found on Suidae, Equidae, Bovidae and perhaps Cervidae) and of certain of the lice of seals. The significance of these resemblances of the Anoplura of rodents to those of other groups is not clear to me, particularly the degree to which they should be regarded as evidence of real relationship or as examples of retention of similar primitive features or acquisition of similar specializations, but I suspect that the truth may be that we are dealing with a case of secondary absence on a large scale, and that the rodents have retained a more representative selection of the Anoplura of the very early placental mammals than have other groups descended from these latter.

(12). CETACEA.

The whales have commonly been considered to have been an early off-shoot from the Creodonta, but Simpson (1945, p. 214) considers this suggestion improbable and suggests that their true origin is more remote. Their mode of life would render the survival of lice on them quite impossible.

(13). CARNIVORA.

Modern Carnivora (Fissipeda and Pinnipedia) certainly arose from the Creodonta, a primitive flesh-eating group whose members flourished during probably the whole of the Paleocene and Eocene periods ; the Creodonta in turn were apparently derived from the primitive insectivoroid stock, from which they may have diverged early in the last third of the Cretaceous period. Late Creodonta and early Fissipeda are so much alike that it is often a matter of great difficulty to decide to which group remains should be assigned. A question of particular importance in connection with several points of my argument is that of the origin of the Pinnipedia or seals. These certainly arose from the Creodonta, perhaps in the late Eocene period, and are known as fossils from the Lower Miocene. A former suggestion that the Phocidae or true seals might have arisen from a different group of the Creodonta than that from which the other Pinnipedia originated is now considered to be improbable. The two main branches of the Fissipeda (Canoidea and Feloidea) must have diverged not very long after the origin of Fissipeda from the Creodonta, since fossils attributed by Simpson to the Canidae and the Felidae are known from Upper Eocene rocks.

The lice of seals and of Fissipeda are discussed separately.

Pinnipedia.

The lice of the seals are of exceptional interest because of the marine habits of their hosts. Mallophaga are absent and have probably been drowned out, for the almost universal occurrence of Mallophaga on the Fissipeda suggests strongly that the original stock of the Pinnipedia must also have been infested. The fact that Mallophaga are present on the otters is no impediment to my suggestion as to the fate of the hypothetical Mallophaga of the seals, for the otters are far less aquatic in their habits.

Anoplura, on the other hand, have successfully survived the return of seals to the sea, their survival being doubtless made possible by the possession by their hosts of a dense under-fur which delays the wetting of the surface of the body. The fact that all three families of the seals are infested with closely related parasites is an exceedingly strong indication that the infestation is primary, especially in view of the fact that the seals can have had practically no contact with other louse-infested mammals since they took to an aquatic life*.

As is only to be expected, the seal-lice have been considerably modified from the type found on their nearest living relatives. These differences have caused the group to be given family rank, but this seems to me to exaggerate their degree of remoteness, and I have no real doubt that they should be referred to the Haematopinidae and are derived from forms closely related to the ancestors of *Linognathus*. The most extreme forms of the seal-lice are admittedly exceedingly unlike *Linognathus*, but if one compares *Proechinophthirus*, the most primitive of the seal-lice (Ferris, 1920-1935, figs. 279, 280, pp. 482, 483), with the type species of *Linognathus* (Ferris, *l. c.*, figs. 206, 207, pp. 243, 343) or with one of the less-specialized forms of *Haematopinus* (Ferris, *l. c.*, figs. 263, 264) it is at once clear that the resemblances are very great. The chief differences from *Linognathus* are that in *Proechinophthirus* the antennae are composed of 4 segments instead of 5, the spiracles are very small and possess a specialized closing device, and gonapophyses in the female genital region are lacking, while *Haematopinus* has the additional difference that the fore-legs are similar to the other two pairs. The number of segments in the antennae is obviously unimportant for "such a character has undoubtedly arisen quite independently at least three times in the Anoplura" (Ferris, 1920-1935, p. 481); furthermore, in one of the seal-infesting genera (*Antarctophthirus*) the antennae are 5-segmented. Nor do I attach much greater importance to the absence of gonapophyses, for in all the genera of seal-lice a dense patch of setae on each side of the genital region marks their former position, suggesting that they have not long been lost. The structure of the spiracles is interesting and important, but is very obviously an adaptation to life on aquatic hosts, and Webb (1946, pp. 95, 96) finds an interesting resemblance between the prothoracic spiracle of seal-lice and that of *Haematopinus*, though he refuses to regard it as necessarily indicative of relationship. The unmodified fore-legs of *Haematopinus* are shared by *Echinophthirus* among the seal-lice. There is another character of *Haematopinus* which is shared by the seal-lice and not by *Linognathus*: in *Haematopinus* the head has the post-antennal angles acute and directed anteriorly, giving this region an extremely characteristic appearance and forming a very conspicuous projection; in the seal-lice this projection is not only always present (least so in *Lepidophthirus*) but is sometimes (*e. g.* in *Antarctophthirus trichechi*) almost precisely of the same form as in *Haematopinus*; in *Linognathus* the projection is absent. The seal-lice may have originated from the *Haematopinus*-stock or the *Linognathus*-stock (I think it certain that they arose from one or the other), but if from the latter it was at a time before the fore-legs of *Linognathus* had been reduced and before the post-antennal angles had been smoothed off.

* The seals of the Arctic are a favourite prey of the Polar bear, but a seal which came into close enough contact with a bear to have an opportunity of acquiring lice from it would be most unlikely to survive. Seals in the Antarctic cannot come into contact with any other mammals except whales.

I have dealt with this matter of the relationships of the seal-lice at some length because of the unusual importance of the light it throws on the relationships of the lice of the Carnivora to those of the rest of the cohort Ferungulata, and the very fortunate fact that the primitive characters retained by certain of the seal-lice are sufficient to demonstrate these relationships very clearly. The deductions which may be drawn from these relationships are discussed elsewhere (p. 556).

Fissipeda.

On the land-Carnivora or Fissipeda, Ischnocera of the family Trichodectidae are of almost universal occurrence on every family, Anoplura of the genus *Linognathus* are confined to the family Canidae, and a single member of the amblyceran family Boopidae occurs on the domestic dog and some other hosts.

Perhaps the most interesting feature of the Trichodectidae of Fissipeda is that they are all much more closely related to one another than to the Trichodectidae of the Artiodactyla and Perissodactyla, because this disposes of any suggestion that the land-Carnivora could have derived their Trichodectidae from their prey; the differences between the Trichodectinae of Fissipeda and Damaliniinae of Artiodactyla and Perissodactyla are probably great enough to justify the subfamily rank given to these groups. Another point of some importance is that the division between the hosts of the genus *Trichodectes s.str.* and those of *Felicola s.str.* is also the division between the superfamilies Canoidea and Feloidea. In my opinion this constitutes proof that the Fissipeda were already infested with a *Trichodectes*-like form before these two superfamilies began to diverge.

With regard to the Anoplura of the Fissipeda the position is different. Ferris (1920-1935, p. 344) noted the close resemblance between *Linognathus setosus* and *L. pedalis* (Osborn), the latter from domestic sheep, and put forward very tentatively the suggestion that the long association between dogs and sheep might have something to do with the apparent anomaly of the occurrence of a *Linognathus* on a carnivore. He found the occurrence of a similar *Linognathus* on foxes in the Arctic regions not very consistent with this suggestion, and the discovery, since Ferris wrote, of a closely-allied but quite distinct species of *Linognathus* on Brazilian Canidae of the genus *Dusicyon* has thrown still further doubt on the hypothesis. The final blow to it is, in my opinion, given by my demonstration (p. 546) of the relationship between *Haematopinus* or *Linognathus* (which I think to be ancestrally not far apart) and the seal-lice. It still remains possible that the Carnivora acquired their Anoplura from some primitive member of the ungulate stock, but the time at which this could have occurred cannot have been later than the divergence of the Fissipeda and Pinnipedia, and it seems to me to be simpler to suppose that the original stock of the whole cohort Ferungulata was infested with Anoplura not distantly related to *Haematopinus* and *Linognathus* and that these have become extinct on all groups of Carnivora except the Pinnipedia and the Canidae.

The case of the genus *Heterodoxus* (Amblycera, Boopidae), found on the domestic dog and certain other Canidae as well as on Australian marsupials, is a difficult one. So long as it was believed that the species on the dog was the same as that on kangaroos it was obvious that the infestations must be secondary and quite recent (probably since the discovery of Australia by Europeans), but it is now known that the species on the dog is distinct from any known from kangaroos unless Plomley's record of two males and seven females of *Heterodoxus spiniger* from *Wallabia bicolor* is reliable, which it probably is not. Unless *Wallabia bicolor*, or some kangaroo or wallaby of which the parasites are not yet known, is the original host of *H. spiniger*, the parasite must almost of necessity have transferred to domestic dogs through the dingo, for the differences from the other known forms of the genus, though almost confined to the male genitalia, are considerable; although Australia appears to have been known

to the Chinese during the thirteenth century, a period of seven or eight hundred years does not seem adequate for the development of such differences. Although I have little doubt that the suggested kangaroo-origin of the parasite is correct, the geographical evidence is rather against it. *H. spiniger* was first collected in Martinique in 1896 (Plomley, 1940). It occurs in many parts of Africa, Australia, America and Asia, but apparently not in Europe, the northern part of the United States, nor Canada, though these are the areas where the occurrence of a parasite transported from Australia by man would seem most probable. There are large numbers of records from the domestic dog and definitely reliable records from jackals and coyotes. Records from hosts not belonging to the genus *Canis* are doubtful; a skin of *Civettictis civetta* from the Belgian Congo from which I once obtained a short series of *H. spiniger*, and a skin of *Crocuta crocuta* from which I took a pair of the same species in Uganda were both old ones which may very well have served as bedding for a dog.* Cummings' record from a crow and Plomley's from man are both obvious nonsense. Werneck's record from *Felis salinarum* is most interesting biologically, but the circumstances of the record (see p. 507) are not such as to give rise to any confidence that the occurrence was a natural one, particularly as *H. spiniger* is abundant on dogs in Brazil. The evidence that *H. spiniger* represents a secondary and relatively very recent infestation on non-marsupial hosts is very strong, but it remains just possible that *Heterodoxus* once had a much wider distribution on placental mammals, of which its occurrence on the Canidae is a relic.

The occurrence of *Felicola subrostratus* (belonging to the Trichodectidae) on the domestic cat and on *Felis silvestris*, and of *Felicola caffra* (as well as *F. subrostratus*) on *Felis lybica*, is a very interesting apparent anomaly, because *Felis lybica* is stated to be the ancestor of the domestic cat and should, therefore, have the same parasites. The available evidence for the natural occurrence of *Felicola caffra* on *Felis lybica* is weak, but confirmation of the occurrence would suggest that this cat may not be the ancestor of *Felis catus* and that it was originally infested by *Felicola caffra* only. Another possible solution of this problem is suggested by the facts that *Felicola subrostratus* is often abundant on its hosts whereas *F. caffra* (of whose host I have dissolved or brushed many skins) is apparently exceedingly rare, and that *Felis catus* and *Felis silvestris*, as well as *Felis catus* and *F. lybica*, are known to interbreed on occasion. It seems conceivable that *Felicola caffra* was the original louse of both *Felis lybica* and its derivative, *F. catus*, but has been almost swamped out on these hosts by competition from the more vigorous *Felicola subrostratus*, acquired by the domestic cat from *Felis silvestris*. Examination of ancient cat-mummies from Egypt might perhaps throw light on this problem, of which a further complication is that *Felicola rostratus*, occurring on two not very closely related members of the Viverridae, appears to be inseparable from *F. subrostratus*.

(14). TUBULIDENTATA.

The sole modern representative of this order, *Orycteropus afer*, was formerly included in the Edentata *s.l.*, but its resemblances to the true Edentata are now considered to be convergent and not indicative of any close relationship. The true position of the order is still not clear, but it has been suggested that the group is a very ancient derivative from the proto-ungulate stock, perhaps the Condylarthra. Simpson expresses this belief by placing the Tubulidentata in the superorder Protungulata of the cohort Ferungulata. Fossil remains of the Tubulidentata are extremely meagre, but the genus existed in the Pliocene and forms doubtfully referable to the order occur in much earlier rocks, including Lower Eocene.

Orycteropus is infested by a single sucking louse, *Hybophthirus notophallus*, a rather remarkable member of the family Haematopinidae. Ferris (1920-1935,

* I once found a number of specimens in Kenya on sacks used as a dog's bed.

pp. 170, 175) regards *Hybophthirus* as being very closely related to the rodent-infesting genus *Scipio*. If this is correct there can be but little doubt that the infestation of *Orycteropus* is secondary, and in this connection it may well be significant that both *Orycteropus* and the hosts of *Scipio* live in burrows and may at times enlarge or utilize each others' dwellings. But I retain an open mind as to the primary or secondary nature of this infestation, because I do not think that the possibility that the resemblances between the two genera are due to the retention by both of similar primitive characters or the acquisition by both of similar specializations is wholly excluded. Webb (1946, p. 91) notes possibly significant resemblances between the spiracle-structure of *Hybophthirus* and of *Haematopinus*, the former being the more primitive.

(15). PROBOSCIDEA.

The earliest known fossils belonging to this order are from the Upper Eocene, and may have been on the direct line of descent of the modern elephants. The group probably split off from the proto-ungulate stock at a date about the last third of the Cretaceous period. The modern genera *Elephas* and *Loxodon* are represented by fossils in the Pleistocene period, but other evidence suggests a much earlier divergence: the connection of Africa with Asia through Arabia is believed to have become impassable to most mammals (probably owing to dessication) in the Eocene or Miocene periods, so that it is most improbable that there has been any contact between the two genera since the Miocene at latest, until man's intervention brought them together in captivity. This point is of great importance with regard to the distribution of the elephant-lice, *Haematomyzus*.

The group Rhyncophthirina, whose sole representative is *Haematomyzus elephantis*, is of exceptional interest because to some extent it stands between the Mallophaga and Anoplura; its systematic position has been very briefly discussed above (p. 390). A very full account of its morphology has been published (Ferris, 1931) and it only remains to note that its resemblances to the Trichodectidae and the Anoplura are sufficiently marked as to leave little doubt (in my mind, at least) that it lies but a short distance off the direct line along which the former evolved into the latter. This opinion is less at variance with that of Webb (1946, p. 98) than might be assumed from our very different translations of the facts into classifications.

In this order of hosts we have one of our best chances of obtaining fossil Phthiraptera, for the occasional specimens of the mammoth which are found ice-preserved and with the skin and hair still more or less intact would be very well worth examining for lice by the dissolving technique. I venture to prophesy that if any lice are found they will include a form very similar to *Haematomyzus elephantis* and perhaps inseparable from modern specimens of that species.

(16). HYRACOIDEA.

The hyraxes are another very ancient group and an unusually conservative one. They are known fossil from as far back as the Lower Oligocene, when a number of genera existed of which Simpson refers two to the extant family Procaviidae. He refers the order Hyracoidea to the superorder Paenungulata, regarding them as being sufficiently related to the Proboscidea to be included in the same superorder. The Hyracoidea probably diverged from the general proto-ungulate stock at some time in the Cretaceous period.

The hyraxes are infested with both Ischnocera and Anoplura, and their infestation with the former is exceptional in that as many as eight species, belonging to four genera and six subgenera, may occur on the same host-form (*Dendrohyrax arboreus adolfi-friederici*, p. 511) in the same locality, and doubtless occasionally on the same individual. On the other hand, certain other hyraxes whose parasite-fauna is fairly adequately known seem to possess only three

genera of Ischnocera (*Heterohyrax s. bakeri*, p. 514) or even only two (*Procavia johnstoni lopezi*, p. 519).

The relationships of the Trichodectidae of hyraxes (with the possible exception of *Dasyonyx*) are undoubtedly with the genera found on Artiodactyla and Perissodactyla, though they also exhibit some interesting and probably significant resemblances to the genera which infest the Carnivora. *Dasyonyx* differs from every other known genus of lice in that the claws of the posterior two pairs of legs are spinose-serrate, and for this reason has been accorded family or subfamily rank, but in other respects it fits in so well with the rest of the group that I am inclined to consider the claw-character as a specialization of little phylogenetic importance. There can be no reasonable doubt that the infestation of the hyraxes with Trichodectidae is primary. It is worth noting that *Eurytrichodectes* seems to be possibly on the verge of extinction, for it is known from only one subspecies of *Dendrohyrax arboreus*, although large numbers of other forms of *Dendrohyrax* (including numerous subspecies of *D. arboreus*) have been searched for lice, and even on this one form it is decidedly rare.

Only one genus of Anoplura (*Prolinognathus*, belonging to the Haematopinidae) occurs on the Procaviidae, and its distribution affords further strong support to the theory of secondary absence, for it occurs only on *Procavia* and *Heterohyrax*—genera in which infestations of Trichodectidae are much lighter, both in number of species and in number of individuals, than in *Dendrohyrax*. There can be no reasonable doubt that the infestation is primary, and I suggest that *Prolinognathus* was once present on all three genera, but has been "crowded out" on *Dendrohyrax* by the extreme success of the Trichodectidae. *Prolinognathus* is stated by Ferris (1920-1935, p. 409) to be "exceedingly close to *Linognathus*"; the latter genus (or slight modifications of it) occurs on most of the Artiodactyla and also on the most primitive family (Canidae) of the Carnivora. Webb (1947, p. 578) suggests that *Prolinognathus* has affinities with the sucking lice of rodents and is close to the ancestral form that gave rise to *Linognathus*.

(17). SIRENIA.

The Sirenia are of little interest in the present connection because of the improbability of their combination of aquatic habits and lack of hair permitting the survival of lice. Simpson refers them to the Paenungulata. They perhaps arose from the paenungulate stock close to the elephants, and are known as fossils from the Eocene period.

(18). PERISSODACTYLA.

The odd-toed ungulates undoubtedly arose from the Condylarthra, like their even-toed relations, but they appear to have diverged from these latter at a very early stage, perhaps in the late Cretaceous. Certain Early Paleocene condylarths are very like early perissodactyls. Perissodactyla are definitely known from the Lower Eocene and some of the Eocene forms are separable into Equoidea, Tapiroidea and Rhinoceroidea.

The relationships of the genera of lice found on Equidae are quite clear, with the possible exception of *Ratemia*. The trichodectid genus *Damalinia*, known from all three Equidae which have been examined, also occurs almost universally on the Artiodactyla; the anopluran genus *Haematopinus* is also characteristic of both Equidae and Artiodactyla. *Ratemia* (also belonging to the Haematopinidae) is unknown except from the Equidae. Ferris (1920-1935, p. 156) writes of *Ratemia* "This is a peculiar genus of somewhat doubtful affinities. It is possibly related to the forms now placed under *Linognathoides* rather than to *Linognathus* as was suggested by Neumann." My own view is that it is a form whose specialization has taken the form of simplification and that it is quite closely related to *Linognathus*. This view, if correct, would fit in well with the relationships of the other lice of the Equidae, for *Linognathus* and

its near relatives are extremely well distributed on the Artiodactyla. *Ratemia* has a very striking superficial resemblance to *Pedicinus* (found on Old World monkeys) but I believe this to be wholly misleading.

This, like the Proboscidea, is a group from which there is a possibility of obtaining fossil lice, for ice-preserved specimens of the woolly rhinoceros are occasionally found. These would be much more likely to be infested than their nearly naked modern relations.

(19). ARTIODACTYLA.

The even-toed ungulates probably diverged from the Condylarthra in the late Cretaceous period or Early Paleocene, for members of one group of the Early Paleocene condylarthrs are very like early artiodactyls. The Condylarthra themselves seem to have had but a short existence; they are known from Lower Paleocene deposits and were extinct as a group by the end of the Eocene, though many of them must have left descendants in the form of true ungulates. The earliest known forms of the Condylarthra are very close in many respects to the early Creodonta (ancestors of the Carnivora), and it seems extremely probable that these two groups had a common ancestor in the lowest Paleocene or perhaps the late Cretaceous; the deeper origin of both groups must have been the first placentals of the mid-Cretaceous. The Condylarthra also show resemblances to the ancestral Primates, and the original stock of the Ferungulata and that of the Unguiculata may have diverged from the stem of the first placentals very close together, if not at the same point.

Of the main groups of the Artiodactyla, the Suiformes had become recognizable by Lower Eocene times and the Tylopoda by the middle of the same period. The earliest known fossil Tragulina in the strict sense are from the Miocene, but certain late Eocene and Oligocene fossils apparently represent a stock ancestral to both Tragulina and Pecora. The Cervidae are known from the Lower Oligocene, the Giraffidae from the Lower Miocene, but many of the earlier fossils might almost as well be called giraffes as deer and it is regarded by Simpson as certain that these two families had a common ancestry. The Bovoidea may have arisen from Upper Eocene forms referred to the Tragulina but the first fossils certainly referable to the group are of Lower Miocene date.

The lice of the main divisions of the Artiodactyla are discussed below under separate headings.

Suina.

The only Mallophaga known from the Suina belong to the amblycerous family Gyropidae. This is a purely South American family which has a very extensive distribution on South American hystricomorph rodents belonging to the Cavoioidea, Chinchilloidea and Octodontoidea, and also occurs rather sporadically on several other orders of mammals. Its occurrence on the pecaries is probably secondary, though it is not wholly impossible that the present-day distribution of the family is residual and that it formerly had a much wider distribution, both geographically and zoologically.

All the genera of Anoplura found on the ungulates belong to the Haematopinidae. Of those found on the Suina, *Haematopinus* is characteristic of the Artiodactyla and Perissodactyla; besides its very general occurrence on the pigs it has a rather sporadic distribution on the Bovidae, is known from all Equidae which have been examined, and there is one unconfirmed but probably correct record from a member of the Cervidae. *Pecaroecus* (confined to the Suina) is of special interest, since Babcock and Ewing regard it as the most generalized member of the Anoplura recorded from an ungulate host; they state that it is most nearly related to *Microthoracius* (from the Camelidae), though showing some resemblances to *Haematopinus*, and it seems likely that *Pecaroecus* is a specialized early offshoot from the stock which later gave rise to *Haematopinus*.

Its possession of eyes is a primitive character*, but the structure of the thorax is more specialized than in *Haematopinus*. The absence of *Linognathus*, or some modification of this genus, on the Suina is to be regarded as secondary.

Tylopoda.

The Trichodectidae are represented on the family Camelidae, the only living family of the order Tylopoda, by the genus *Lepikentron*, which is very close to *Damalinia* and possibly inseparable from it.

The only anopluran genus known from the Tylopoda is *Microthoracius*, which (like *Pecarocetus*) appears to be a specialized development from the *Haematopinus*-stock. Although in several respects it is more specialized than *Haematopinus*, this genus possesses eyes, though these have lost their pigment and are doubtless on the way towards complete suppression.

Tragulina.

Our knowledge of the lice of this group is exceedingly scanty, but we now know that the chevrotains are infested with chewing lice of the genus *Damalinia*. As would be expected from the small size of the hosts (see Hopkins, 1943) these lice are of tricholipeuroid form. No Anoplura are yet known from the Tragulina, but their occurrence is very probable.

Pecora.

The deer are infested with Trichodectidae of the subgenus *Cervicola*, which shows an almost exactly parallel series of forms with the *Damalinia* of Bovidae, elongate forms with a concave or notched frons occurring on the smaller species of hosts and broader species, usually with a convex frons (*Rhabdopedilon*), on the larger species. The differences from *Damalinia s.str.* are very small but I think that *Cervicola* is a valid subgenus.

Two genera of Anoplura seem to occur on deer, but the occurrence of *Haematopinus* on this family rests on one unconfirmed record; this is very tantalizing, for if the record were confirmed it would fit in excellently with the somewhat sporadic occurrence of the genus on other ungulates and with the principle of secondary absence; the characters of the species are such as to suggest that the record may very probably be correct. The other genus, *Solenopotes*, is undoubtedly very closely related to *Linognathus*, the commonest genus on the Bovidae, and apparently occurs on all deer.

Ferris (1920-1935, p. 365) very rightly thought that the occurrence of *Linognathus* on the Giraffidae needed confirmation because both records were from zoos in Holland and the giraffes might well have been contaminated from a common source. But I have now collected *L. brevicornis* in very large numbers from the skin of a giraffe calf that had not left Kenya and had only been in captivity a very short time, and have also obtained it in considerable numbers from two wild skins. The fact that giraffes and Bovidae are infested with *Linognathus* while the deer possess the closely-related genus *Solenopotes* can be regarded as support for the belief of some mammalogists that the Giraffidae are more closely related to the Bovidae than to the deer, but may mean *Solenopotes* evolved from *Linognathus* on the deer after the latter had diverged from the common stock from which it seems to be accepted that all three main divisions of the Pecora arose, while the Bovidae and Giraffidae have retained relatively unchanged the *Linognathus* which infested the original stock of the Artiodactyla. Especially because of the occurrence of *Linognathus* on Carnivora I greatly prefer the second alternative, which is consistent with the suggestion (Simpson, 1945, p. 267) that the common stock of Giraffidae and Cervidae perhaps ought to be "considered giraffid, with cervids arising from giraffids."

* Though Webb (1948 a) has shown that vestigial eyes are present in *Haematopinus*.

The Bovidae are universally infested with ischnoceros Mallophaga belonging to the family Trichodectidae and (with the possible exception of *Holakartikos*) to the genus *Damalinia*. *Holakartikos* is at least very closely related to *Damalinia*.

Practically all Bovidae are also infested with *Linognathus*, and very frequently by two species of the genus, of which one is always long-headed and the other short-headed. *Haematopinus* is not infrequent on the Bovidae but is confined to the large or very large species of hosts.

Artiodactyla in general.

We know the lice of Artiodactyla very much better than those of most groups, and the outlines of the picture are perfectly clear, though much detail remains to be filled in. A gratifyingly large number of the records are from wild hosts and wholly reliable.

No Amblycera occur, except for the probably secondary infestation of the peccaries with Gyropidae. Ischnocera are not known from the Suina nor from the Giraffidae but these latter have certainly not been sufficiently examined. On the remaining groups Trichodectidae are universal and all belong to the genus *Damalinia* or very closely-related genera; the species on different species of hosts are almost invariably different, the few exceptions appearing to be mostly (but not all) due either to misdeterminations of the parasites or to the hosts not being really specifically distinct.

With regard to the Anoplura of Artiodactyla, the genus *Linognathus* is universal on the Bovidae and occurs also on the Giraffidae. *Solenopotes*, on the Cervidae with one probably secondary occurrence on cattle, has evolved from a form similar to *Linognathus*, while *Pecaroecus* and *Microthoracius* are closer to *Haematopinus*, a more primitive genus than *Linognathus*. The distribution of this *Haematopinus*-group of genera is of great interest: *Pecaroecus* is in at least one respect the most primitive of them, since it possesses well-developed eyes; it occurs on the peccaries, belonging to the most primitive extant suborder (the Suiformes) of the Artiodactyla, and is replaced on the true pigs by *Haematopinus*, which has only vestigial eyes. On the Camelidae the group is represented by *Microthoracius*, which also has vestigial eyes. The genus *Haematopinus* occurs universally on the true pigs and sporadically on a few of the Bovidae, in the latter case only on the larger members of the family—an obvious case of secondary absence on the smaller forms. This group of genera exhibits well one of the great difficulties in the way of the systematist who attempts to erect a natural classification of the Anoplura: the combination of primitive and specialized characters in the same genus, with the probability that similar specializations (particularly the loss of eyes) have taken place independently in different groups. Instances of this phenomenon are numerous: a reduction in the number of antennal segments to four “has undoubtedly arisen quite independently at least three times in the Anoplura” (Ferris, 1920–1935, p. 481); in the distantly related genera *Ratemia* and *Pedicinus* the number of abdominal pleural plates has in each case been reduced to three, giving the two genera a misleading appearance of close relationship, and the first pair of legs has become reduced in size in at least two wholly independent cases (the *Linognathus* group and the lice of seals).

There can be no doubt whatever that the infestation of the Artiodactyla with both Trichodectidae and Haematopinidae is primary; in both groups of lice the genera are so widely distributed on this order of hosts, so closely related among themselves, and so different from those of other orders of mammals (except in the case of orders also belonging to the cohort Ferungulata) that the infestations could not possibly have had a secondary origin. Moreover, the fact that the relationships of the lice of various very distinct branches of the Ferungulata are nearly all with one another rather than with the lice of other cohorts

not only supports the view that the cohorts are natural divisions but also suggests strongly that the louse infestations are primary so far as the cohort is concerned, and not merely the orders composing it. *Linognathus* and *Haematopinus* (or very close relatives) both have such a wide distribution on the Ferungulata that it is certain that both must represent primary infestation of the ungulates (*s.l.*) at least and almost certainly of the Carnivora as well.

VI. THE ANTIQUITY OF LICE AS PARASITES OF VERTEBRATES.

Since lice are unknown as fossils, any evidence as to their antiquity must be indirect and must be based on examination of their present distribution on groups of hosts the antiquity of which is approximately known from the direct evidence of fossils, and occasionally in geographical areas the approximate age of which is known. The argument is a simple one: that if two branches of a mammalian stock are both infested with closely-related lice, then the stock from which both branches diverged must also have been infested with similar lice; if therefore, we can establish the date at which divergence of the host-branches took place we have set an upper time-limit for the infestation of the group with lice, which may be earlier but cannot be later. In any such examination of the antiquity of mammal-lice the Anoplura and Rhyncophthirina are of special significance because they are unknown except on mammals and must be assumed to have evolved on this group of hosts, whereas the Amblycera and Ischnocera occur even more abundantly on birds and their infestation of mammals may perhaps be secondary. Any deductions we may obtain must, of course, be inconclusive, the evidence being of such a nature as to permit of our establishing probabilities but not facts. Our argument must be based almost exclusively on those instances in which there is no reason to suspect that an infestation may be secondary, and we are not entitled to draw any weighty deduction from the absence of lice (or any group of them) on a particular group of hosts, because of the probability that this absence may be secondary. Making all allowances for the imperfection of the evidence and its contamination by cases of secondary infestation, I believe that from the present host-distribution of the Phthiraptera it is possible to make deductions which, while inevitably falling short of scientific proof, have as their basis sufficient evidence to establish a very high degree of probability.

(1). PREVIOUS ATTEMPTS TO UTILISE THE EVIDENCE.

The earliest attempt to deduce the antiquity of lice from their host-distribution of which I am aware was made by Harrison (1914, p. 9) when he put forward a tentative suggestion that "the adoption of a parasitic habit by Mallophagous insects occurred even as far back as late Mesozoic time"; two years later (1916 *a*, p. 257) he restated his belief that this mode of life dated "from late Jurassic or Cretaceous times", and still later (1928 *a*, p. ix) he suggested that the period was the Jurassic. He accepted without question the assumption that the first Mallophaga parasitized birds (an assumption which I regard as probable but unsupported by conclusive evidence) and considered that they took to a parasitic life on vertebrates at a time when they had not evolved beyond the stage represented by the most primitive of the Amblycera "and that they parasitized both birds and marsupials before the true mammals had differentiated out." My own deductions from the evidence not only fully support Harrison's main contention, but suggest a still earlier date for the origin of the Mallophaga as parasites of vertebrates.

Ewing (1929, p. 93), though not concerned with deducing a date for the origin of the Mallophaga, attempts to prove that they originated on birds. He asserts that Harrison "considers the Mallophaga of the Australian marsupials (family Boopidae Mjöberg) as being the most primitive"—a statement for which I can find no basis in Harrison's work. He then states that the conclusion as to the

primitive nature of the Boopidae " is based upon a highly debatable assumption, *i. e.* that the biting lice originated as mammal parasites ", whereas in reality Harrison made no such assumption but accepted the assumed origin of the group on birds. After reminding us that the Mallophaga are practically universally present on all birds but are absent on several large and important groups of mammals, Ewing continues as follows :—

" Then since the evidence is so strong indicating the origin of the biting lice from the Corrodentia would one not look for the most generalized types on the more ancient of the land birds ? Here we are met by the fact that the lice upon the large flightless birds, the Palaeognathae, belong to the more specialized order, or the Ischnocera. Evidently these lice, some of which are peculiarly specialized in being asymmetrical, are of a relatively recent acquisition by the hosts. Of the land groups of birds of flight it is precisely upon the commonly accepted most ancient group, the Galliformes, that we find the most generalized forms of lice, those of the genera *Menopon* and *Menacanthus* and other nearly related genera. These lice are distinguished from those occurring on the Australian marsupials by only trivial characters hardly of sufficient importance to be accorded generic significance. Could not the Australian marsupials have obtained their lice from birds just as the domestic dog in North America has obtained one of its louse species, *Heterodoxus longitarsus*, from an Australian marsupial ? Certainly American marsupials did not get biting lice from Australian marsupials, but rather from rodents with which they were associated."

Ewing's argument is so full of flaws that it becomes difficult to deal with it. I am quite unable to understand why the admitted descent of all lice from the Psocoptera (Corrodentia) should be considered to be evidence for the evolution of the Mallophaga on birds rather than on mammals. I think I have proved (pp. 427-432) that the absence of Mallophaga on certain groups of mammalian hosts is almost certainly secondary, but I must modify Ewing's statement about the distribution on birds of the groups Amblycera and Ischnocera, for Amblycera are absent or very rare, not only on the Palaeognathae, but also on the Tinamiformes, Sphenisciformes and Gaviformes, all very primitive groups. The case of the Tinamiformes is particularly instructive because (in spite of Ewing's statement that the Galliformes are commonly accepted as the most ancient group of terrestrial birds of flight) ornithologists are in general agreement that the Tinamiformes are considerably more ancient. On the Tinamiformes we find an enormous development of the Ischnocera and only two or three exceedingly rare species of Amblycera. It seems to me that it would be more logical to argue that, since all the most primitive groups of birds are devoid of Amblycera (or nearly so), the birds must have acquired their amblycerous fauna from marsupials, than that the marsupials derived their Amblycera from birds. I do not, however, argue in this way because I consider that the absence of Amblycera on the more primitive birds is very probably secondary.

Nor do I agree with Ewing's statement that the differences between the Mallophaga found on Australian marsupials and the bird-infesting genera *Menopon* and *Menacanthus* are trivial ; Harrison (1915, p. 124) considered that these differences were worthy of family rank. Further, although the acquisition by the great flightless birds (ostrich, emu and rhea) of their obviously closely-related Mallophaga may perhaps have been " relatively recent " it cannot have occurred later than the Cretaceous period, when the land-bridge between Africa and South America broke down. I have already stated (p. 538) my belief that there is no certainty that the American marsupials derived their biting lice from American rodents instead of *vice-versa*.

Webb (1946, p. 100) has also dealt with the origin of lice and considers that they originated on birds. His argument would be much more convincing if he had been able to examine members of the Boopidae and had found that these had spiracles of a less primitive type than those of bird-infesting Amblycera. Moreover, I cannot see that development of Amblycera from psocids is more likely to have taken place in a bird's nest than in a mammal's nest. The balance of probability seems to me to be very slightly in favour of the Amblycera having originated on birds, and a little more strongly in favour of the Ischnocera

having migrated from birds to mammals (particularly in the case of *Trichophilopterus*). I entirely agree, on totally independent grounds, with Webb's suggestion that the Anoplura are derived from the same ancestral stock as the Trichodectidae.

(2). EVIDENCE FROM MAMMALS.

Anoplura.

Undoubtedly primary infestations of sucking lice occur on the Perissodactyla, Artiodactyla, Hyracoidea, Pinnipedia, Rodentia, Lagomorpha and Primates; those of the land-carnivores, the Dermoptera and the Insectivora are probably primary (though *Polyplax* on Insectivora is here regarded as secondary), and that of the Tubulidentata is perhaps secondary.

The first two of these host-groups are derived from the Condylarthra and their Anoplura are very closely related, so it seems certain that the Condylarthra were infested with Anoplura; in this connection it is to be noted that both groups of hosts are herbivorous, rendering acquisition of lice from other mammals excessively improbable. The Hyracoidea, if not derived from the Condylarthra, must be descended from a kindred but still older stock; their Anoplura are very close to *Linognathus*, so that they afford strong confirmation of the suggestion that the earliest ungulate mammals must have been infested with a *Linognathus*-like genus of lice.

The Pinnipedia are mainly flesh-eaters, but their food does not include other mammals, so that it would be almost impossible for them to have become secondarily infested. But the Pinnipedia are derived from the Creodonta, so these also must have borne Anoplura. Moreover, the seal-lice show obvious traces of derivation from a form not distantly related to *Haematopinus*, linking these lice closely with the *Haematopinus*-group of genera found on so many different groups of the ungulates (both Perissodactyla and Artiodactyla) and making it almost certain that the original stock of the Ferungulata must have been infested with a louse very near to *Haematopinus*. Similarly, the almost certainly primary infestation of the ungulates with *Linognathus* or related forms links up with the occurrence of this genus on Canidae and greatly adds to the probability that the sucking lice of the Canidae are a residual infestation and that the absence of such lice on the other land-Carnivora is secondary. There is fossil evidence which suggests that the Condylarthra and the Creodonta had a common ancestor, and the relationships between their sucking lice very strongly support this suggestion, but the geological evidence shows that such an ancestor could not have existed later than the lowest Eocene and was more probably of late Cretaceous date. The latest date we can assign to the Anoplura, on the evidence just discussed, is the lowest Eocene period.

But the Anoplura also occur as undoubtedly primary infestations on the Rodentia and the Primates. The origins of the Rodentia are so poorly understood that the group is of but little use to us in drawing our deductions, but rodents are known from the Paleocene and it seems improbable that they had a common stock with any other orders of mammals (except perhaps the Lagomorpha) later than the middle of the Cretaceous period. The origins of the Primates are better known, and their relationships to the Condylarthra-Creodonta stem are not very close (it seems significant that the Anoplura of these two stocks are also apparently not very closely related). It seems certain that these two stocks cannot have had a common ancestor later than the first placental mammals, before the middle of the Cretaceous period.

The evidence is all in agreement and makes it very nearly certain that the Anoplura infested the first placental mammals during the middle of the Cretaceous period. Moreover, these lice must have been true Anoplura and not annectant forms between the Mallophaga and Anoplura, because all three host-stocks discussed (Primates, Rodentia and the descendants of the Condylarthra and Creodonta) are infested with lice of the true anopluran type. It

is permissible to suggest the possibility that the Anoplura are not much older than the mid-Cretaceous period, because of the apparent absence of the group on non-placental mammals, but this absence may be secondary.

With regard to the date of the evolution of the Anoplura, the distribution of genera may be used as a check on what has been argued from the distribution of the group as a whole. The Camelidae of South America (llamas) are infested with *Microthoracius*, a highly distinctive genus which has recently been re-discovered on the true camels of North Africa, the species found on the African camels being very closely related to those found on llamas. The latest known fossils of Old World Camelidae which share the characters distinctive of the llamas come from Lower Pliocene deposits, so the genus *Microthoracius* must then have been already differentiated and may, of course, be very much older. But Camelidae are known from the Upper Eocene, so it is altogether improbable that the genus *Microthoracius* had not already begun to differentiate from the common stock of the Anoplura of ungulates in Eocene times. If the genus *Microthoracius* is of at least Eocene date, it seems practically impossible for the family Haematopinidae to be later than the Paleocene, or for the suborder Anoplura to be later than the Cretaceous, which is the date suggested by the evidence previously discussed. Similarly, I have argued above that genera akin to *Linognathus* and *Haematopinus* probably existed in the late Cretaceous period.

Again, the genus *Pediculus* is common to man and the chimpanzee, and man is believed to have diverged from the rest of the great apes in the early Miocene, so *Pediculus* must have existed at least in the early Miocene. But *Pediculus* is closely related to *Pedicinus*, which infests the cercopithecoid monkeys. The latter probably date from the Eocene period, so a genus ancestral to *Pediculus* and *Pedicinus* was probably extant during the Eocene.

Rhyncophthirina.

The occurrence of the same species of *Haematomyzus* on both *Elephas* and *Loxodonta* is of very great interest, for these two genera are both known as fossils from Pleistocene rocks. The fact that the two genera are not only both infested by *Haematomyzus*, but by the same species of that genus, gives an indication of the enormous length of time during which a parasite may persist unaltered, and suggests that the species *Haematomyzus elephantis* may already have been a very ancient form during the Pleistocene. In any case the species can hardly be later than the Pleistocene period, and the genus must obviously be very much older.

In considering the earlier history of the Rhyncophthirina we are faced with the difficulty that the only two twigs of the elephant-stem which have persisted to the present day diverged relatively recently. In this connection the alleged occurrence of *Haematomyzus* on a rhinoceros would be of immense interest if there were the slightest reason for supposing it to be natural, but this is not the case. Not only does the sole record come from a zoo, but the Rhinocerotidae are widely sundered phylogenetically from the elephants, so that it is excessively improbable that any member of the Rhyncophthirina which occurred naturally on them would belong to *Haematomyzus* and still more unlikely that it would be *H. elephantis*.

In the absence of better evidence we can only suggest the probability that the original Eocene stock from which the Proboscidea evolved was infested with Rhyncophthirina, and the further probability that the group is much older than this. Since the much more specialized Anoplura have been shown (p. 556) to have been almost certainly widely distributed not later than the middle of the Cretaceous period, it seems unlikely that the relatively primitive Rhyncophthirina are of later date than the early Cretaceous, but the evidence is too weak to permit of more than suggesting this date as a possibility.

Ischnocera.

With the *Ischnocera* we encounter the difficulty that they are found on birds as well as mammals, so that the infestation of the latter may have been derived from the former. This objection is particularly applicable in the case of *Trichophilopterus*, which perhaps originated relatively recently from a bird-infesting form and which will not, therefore, be discussed. It hardly applies to the Trichodectidae, which possess at least one feature (the presence of gonapophyses in the female) that is absent in all the known lice of birds except *Osculotes*. Moreover, the Trichodectidae of different groups of mammals are all so obviously inter-related as to make it certain that the surviving groups are all descended from one common ancestor, whether that ancestor evolved on a mammal or was an acquisition from a bird. The Trichodectidae seem to me to be very close to the stem from which the Anoplura branched off, and I strongly suspect that they are the relatively unchanged descendants of the common ancestor of *Ischnocera*, *Rhynchophthirina* and Anoplura.

The present distribution of the Trichodectidae on the orders of mammals closely resembles that of the Anoplura, undoubtedly primary infestations occurring on the ungulates and Carnivora, while the infestations of the Rodentia and Primates are very probably primary. The chief difference is that among the carnivores the seals lack Trichodectidae while the land-carnivores are almost universally infested with this family of lice. This distribution does not, of course, mean that there has been a parallel evolution of Anoplura from *Ischnocera* on each of the mammalian stems concerned, but that the original common stock from which these stems diverged must have been infested with Trichodectidae as well as with Anoplura. Trichodectidae must have been mammal-parasites during the Cretaceous period and must then have parasitized the first placentals. Below this point we are reduced to conjecture, for Trichodectidae are not known from any non-placental mammals. But it is altogether possible that the ancestors of the Trichodectidae parasitized the Pantotheria during the later part of the Jurassic period.

Again valuable confirmatory evidence can be obtained from the distribution of groups within the family Trichodectidae. The Carnivora are infested with a number of natural groups which merge into one another so completely that I refuse to regard most of them even as subgenera though others regard them as genera. Of these groups *Trichodectes s.str.* occurs exclusively on Canoidea, as also do various groups that I regard as referable to this rather than to *Felicola*, the latter group is confined (as *Felicola s.str.*) to the Feloidea, while *Suricatoecus*, which I consider to represent a stage in the evolution of *Felicola* from *Trichodectes*, occurs on both Canoidea and Feloidea. Far the simplest explanation of these facts seems to me to be that the original Fissipeda were infested with a genus extremely similar to *Trichodectes s.str.*, that this had already given rise to *Suricatoecus* before the Canoidea and Feloidea diverged, and that on the Feloidea (but not on the Canoidea) *Suricatoecus* evolved further to produce *Felicola s.str.*, *Suricatoecus* subsequently dying out on most of the forms of both Canoidea and Feloidea. But if *Suricatoecus* was present on the common stock of the Canoidea and Feloidea it must have existed in the Upper Eocene period, when these two superfamilies had apparently already diverged. And if an extant genus (or subgenus) of Trichodectidae was in existence during the Eocene period, then the lowest Eocene or even the Paleocene is surely too late a date for the evolution of the family as a whole, and an early date in the Cretaceous is much more probable; a still earlier date is, of course, not excluded.

Amblycera.

Here, again, we are dealing with a group which parasitizes birds as well as mammals, and which may have been secondarily acquired from the former by the latter.

Amblycera occur on Rodentia, Primates, Suina and marsupials, the families concerned being the Gyropidae and Boopidae. The Gyropidae are so distinct from all other Amblycera* and so widely distributed on certain groups of rodents that their infestation of the rodents must be regarded as primary, but they occur so sporadically on Primates and Suina that their infestations of these groups must be assumed to be secondary. A primary infestation of the rodents takes us back to about the middle of the Cretaceous period, below which date we are reduced to guess-work on account of the obscure relationships of the Gyropidae. One is at liberty to assume either that the Gyropidae were then of much wider distribution on mammals and were linked up with the other mammal-infesting Amblycera, or that they were independently acquired by the ancestors of the rodents from birds. I greatly prefer the former hypothesis because of the isolation of the Gyropidae from all bird-infesting genera and the fact that they seem to have a distant relationship to the Boopidae.

The Trimenoponinae and Boopinae are of much greater interest because they are the only lice known to occur naturally on non-placental mammals. I have discussed these groups above (pp. 536-538) and have stated my belief that they are closely related and that the occurrence of Trimenoponinae on South American marsupials is probably primary, while the infestation of the Australian marsupials with Boopinae is certainly primary. From this there follows a very strong probability that the original stock of the marsupials was infested, and since marsupials are known to have existed in the Cretaceous period it seems exceedingly probable that Amblycera were then parasites of marsupials. There is no reason to suppose that they are not very much older than this, and it is entirely possible that they occurred on the Pantotheria. If the marsupials acquired their Amblycera from birds this may have happened during the Jurassic period or at the very beginning of the Cretaceous, but if Amblycera evolved on mammals the group may have parasitized the original stock of the mammals at the end of the Triassic period. In this connection the absence or great rarity of Amblycera on the most primitive surviving groups of birds is interesting but by no means conclusive because of the probability of it being secondary. Nor is it necessary to assume that Amblycera cannot have infested the ancestors of mammals earlier in the Triassic period before true mammals (even of the monotreme type) had appeared, for the fact that the monotremes have hair not differing in essentials from that of marsupials and placentals shows that hair must have been evolved at the time the first mammals appeared, and suggests the possibility that some of the later ictidosaurian ancestors of mammals may also have been hairy. Even if this was not the case, the evolution of hair from scales must have involved the appearance of intermediate conditions and there is no reason to suppose that none of these intermediate types of skin-covering provided suitable food and shelter for the hypothetical very unspecialized Amblycera which are the only type of lice that could then have been in existence.

Phthiraptera.

Considering the whole of the evidence derived from the distribution of lice on the mammals, and taking first the more specialized (and therefore presumably younger) groups, the Anoplura can hardly be more recent than the period when the Condylarthra, the Creodonta, the Primates and the Rodentia were all represented by one common stock, which is about the middle of the Cretaceous period.

The available evidence with regard to the Rhyncophthirina is too scanty to permit of more than a suggestion that the group probably occurred before the Eocene period and is not likely to be younger than the Anoplura.

The Ischnocera as parasites of birds will be considered later, but as parasites

* Their affinities perhaps lie with the Boopidae rather than with any bird-infesting group.

of mammals they not only must have occurred in the Paleocene, but at that date the principal mammal-infesting family was the Trichodectidae, just as it is today. The Ischnocera must have occurred on mammals in the Cretaceous and the infestation may even go back to the Jurassic but the absence of this group on the marsupials, though inconclusive, is somewhat against so remote an origin; an early Cretaceous date is more probable.

If we accept my suggestion that the resemblances between the Boopinae and the Trimenoponinae are evidence of genuine relationship and not of convergence, then the Amblycera probably infested marsupials at a date not much later than the origin of the latter, which is at latest the early Cretaceous period. Attempts to trace the Amblycera as mammal-parasites beyond this period are frustrated by the possibility that the earliest marsupials may have acquired their Amblycera from birds.

(3). EVIDENCE FROM BIRDS.

The ancestry of the birds is, unfortunately, much less well established than that of the mammals, at least so far as the different orders are concerned. The first known bird is *Archaeopteryx*, from the Upper Jurassic, and the group probably evolved in the Upper Triassic period, but the first unquestioned ancestors of modern groups occur in the Upper Eocene, when the main orders and families were already well marked. There can be no doubt that these must have arisen from the rich and varied avifauna of the Lower Eocene, and these, in turn, from the toothed birds of the Cretaceous, but the affinities of all the forms which are older than the Upper Eocene are in dispute.

No birds are infested with Anoplura, but all which have been adequately examined possess Mallophaga. The most primitive groups are apparently almost or entirely devoid of Amblycera, but on the higher groups both Amblycera and Ischnocera are universally present. An interesting point is that the Ischnocera of the most primitive groups of living birds almost all possess the primitive "circumfasciate" type of head-structure which is also the only type found in the Trichodectidae; this type of head-structure persists in lice from birds at least as high up the scale as woodpeckers, but on all the higher groups of birds non-circumfasciate genera of Ischnocera tend to be dominant.

I have formerly used the absence of Amblycera as an argument for the ancient nature of certain groups of birds, but if we are to accept the unproved but generally accepted assumption that the Mallophaga evolved on birds, this is too bold an argument, for if this assumption is correct the absence of Amblycera on the lowest orders of birds must necessarily be secondary. Without accepting or rejecting the assumption that the Mallophaga arose on birds, I agree that the absence (or great rarity) of Amblycera on the most primitive groups is probably secondary.

The facts that no birds which have been sufficiently examined are without Mallophaga, and that each order of birds has at least some genera of Mallophaga which are not found on any other order, are conclusive proof that Mallophaga must have occurred on birds at a time before the present orders had evolved, *i. e.*, not later than the Lower Eocene and in all probability very much earlier. On this point there is very strong supporting evidence: the ostrich, emu and rhea, Ethiopian, Australian and South American respectively, are all infested with Ischnocera which are obviously closely related, and which therefore cannot have been independently acquired by each of these hosts. But all three hosts are flightless and the land bridge between Africa and South America broke down during or before the Cretaceous period, since when there can have been hardly any contact between ostriches and rheas, though it is possible that there may have been a certain amount of later contact through Holarctica. The ancestors of these birds must, therefore, in all probability have been infested by Ischnocera during the Cretaceous period. Since at that date the Ischnocera were already in existence, it seems impossible that the much more primitive

Amblycera began to be parasites of vertebrates later than the Jurassic, and entirely possible that the period was the Upper Triassic, when the first birds are believed to have appeared; the uncertainty as to whether the Mallophaga evolved on mammals or on birds forbids our asserting on which group of hosts these very early Mallophaga occurred, but I consider it extremely probable that during the Jurassic period, at least, Mallophaga occurred on both birds and mammals.

(4). EVIDENCE FROM FOSSILS.

We have now discussed the distribution of the Phthiraptera on mammals and on birds and have deduced from the evidence a very early date for the origin of the group as parasites of these two classes. Before we proceed to make any deductions from the distribution of lice on the mammals and birds together, it is incumbent on us to see if there is any geological evidence which conflicts with the deductions we have so far drawn. Although lice are not known as fossils, many other groups of insects are, and it is from these latter groups that our evidence must be drawn. In this connection we must remember that the Phthiraptera belong to the more primitive hemimetabolous division of the insects.

The first undoubted known remains of insects occur in the Devonian, and by the Carboniferous period they are not only numerous but begin to show strong affinities to many of the extant orders of the hemimetabolous group. In the Triassic most of the insect-remains are referable with confidence to the existing orders and by the Jurassic many of them can clearly be referred to existing families; Baker (1931, p. 191) notes the occurrence in the Lower Eocene strata of fossil larvae of the Oestridae or bot-flies, parasites belonging to one of the highest groups of one of the most specialized orders of insects (the Diptera). No date, later than the Carboniferous, which we care to suggest for the origin of an extant order of hemimetabolous insects would be at variance with the geological evidence, and the fact that the Jurassic insect-remains are often referable to existing families even suggests that the Jurassic is too recent a date to look for the emergence of an order, though it must be admitted that a new order might arise at any time when conditions (in this case the existence of hosts with a suitable skin-covering) became favourable.

(5). THE EVIDENCE AS A WHOLE.

Now let us take the evidence as a whole. I have summarized above the evidence derived from the distribution of lice on the various groups of mammals, and claim to have proved (as nearly as is possible from the available evidence) that the Anoplura must have existed in the mid-Cretaceous period, the ischnocerous family Trichodectidae in the early Cretaceous period or perhaps the Jurassic, and the Amblycera in the Jurassic. All these dates are the latest which I consider it justifiable to suggest on the evidence; earlier dates are by no means excluded, though there is a little evidence which suggests that the Anoplura may not be much older than the middle of the Cretaceous period.

The evidence derivable from the distribution of the Mallophaga on birds is much less satisfactory because we know far less about the origins of the different orders of birds than of those of mammals, but it demonstrates the great probability of the presence of Ischnocera on birds in the Cretaceous period and suggests the improbability of a later date than the Jurassic period for the first infestation of birds by Mallophaga, with nothing to suggest that an earlier date is unlikely.

The evidence of fossil insects not only does not conflict with the deductions drawn from the present-day distribution of lice, but even suggests the possibility that the Jurassic may be too late a date to expect the emergence of a new order, and that for this we ought to seek not later than the Triassic period.

It is particularly to be noted that the various lines of evidence, each inconclusive when taken by itself, all support one another. Not one of them is inconsistent with my suggestion that the first Mallophaga must have been parasites of vertebrates not later than the early Jurassic period, and in all probability in the Triassic.

The almost universal occurrence of lice on both mammals and birds inevitably suggests the possibility that they occurred on a common ancestor of these two groups, but Professor Broom tells me that no such common ancestor could have existed later than the Lower Permian period. The complete absence of the Phthiraptera on modern reptiles seems to exclude so early an origin for the order, though it is doubtful if lice could live on a scale-covered skin. Unfortunately we do not know what was the skin-covering of the Cotylosauria of the Lower Permian.

I suggest that the sequence of events was more or less as follows: in the late Triassic period primitive hemimetabolous insects of the same stock as the Psocoptera found food and lodging of a suitable kind on the skin of either the ancestors of the mammals (possibly still reptilian) or the very early birds; both the ancestors of the mammals and the early birds were for the most part carnivorous, the Proto-Mallophaga were not yet at all specific in their choice of host, and transfer took place from the mammal-ancestors to the birds (or *vice-versa*) as the successful predator devoured its prey. It is tempting to suggest that the Amblycera may have arisen on one of the groups of hosts and the Ischnocera on the other, but there seems to be no evidence whatever in favour of such a suggestion and I think it much more probable that both groups developed on the same host-class and transferred to the other before even feebly specific host-associations had developed. It seems impossible to decide whether the ancestors of mammals or the early birds were the first groups to be infested by Mallophaga. By the time the main branches of the placental mammals had diverged (probably in the mid-Cretaceous) not only had the Ischnocera evolved (probably in the Jurassic or earlier) from the Amblycera, but the existing family Trichodectidae was already extant and host-specificity must have already appeared, for after this period it would have been practically impossible for the herbivorous Condylarthra to become secondarily infested. The Anoplura probably first appeared during the Cretaceous period and in any case not later than the divergence of the main branches of the placental mammals.

VII. SUMMARY.

The Phthiraptera or lice are divided into three main groups or suborders Mallophaga, Rhyncophthirina and Anoplura, of which the first-named is further divided into the superfamilies Amblycera and Ischnocera. All the Phthiraptera are derived from one stock, which appears to have been an off-shoot of the Psocoptera.

All the lice are obligatory ectoparasites of mammals or birds; the Rhyncophthirina and Anoplura occur exclusively on mammals, while the Amblycera and Ischnocera are found on both mammals and birds, though the families found on the two host-classes are different. Lice belonging to at least one of the main divisions occur on all the large orders of mammals except the Chiroptera. Evidence is produced that lack of lice (or of certain groups of lice) on given groups of hosts is very often due to secondary absence, and it is suggested that such instances of secondary absence are frequently due to competition, either between the different groups of lice or with other groups of ectoparasites. A host-list of the lice of mammals is provided, so that the reader may evaluate for himself the deductions made.

The entire life-history of all the lice takes place on the host, and the food is blood, hair or feathers, skin-debris, and probably mucus and sebaceous matter, all provided by the host; the food is different for each of the suborders of lice.

The absence of the necessity for any part of the life-history to take place off the host has made possible host-associations which are more extremely specific than in the case of any other large group of ectoparasites, and this in turn has rendered successful interspecific transfer of louse-species excessively difficult. Even transfers which result in the death of the transferred lice within a brief period are very uncommon in natural conditions except in the case of predator and victim, but in the latter instance opportunities for such transfers must be common. The paucity of authentic records of lice occurring in natural conditions on a host to which they are not normal must mean that there is some factor which inhibits the successful establishment on the predator of a louse-infestation derived from its prey, and there is strong evidence that this factor is that the food-supply available on the strange host is, with rare exceptions, unsuitable, or even lethal, to the invading lice.

The extreme specificity of the host-associations of the lice leads to the most interesting feature in the study of the order, because there is overwhelming evidence that the vast majority of lice have infested the groups of hosts on which they now occur ever since the date when these host-groups became differentiated from their parent stocks. Because evolution has almost invariably proceeded more slowly in the lice than in their hosts, the relationships between the former may often be used to trace the phylogeny of the hosts in cases in which evolution of the latter has proceeded so far that their relationships have become obscure.

No lice are known as fossils, but their present host-distribution can be used, coupled with the evidence derived from fossils of the host-groups, to furnish evidence as to the antiquity of the various groups of lice. From such evidence I have deduced that the Anoplura cannot be of later origin than the middle of the Cretaceous period, that the Ischnocera existed in the early Cretaceous or the Jurassic, and the Amblycera in the Jurassic, earlier dates not being in any way excluded; the evidence with regard to the Rhyncophthirina is too scanty to permit of more than a suggestion that this group is probably much older than the Eocene period and may well have existed in the Cretaceous. It is perfectly possible that the ancestors of the Amblycera (the most primitive of extant groups of lice) may have begun to be ectoparasites of vertebrates during the later part of the Triassic period, and that they then parasitized either the very earliest mammals and birds or the still reptilian ancestors of these two groups.

It may be useful to summarise also the lines along which it seems to me that future work should proceed in order to make the maximum additions to our knowledge of lice:—

(i). *Collecting*.—Very much more collecting is necessary, especially in the Oriental Region, and so far as possible this should be combined with population-studies such as have been carried out in the case of *Pediculus humanus*; these studies are likely to give results of particular interest in cases of multiple infestation. In this connection the dissolving-technique has given us a method whereby big game hunters can add very greatly to our knowledge with very little trouble to themselves, for many who would be unable to spare the time to collect lice by other methods would find it easy to rip off and dry a few skins for subsequent examination. It should not be forgotten that many large mammals are inevitably doomed to become very rare or even extinct with the development of the countries in which they dwell, so that no time should be lost in ascertaining the parasite-fauna of such threatened species before it is too late. Collections made from captive hosts or from skins in museums are capable of being of great value, and museums should never destroy unwanted specimens (such as faded skins from specimens which have been on exhibition) without giving a specialist on lice the opportunity of dissolving them, but such collections are far less reliable than those from wild hosts and should only be regarded as supplementary to the latter; single specimens from captive hosts or from skins should not be described. Much remains to be ascertained about the parasites of our common

domestic mammals, and some of these offer a particularly fruitful field for observations on the question of ecological niches. The specialist should show much more care than is often the case with regard to the recording of data concerning the host of his parasites; all available relevant facts should be placed on record, particularly the number of lice obtained, the number of host-individuals from which they were collected, and whether the host was wild or captive. The collector often does not yet realize how easily contamination may occur, and the specialist too frequently shares his failure to appreciate this point and therefore publishes "facts" which are sheer nonsense; in my opinion it is the duty of the specialist to refrain from publishing records which are not almost certainly reliable.

(ii). *Systematic work.*—The quality of our systematic work on lice has improved immensely in the last thirty years, though there is still room for further improvement, especially with regard to very closely related species and subspecies; in my opinion any constant difference (however small) between different communities of lice should be recognized, and this is a strong argument for the examination of long series whenever possible. Bad methods of mounting specimens for examination have been responsible for much bad systematic work and must be abandoned, and we must also cease identifying specimens with inadequately-described species from another host from which material is not available. We still badly need a good super-generic classification of the Anoplura. Description of new species from material the host of which is not known serves, in my opinion, no useful purpose. Revisions should be directed to genera (or groups of genera) of lice, not to the fauna of geographical areas.

(iii). *Experimental work.*—Experiments on the biology of lice are so few, except in the case of *Pediculus humanus*, that they can hardly be regarded as having begun. Points on which information is specially desirable include the factors which result in host-specificity, the degrees of relationship between hosts within which these factors operate, and the results of transferring lice of a given species to a host already infested with a closely related species or with a different subspecies of the same louse. It would also be of very special interest to observe whether successful transfer of a louse to an abnormal host will eventually result in morphological changes in the louse, and this could probably most easily be done by transferring specimens of a known human strain of *Pediculus humanus* to uninfested individuals of *Ateles* (spider-monkeys) and examining samples of the resulting populations at intervals over a long period.

VIII. LITERATURE CONSULTED.

From the list below I have omitted many papers which I consulted but found to contain neither records of lice from mammalian hosts nor important information on subjects dealt with in this paper, and I have made no attempt to make an exhaustive examination of the immense bulk of economic literature on the lice of man and his domestic animals. A few important papers which I have not seen are included in the list, in brackets.

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* Parts I-IV of this work are paged consecutively, parts V-VIII have independent pagination at the top of the pages and pagination consecutive with that of the earlier parts at the bottom. All references are to the consecutive pagination.

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