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FLEAS, FLUKES & CUCKOOS

THE NEW NATURALIST

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THE NEW NATURALIST

FLEAS, FLUKES &
CUCKOOS

A STUDY OF BIRD PARASITES

by

MIRIAM ROTHSCHILD

and

THERESA CLAY

*With 99 Black and White Photographs
4 Maps & 22 Drawings*



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To
Charles Rothschild

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CONTENTS

	PAGE
EDITORS' PREFACE	ix
AUTHORS' PREFACE	xii

PART ONE

CHAPTER

Introduction	1
1 Parasitism	6
2 Commensalism	11
3 Symbiosis	20
4 The Effect of Parasites on the Host	30
5 The Effect of Parasitism on the Parasite	38
6 The Origins of Parasitism and the Evolution of Parasites	47

PART TWO

Introduction	56
7 Fleas	61
8 Feather Lice	118

PART THREE

Introduction	158
9 Protozoa	159
10 Worms	176

CONTENTS

	PAGE
11 Flies	211
12 Mites	224
13 Micro-Parasites	235
14 The Fauna of Birds' Nests	245
15 Skuas	253
16 The European Cuckoo	256
 BIBLIOGRAPHICAL APPENDIX	 269
INDEX OF POPULAR AND SCIENTIFIC NAMES	283
GENERAL INDEX	296
INDEX OF SCIENTIFIC NAMES OF BIRDS MENTIONED IN THE TEXT	 302

ILLUSTRATIONS

		FACING PAGE
Ia	Starling Louse	6
Ib	Quill Louse	6
II	Great Spotted Woodpecker	7
III	Great Tit removing cap from milk bottle	14
IVa	Robin perched on spade	15
IVb	Hen Blackbird sunning	15
V	Phoresy	22
VI	Barn-Owl feeding Rat to young	23
VII	Effect of parasite on host	30
VIII	Young Starling preening	31
IX	Louse-flies	34
X	Pronotal comb of Mammal Flea and Bird Flea	35
XI	The two main types of Fleas	50
XII	Mouth-Parts showing adaptations to specialised methods of feeding	51
XIII-XIV	The Receptaculum Seminis of Female British Bird Fleas and Mammal Fleas	66-67
XV-XVI	Terminal Portion of Male British Bird Fleas	82-83
XVII	Common House-Martin Flea	98
XVIII	Life-Cycle of Flea	99
XIX	Pygidium of Flea	114
XX	Swan	115

ILLUSTRATIONS

XXI	Feather Louse from Common Tern	130
XXII	The two main types of Feather Lice	131
XXIII	Different kinds of Feather Lice	146
XXIV	Eggs of Wing Feather Louse	147
XXV	<i>Trypanosoma</i>	162
XXVI	Sand-Martins preparing to migrate	163
XXVII	Fluke, Roundworms and Tapeworm	178
XXVIII	Intermediate hosts of Herring-Gull Fluke	179
XXIX	Biting Midge	210
XXX	Mosquitoes which feed on Birds	211
XXXI	Feather Mites	226
XXXII	Sheep Tick	227
XXXIIIa-b	Common House-Martin Flea	242
XXXIIIc	Leg of Shearwater Flea	242
XXXIVa	Cormorant Colony	243
XXXIVb	Shearwater at entrance to its burrow	243
XXXV	Sand-Martin at nest burrow	258
XXXVI	Bed-bug and Swallow-bug	259
XXXVII	Whitethroat removing parasites?	264
XXXVIIIa	Arctic Skua	265
XXXVIIIb	The Cuckoo	265
XXXIX	House-Martins collecting mud for their nests	268
XL	Birds congregating on the sea shore	269

EDITORS' PREFACE

AN OBJECT of the *New Naturalist* series is the recognition of the many-sidedness of British natural history, and the encouragement of unusual and original developments of its forgotten or neglected facets. One such facet is the study of parasites, a study all too long regarded as curiosity about mere curiousness, or as excursions into backwaters. Some popular books that have been written on the subject have stressed the unusual, the mysterious, often the macabre. Few have taken the subject truly seriously. This book, which is at the same time an able (and entertainingly written) popular exposition, and an original and new scientific synthesis, will put things in a new and true perspective.

"Birds," the authors quote from A. E. Shipley, "are not only birds but aviating zoological gardens." This book is the first guide to those gardens: it is the study of a community of animals, plants and bacteria that is just as real, as any of the communities of the wood, the stream, the field, or the sea. For the outside and inside of the body of a bird (or for that matter, any other vertebrate animal) harbours, and shelters a vast population of organisms, of many species, whose way of life, relationships and importance are little-known and poorly understood.

Birds are the most intensively-studied animals in the world—yet only a few naturalists consider the existence of the birds' relationships with the vast network of organisms that comprises their parasite-community. Only a mere handful is interested in the subject. But because birds are otherwise so well-studied, they make the best starting-point for a development of the picture of parasites alive and at work. It was fortunate for the *New Naturalist* that this view had been held for many years by the two able workers whose researches and wide scholarship have here borne fruit.

This book, then, leads the reader to the lessons to be learned from the life of parasites, *via* the particular parasites of birds. To

EDITORS' PREFACE

restrict the subject in this way forces a selection from a plethora of examples (of which many are of the same kind) : but it does not result in the loss or omission of any important general conclusions.

This is the first book devoted entirely to the various groups of parasites which live in or on birds. It describes not only the mutual impact of parasite and host, but the extraordinary modifications of the parasites' sexual habits, life-cycles and anatomy which are associated with their loss of independence. The authors also touch upon other curious relationships—between birds and Hymenoptera (wasps and ants), birds and whales, birds and cattle, birds and cuckoos, birds' nests and insects and mites.

Miriam Rothschild is a member of the famous family of merchant bankers, and a sister of the present Lord Rothschild, who is also a prominent zoologist. Like her late father, the Hon. N. Charles Rothschild, she has always regarded parasitology as an hobby, but has approached it scientifically. Since taking her zoological training at London University she has carried out much experimental work at the Marine Biological Station at Plymouth. Of about sixty scientific papers that she has published, at least forty deal with parasites. She is probably the world's greatest authority on bird-fleas.

Theresa Clay, for her part, is probably the world's greatest authority on bird-lice and has published over forty scientific papers on the subject. She has travelled widely accompanying scientific expeditions to Africa, Arabia, Pakistan, North America, Iceland, and the European Arctic. Like Miriam Rothschild, she is a trained zoologist—a graduate of Edinburgh University ; and is now a member of the staff of the British Museum (Natural History).

Fleas, Flukes and Cuckoos points to many interesting fields for research. All *New Naturalist* books tend to synthesise our knowledge of a subject, to demonstrate deficiencies in that knowledge, and to point to new goals. In this book the unsolved problems advertised, and the new avenues charted but unexplored, seem to us to be more numerous than in any other that we have so far had the pleasure of editing. There is not even one worker in Britain who is wholly occupied with that extraordinary group of animals, the trematodes or flukes. If this lucid, informative and interesting book, so unusually illustrated, does not stimulate a new surge of research it will be no fault of the authors, and no credit to British naturalists.

THE EDITORS

AUTHORS' PREFACE

THROUGHOUT this volume an attempt has been made to keep the parasitic relationship in the foreground. In Part I we have dealt with the more general aspect of the subject, and in Part III a brief survey is given of the various groups of parasites which attack birds in Great Britain. In Part II we have tried to present a close-up of two contrasting types of parasitic insects, the feather lice and fleas, in order to illustrate in greater detail the intimate relationship which exists between host and parasite.

The ground we have had to cover is extensive. Some of the groups of bird parasites contain hundreds of species of which many are well known to specialists but are not yet described or named. In the fleas, louse-flies, ticks and tongue-worms only, four exceptionally small groups, we have been able to give a complete list of the species recorded from British birds. In other sections, notably the worms, mites and the fauna of nests, we have merely skimmed the surface of the subject. In those classes in which the existing classification is considered unsatisfactory and probably of a temporary nature only, references to sub classes and orders have been avoided as far as possible. In this edition (third edition, fourth impression) space has not permitted alterations in the text, but merely the correction of errors and misprints, and we have included some new and very important references in the bibliographical appendix. We have also tried to keep the four small groups mentioned above up to date by noting the recent additions on pages xiii to xiv. We have attempted to define "parasitism," "commensalism" and "symbiosis" in the text. The American Society of Parasitology's Committee of Terminology decided that "the present confusion necessitates the definition of the term [symbiosis] whenever it is used" and we think this is true of all three terms. We should, however, like to draw the reader's attention to the rather different definition of these terms by authors such as Davenport (1955) and Allee *et al.* (1949). In order not to overburden the text with "Latin"

AUTHORS' PREFACE

names we have assumed that the reader is familiar with the popular names of British birds, and have included their scientific names in the index only. We have followed the classification and nomenclature in Witherby's *Handbook of British Birds* (1938-1941).

Unfortunately it is quite impossible to name all those who have personally assisted us in the preparation of this book or to refer by title to the extensive literature we have consulted. In the chapter on fleas alone we have quoted from over a hundred papers. We should nevertheless like to express our special gratitude and sincere thanks to all those who have supplied us with specimens, information and criticism, and to all the photographers and draughtsmen who have contributed to the illustrations in this volume. Mr. A. L. E. Barron in particular has lavished infinite care and skill upon the execution of thirty microphotographs which, in many cases, presented great technical difficulties, and Mr. Arthur Smith has produced the excellent black and white drawings. We should like to thank the Editors of the *Proceedings of the Zoological Society of London*, for permission to reproduce Plate XXIV, and the Editors of the New Naturalist series themselves for all the trouble they have taken on our behalf. Mr. Eric Hosking took the magnificent photograph of birds crowding on the sea-shore (Plate XL) especially for this volume—a photograph which has already become famous.

M.R.
T.C.

September, 1949

ADDITIONS TO THIRD EDITION

Chapter 7: Fleas (Aphaniptera).

The hen stick-tight flea (*Echidnophaga gallinacea*) has been recorded by Thompson (1952) on a migrating White Wagtail (*Motacilla a. alba*) a bird which winters in Africa, captured at Skokholm Island. (See pages 71, 84 and 108).

Waterson left out of his count 40 aberrant females (Smit, 1955), so there were actually 2,408 (59%) females to 1,672 (41%) males. (See page 79, line 21).

It is now considered (Smit & Allan, 1955) that *C. farreni* in North Africa is only a variety. A distinct subspecies, however, occurs in Japan and China. (See page 85).

C. riparius has now been found in Transbaikalia (Smit & Rothschild, 1955), which suggests that it spread to the U.S. from the west. (See page 89).

Recently *C. borealis* has been found in moorland districts on the mainland of Britain, and several cases of hybrids between it and *C. garei* have been recorded from this habitat. (See page 89, map 2.)

Ceratophyllus lunatus has now been found in the nest of *Anser leucopsis* in Greenland. (See page 95).

Ceratophyllus styx has recently been split into two subspecies, both of which occur in Britain, *C. styx* Rothschild 1901 and *C. styx jordani* Smit 1955. Hybrids are produced where the two subspecies meet. (See page 113).

Ceratophyllus vagabunda insularis has recently been recorded in Belgium. (See page 115).

Chapter 9: Protozoa.

Baker has recently (1955) found a Plasmodium, probably *P. relictum*, in three rooks, a jackdaw and a blackbird in Hertfordshire. (See page 165).

Baker (1955) has recorded five species of *Leucocytozoon* from birds in Hertfordshire, namely *L. majoris*, *L. sakharoffi*, *L. marchouxi*, *L. dubreuli* and *L. danileuskyi*. (See page 169).

Recently Baker (1955) has discovered that *Trypanosoma avium* is transmitted by the louse-fly *Ornithomyia avicularia*, in which it undergoes cyclical development in the gut. Birds become infected by ingesting infective louse-flies. (See page 172).

ADDITIONS TO THIRD EDITION

Chapter 11: Louse-flies (Hippoboscidae).

Ornithomyia lagopodis is now considered as a synonym of *Ornithomyia fringillina* (See page 213).

There have been two additional records of *Lynchia albipennis* (= *Ornithoponus ardaea*) from Britain: one from the little bittern (*Ixobrychus m. minutus*), and the other from the bittern (*Botaurus s. stellaris*). (See page 214).

There is a record of one specimen of *Olfersia spinifera* from a stray Man O' War bird in the Inner Hebrides in 1953. This is a host-specific parasite of the Fregatidae. (See page 214).

Chapter 12: Ticks (Ixodoidea.)

Ixodes passericola is also recorded from blue tits, great tits and a few other species, and there are two records of *Haemaphysalis cinnabarina* from a mistle-thrush and a skylark. (See page 231).

Chapter 13: Microparasites.

Poulding has recently recorded five cases of Aspergillosis in sea gulls in Britain. (See page 243).

PART ONE

INTRODUCTION

Then said they, What shall be the trespass offering which we shall return to him? They answered, five golden emerods, and five golden mice, according to the number of the lords of the Philistines: for one plague was on you all and on your lords.

I SAMUEL 6 : 4

THE CHILDREN OF ISRAEL knew that the bubonic plague was intimately connected with rats. Indeed, a profound and intensive study of the Bible might well have prevented, or at any rate reduced, the ravages of the Great Plague of London. There is no hint, however, that the ancient Hebrews were aware of the sinister role played by the rat fleas, which, by their promiscuous feeding habits, spread the plague bacillus from rodent to rodent and from rodent to man. The writers of the Old Testament concentrated on essentials and, in this case, were entirely justified in focusing their attention on the rats and mice themselves, for they are the true hosts of the bacillus in question.

To-day, in studying bubonic plague a large section of parasitology and many of its related problems must be considered. A detailed knowledge of the parasitic bacteria which cause the Black Death in rats and, secondarily in man, is, of course involved, but it is also necessary to study associated animals such as fleas, which act as carriers and spread the disease, as well as a whole series of complex factors, like climate, food and the habits and behaviour of the living organisms involved. At one end of the chain we are concerned with the minute differences in the sex organs of fleas and at the other with the international grain commerce of man.

The complicated relationship between parasites and their hosts is one of the chief lures of parasitology. As children we puzzled over the old woman who lived in a shoe, but such a situation appears commonplace compared with that of the worm which lives exclusively under the eyelids of the hippopotamus and feeds upon its tears. To us, at any rate, the parasite's existence seems strange—whether we are concerned with a threadworm which passes its time partly in a bird's heart and partly in an insect's mouth, or a bed-bug which hides in cracks and crevices, and at night steals out to suck blood surreptitiously from a sleeping beauty's breast.

It is only during the past hundred years that parasites, in their role as carriers of disease, have stolen the limelight. It is now quite usual to regard insects and ticks as the makers of history, the moulders of man's destiny and as one of the real enemies of the human race. It was possible to see and hear Hitler and Goebbels but it is impossible to perceive the plague bacillus spreading poison or the malaria *Plasmodium* bursting open red blood corpuscles. The small size of many parasites makes them rather difficult to study. In order to find out something about them it is necessary to spend a considerable amount of time in the laboratory observing minute structural differences between one animal and another with the aid of a microscope, and searching for small and elusive stages of their life-cycle. This work can be both time-consuming and extremely tedious, although at other times it can be exciting and even dangerous—"Image of war without its guilt."

The most difficult problem to contend with in writing a book of this sort is the fact that most parasites are obscure animals of which the majority of field naturalists know little or nothing. If we analyse the reasons why any particular natural history book strikes us as "very good" we generally find that it has increased our knowledge of a familiar and well-loved subject. Ford's book on butterflies is an excellent example of this kind. There is nothing new in this observation, for everyone is aware that gossip about strangers is dull, whereas gossip about one's friends is highly delectable. There is a tendency in all human beings, however, to laugh at the discomfiture of others. The thought of a tapeworm as long as a cricket pitch living secretly in the stomach of a film star, or a beetle quietly chewing the feet of a close-sitting hen arouses in us a feeling of macabre amusement. This is, perhaps, fortunate, for it does not matter what initiates the naturalist's interest, so long as it is aroused. Soon interest leads to familiarity and,

in this case, familiarity breeds love. Many helminthologists find the diffuse kidneys of intestinal worms not only profoundly interesting but objects of considerable beauty. But this, like the aesthetic pleasure derived from pictures painted by Picasso, although real enough, is an acquired taste.

Birds are no more victimised by parasites than any other class of vertebrates but, except for the fish lice (Copepoda) and a few other exclusively marine animals, they are attacked by representatives of most of the well-known parasitic groups, ranging from unicellular Coccidia to the more familiar cuckoos.

The ordinary "normal" bird supports a large number of both relatively harmless and harmful parasites (see fig. 1), the presence of which is largely unsuspected by naturalists as a whole. In fact, it comes as rather a shock to the ornithologist as well as the bird lover to discover the ills to which avian flesh is heir.

Their feathers are eaten and sometimes completely destroyed by lice and mites. The superficial layers of their skin and its waxy exudation are devoured by certain flies. Mites and tongue-worms also invade the nasal cavities, the bronchial tubes, air sacs and lungs and feed upon their secretions. Fleas, lice, mosquitoes, midges, bugs, leeches and ticks suck their blood from outside. Protozoa (one-celled organisms), such as the malaria parasite, destroy the red blood corpuscles from inside the body. Other Protozoa, the trypanosomes, are found in the bone-marrow and lymph vessels, and flagellates swarm in the crop and mouth. Varieties of worms are located in almost every organ of the body, the subcutaneous tissues, the muscles, the eye, the brain, the trachea, liver, kidneys, gall-bladder, bile-duct, reproductive organs and the alimentary canal. Leeches fix themselves inside the vent and sometimes in the throat-pouches of pelicans.

Moreover, there is not only a large variety of species of parasites which can attack birds, but sometimes very large numbers of one sort of parasite are found in a single individual. Thus, over 10,000 nematode worms are recorded from the intestine of a grouse and more than 1,000 feather lice from the plumage of a single curlew. Shipley was so impressed by the variety and number of their parasites that he exclaimed, "They are not only birds but aviating zoological gardens."

The life history of the malaria parasite of man, perhaps the most important discovery in the whole field of human parasitology, was worked out on a closely related species from wild birds. The life-cycle

of the human blood fluke, which was a serious plague throughout the Middle East, could easily have been elucidated in this country and much time and effort saved if we had made use of the similar type of worm found here in the veins of ducks and gulls. From the utilitarian biologist's point of view it is difficult to over-estimate the importance of studying parasites. Birds which harbour many species closely related to those normally infesting man render us a silent but inestimable service by their sad experiences. Most of the successful anti-malaria drugs are first tried out on canaries.

From the naturalist's point of view, which is necessarily a rather different one, parasites are equally important. Broadly speaking, the public are no longer interested in evolution. The man in the street, who has survived two world wars, together with mustard gas and the atomic bomb, now accepts the suggestion that he is descended from the apes without either indignation or surprise. Evolution has, however, remained the lodestar of our generation of naturalists, and parasites are, perhaps, the organisms in which evolution is most obvious. Their mode of life has imposed certain definite morphological and physiological modifications upon them—a sort of gigantic secondary experiment in evolution, which, if properly studied, must prove profoundly illuminating. Moreover parasites act as pointers and guides to the evolution and relationship of their hosts. Between these two an eternal and curious struggle is in progress. The host's reactions are wholly hostile but the parasite is forced to adopt a compromise. It has to restrict its activities in such a way that it does not immediately endanger the host's life and thus jeopardise its own food supply and chances of reproduction. Parasites which neither stimulate the host to violent reactions nor inflict upon it serious permanent injury are said to be "well adapted" to their mode of life.

There are in nature certain associations in which the organisms concerned suffer no ill effects and, on the contrary, are assured either unilateral or mutual benefits. These relationships, which are known as commensalism, symbiosis, and phoresy (see p. 18) may represent transitional stages in the development of the parasitic habit. Some hold the view that they precede parasitism. Others, with a more idealistic outlook, consider that adaptation has here evolved beyond the parasitic relationship, with the elimination of harmful effects and a gradual substitution of mutual benefit. Whatever the truth may be it is clear that a study of the borderline associations is of consider-

able importance if we wish to understand the parasitic relationship itself.

It is, of course, a truism that all living organisms are inter-dependent, but the origins and development of that acute dependence displayed by parasites and commensals has a special fascination. At one end of the scale there is a rove beetle which can apparently only breed in birds' nests where the temperature is raised to about 40 degrees centigrade by the presence of nestlings and, at the other end, the cuckoo, which has also to seek out the nests of small birds in which to lay her eggs. Once on the track of this sort of relationship, the naturalist becomes more and more curious. He just has to go on.



Bird-bottle fly, *Protocalliphora azurea*, resting upon
a flower (x 4.7)

CHAPTER I

PARASITISM

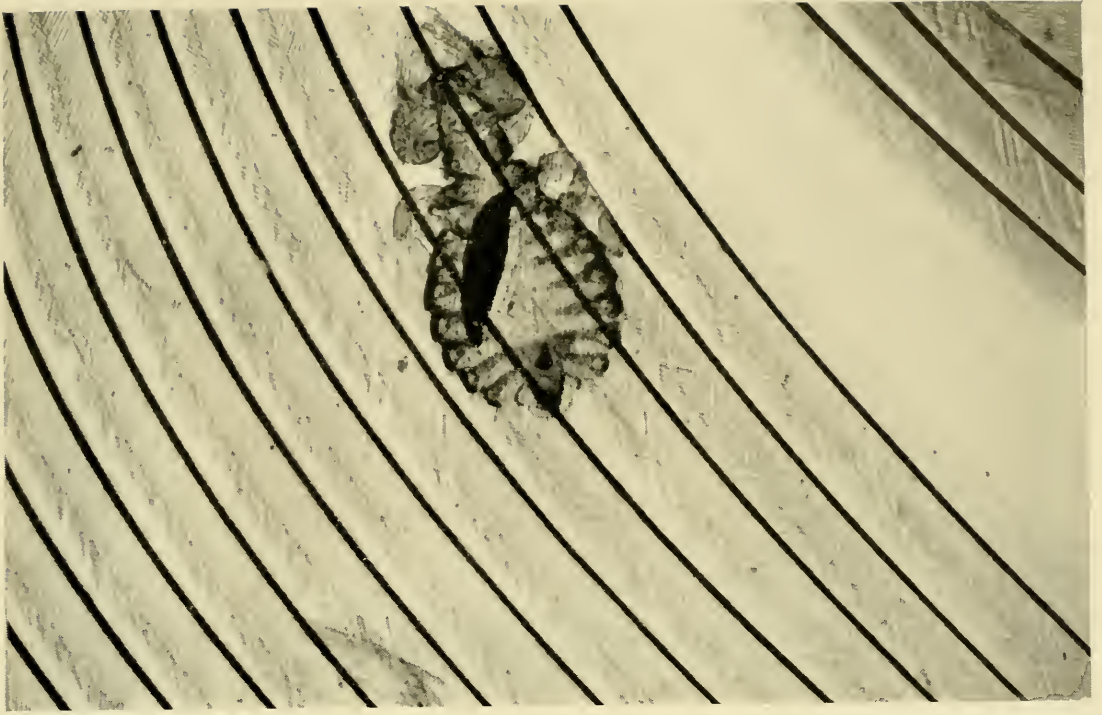
Almost
All the wise world is little else, in Nature,
But parasites and sub-parasites.

BEN JONSON

THE WORD parasite means, literally, one which eats beside another, but the modern biologist cannot accept this as a definition. It is too elastic and too vague. The term is now generally used to indicate strict dependence between two organisms, one of which, at any rate, during some period of its life, lives at the expense of the other. The word parasite is often used in a broader sense to mean any animal or plant which is dependent upon a host—and it is left to the reader to decide for himself how exactly to define the term host.

Ultimately all animals depend on plants or other animals for their source of energy. They must eat to live. Plants may subsist on an ethereal diet—largely air and water flavoured with sunshine—but animals require more substantial if less romantic fare.

Many biologists see in a parasite a form of predatory animal. Instead of killing and devouring its prey whole, it can, by virtue of its smaller size, live on the host or in it, and eat it little by little. The robin, for example, has a number of relatively large carnivorous enemies such as hawks, cats, rats and stoats which prey upon it and devour it whole. It also supports a far greater number of animals smaller than itself (Fig. 1) which are parasitic and live by gradually eating relatively minute portions of its body. Elton has described the difference between a carnivorous and a parasitic mode of life simply as the difference between living on capital and income. If, however, an animal becomes a parasite, the problems which confront it and the *consequences* of its mode of life are unquestionably different from those of a free-living



R. McV. Weston

a. Starling louse clinging to feather ($\times 29$)



W. H. Pollen

b. Quill louse inside wing-feather shaft of curlew ($\times 23$)



Plate II

Eric Hosking

Great spotted woodpecker: the parasitologist can provide a valuable clue to the classification of this group of birds

animal. Possibly there is some justification for those biologists who consider these two habits of life—which are found everywhere and which have been evolved as part of the general struggle for food and shelter—as fundamentally distinct.

In nature we find extremely varied and diverse types of parasitism. It is an easy matter to point to a louse and say with confidence, "There is a parasite." It is equally obvious that a golden eagle is a bird of prey. On the other hand it is difficult to decide if certain larval water beetles and leeches, which sometimes kill and eat their prey outright and at other times merely abstract a little fluid from living victims, are carnivores or parasites. It is also obvious that there is a wide gap dividing the type of parasitism displayed by a worm which lives permanently in the veins of a sea-gull, immersed in a perpetual food bath of blood, and a female gnat which occasionally visits the gull, punctures its skin and withdraws a few drops.

Certain of these animals are described as *obligate and permanent parasites*. The Protozoa which cause avian malaria, the tapeworms and the feather lice, for instance, are compulsorily parasitic throughout their lives. Tapeworms and *Plasmodium* live inside the bird (endo-parasites), feather lice on the outside (ecto-parasites), but they are always dependent upon their hosts and cannot live apart from them. For these parasites, prey and environment merge and become one.

Although so-called obligate parasites are at some period of their lives dependent upon a host, many of them are able to spend long spells in the free state and it is normal for them to do so. Ticks gorge themselves with blood and then drop off the birds into their nests or on to the ground and remain there until they have digested the meal. Bugs hide in cracks and crevices or in the deeper layers of the nest during the day, but steal out at night and feed upon their roosting host. Leeches drop back into the water after engorging around the mouths of cattle and horses drinking in ponds or streams. These animals are generally referred to as *periodical parasites*, whereas those which are dependent on a host during one stage of the life-cycle only, are designated as *temporary parasites*. A good example of the latter type is a beautiful metallic fly (*Protocalliphora azurea*) which as an adult insect hovers over flowers in the sunshine and sips nectar and dew, but as a larva lives by sucking the blood of nestling birds. Another fly, *Carnus hemapterus*, is parasitic as an adult but the larva is a scavenger and dung-eater in the nest. Many Diptera (flies) can be included in both categories. Gnats, midges and

blackflies are only parasitic in the adult stage and they too only visit the host at irregular intervals, some by day and some by night. Very little is known about the biology of these species and it is not quite certain whether all are true obligate parasites. Some may be more correctly included in the group of animals classed as *facultative parasites*. These can live and complete their life-cycles as free animals, but resort to parasitism if circumstances are favourable. For example, certain fly larvae which normally live on dead and decaying matter in nests are attracted to any sores which may be present on the bodies of the young birds. They may invade these areas and from then onwards feed upon the exudations and the putrefying flesh in the cavity of the wounds.

There are also very large numbers of organisms which can be called *accidental parasites*. Certain Protozoa, maggots and worms are over and over again accidentally ingested by birds and other animals and can survive for varying periods. They feed upon secretion or even living body tissues although this is in no way their normal mode of life.

Among these groups we recognise many degrees of dependence, different and contrasting life-cycles and great variation with regard to the mutual reactions of host and parasite. The feather lice and mange mites, for example, which are so-called permanent obligate parasites, pass generation after generation on the same individual animal, even their eggs being attached to the outside or buried within the tissues of the host. On the other hand, certain worms and many of the Protozoa pass through two or more hosts and, certain phases of their lives present a great contrast, part being spent in warm- and part in cold-blooded animals. Again, the egg stage, or the spore and cyst stage, of obligate parasites often passes from the host into the outside world, and is the means by which another animal is reached and the life-cycle recommenced.

Perhaps the most fascinating form of dependence among bird parasites is what is now defined as *brood parasitism*. The feeding and rearing of the young is entrusted to a different species of bird. This type of behaviour is not uncommon in the animal kingdom as a whole but it is very rare among vertebrates. Established brood parasitism in mammals is unknown, although in isolated instances and under domestic conditions certain species will voluntarily rear the young of others. The European cuckoo is the best known type of brood parasite among birds and the only one found in Britain. It is an obligate parasite, incapable of rearing its own young. There are, however, numbers of

birds, apart from the cuckoos, which practise brood parasitism, to a greater or lesser degree. The cow-birds (Icteridae) of America, the honey-guides (Indicatoridae), and certain weavers (Ploceidae) especially the widow-birds of Africa, adopt a similar mode of life.

Not all these birds are as harmful to their hosts as the European cuckoo, for in several species the foster parents rear the intruder as well as their own young, which is left unmolested in the nest along with the rightful owners.

Some birds, of which the skuas (Plate XXXVIIIa) are good examples, live by a curious form of food robbing known as *clepto-parasitism*. They are large and powerful birds, capable of killing their prey in the usual predatory manner, but instead they prefer to chase other sea birds and by their relentless attacks force them to drop the prey they have captured or to disgorge their last meal.

Obligate parasites, facultative parasites, temporary or permanent parasites, brood parasites, clepto-parasites, endo- or ecto-parasites—all these categories have been invented by us for our own convenience in order to simplify the task of description and exposition. They are arbitrary classifications which do not bear critical analysis, and in nature these types are found to merge gradually into one another. Moreover, it is true to say even when closely related species of both host and parasite are involved, no two parasitic relationships are exactly alike.



Fungus, *Aspergillus fumigatus* ($\times 293$),
a facultative parasite in the lungs of birds

COMMENSALISM

And thou shalt eat bread at my table continually.

II SAMUEL 9 : 7

IF TWO animals live in close and harmless association with one another, from which circumstances only one partner derives benefit, the relationship is known as commensalism. Although widespread throughout the animal kingdom, this somewhat mysterious phenomenon is rarer than parasitism and not so easily recognised. If both associated partners receive an advantage the relationship is known as symbiosis.

The most usual form of commensalism is one in which the smaller and weaker of the two animals steals a little food from the larger animal without causing it any appreciable loss or inconvenience. Thus, a small species of muscid fly accompanies large blood-sucking clegs (*Tabanidae*) and laps up a little of the blood which may be left oozing from the wound on the victim's skin. Although strictly speaking the term commensal should be applied to mess-mates only, in many such associations the benefit received is one of shelter and indirect protection from enemies rather than nourishment, while in others both these advantages are conferred simultaneously. A minute worm, for example, lives relatively safely in the groove on the arms of certain starfish and when the host is feeding it wriggles up to the vicinity of its mouth and surreptitiously catches a few stray morsels. In this way it obtains free board and lodging. A more famous association exists between the remora, or sucking-fish, and whales and sharks. The remoras attach themselves to the undersides of their giant companions by means of an adhesive disc on their heads and thus obtain transport, protection and any superfluous food accidentally dropped or discarded in their vicinity. They also enter the gill cavities and mouths of large bony

fish such as sword-fish and sun-fish and are carried about with them, literally taking the food from their mouths.

In most cases of commensalism it is easy enough to see why the active beneficiary clings to the association, but it is far more difficult to understand why the passive partner tolerates the other's presence. One is sometimes tempted to believe there must be a psychological explanation which cannot be observed from the outside.

For instance, a man from Mars would find it a simple matter to understand the relationship between a shepherd and a sheep dog, or a hunter and his hounds. On the other hand, he might well be puzzled at the seemingly one-sided benefits enjoyed by pekinese and pug-dogs. At present no one is in a position to say whether or not the starfish receives agreeable sensations from the worm wriggling up its ambulacral grooves. Is it possible that a remora, twitching in their buccal cavities, assuages feelings akin to loneliness and boredom with which the sun-fish and sword-fish are otherwise afflicted? We do not know.

On the whole commensal relationship among birds is unusual and when it does occur it is chiefly limited to the breeding season. It is, however, common knowledge that many species of birds associate in flocks, especially for feeding and during migration. The significance of most of these associations—if indeed they have any special significance—is completely unknown. In the case, however, of wigeon and brent geese, which are often seen together at their feeding grounds, the duck can be described as commensals, for on such occasions they feed on the débris of eel grass (*Zostera*) which the geese have pulled up and broken into convenient lengths. Nevertheless, the wigeon are quite capable of breaking up the *Zostera* themselves if there are no geese about. In Lapland, waxwings have been seen feeding on the berries of mountain ash, and scattering a quantity of pulped fruit on the ground below. There, flocks of redpolls were waiting to eat up the débris. They appeared unwilling to feed on the whole berries and followed the waxwings from tree to tree. In south east Africa, Swynnerton has watched swallows and bee-eaters accompanying a party of bulbuls (*Pycnonotidae*) which were feeding on ripe guavas. They were catching the insects accidentally disturbed by the bulbuls.

In more familiar surroundings a casual commensal relationship may be observed between the robin and the mole. As the mole tunnels just below the turf and throws up fresh soil in the form of the familiar mole

“hills” the robin watches intently from some convenient bush and quickly seizes any invertebrates which are exposed on the surface.

Certain petrels and the great shearwater follow in the wake of whales and porpoises and devour their faeces. In the South Seas, the sheath-bills (*Chionidae*) enjoy a curious relationship with various colonial nesting birds, which is part parasitic, part commensal and part symbiotic. They haunt their breeding sites and steal many eggs and scraps of food, but they also act as scavengers and obtain a considerable part of their nourishment by eating the remains of crustacea found in the faeces of birds, especially of gentoo penguins (*Pygosceles taeniata*). When the Weddell seals are bringing forth their young the sheath-bills, like the ivory gulls in the arctic, will follow them out to the pack-ice and feed on the placental blood and afterbirth of the new born cubs. One observer saw several of them attempting to eat the umbilical cord while it was still attached to the baby seal.

In Africa, the carmine bee-eater (*Merops nubicus*) rides on ostriches, bustards and certain large mammals using them as perambulating perches. It catches the insects which pass within reach of the “host” or are stirred up in the grass. Once Myers saw a bee-eater fall off when the bustard broke into a run but it flew after it and soon settled again. This bird will also exploit bush fires fearlessly and darts in and out of the flames to catch escaping insects. The native Mandigo name means “nephew of the burning.”

In the tropics there are numbers of spectacular examples in which certain birds habitually nest in close proximity to dangerous social insects such as ants, termites, bees and wasps. At first sight it would appear that the benefit is always one-sided and while the birds obtain protection from the presence of the insects, the insects themselves derive no advantage from the association whatsoever. However, increased knowledge about the birds concerned suggests that often mutual benefit is involved and such examples will, therefore, be considered in a subsequent chapter (p. 26). A case in which the insects appear to gain no advantage at all concerns a South American parrakeet (*Eupsittula canicularis*) which is an obligate commensal of certain termites. It breeds exclusively in their carton nests which it hollows out for the purpose. The parrakeet never uses unoccupied termitaries, although plenty are available. When building operations begin the termites rush to the scene of action and try to repair the damage. They sometimes appear to make half-hearted attempts to drive off the adult birds but they soon desist and leave them

unmolested. They could easily kill the naked and defenceless young when they hatch but, mysteriously enough, these are left unscathed. It is obvious that the parrakeets benefit from the association. The termites are irascible and their bite very painful. It is unlikely that egg thieves would brave their fury in order to rob the parrakeet's nest. Moreover, the termitary itself is hard and durable and also exceedingly warm. Occasionally the adult birds even make a meal off their hosts. It is certainly difficult to understand why the insects tolerate the presence of these tiresome intruders.

There are also several species of woodpeckers, kingfishers and parrots, in both the African and oriental regions, which are obligate commensals of vicious ants and, like the parakeet, build, lay and rear their young in the heart of the ants' nests. In one or two instances it is known for certain that the woodpeckers habitually feed on the ants concerned. The species of ants found in Britain do not lend themselves to this type of association as they are not builders of carton nests. In Sweden, however, Durango has seen three nests of the long-tailed tit placed in close proximity to ant-hills of *Formica rufa*. On one nest the wood-ants were swarming all over the outside. He observed that squirrels avoided the areas where the ants occurred in large numbers. This insect is a common species over a considerable area in Britain, and where it occurs it is worth while keeping a sharp look out for incipient associations between it and breeding birds—not necessarily the long-tailed tit. It is generally species constructing domed nests which establish such relationships with noxious insects, and the wren is therefore a bird to watch in this respect. The question of birds nesting near bees and wasps in this country is considered in the following chapter.

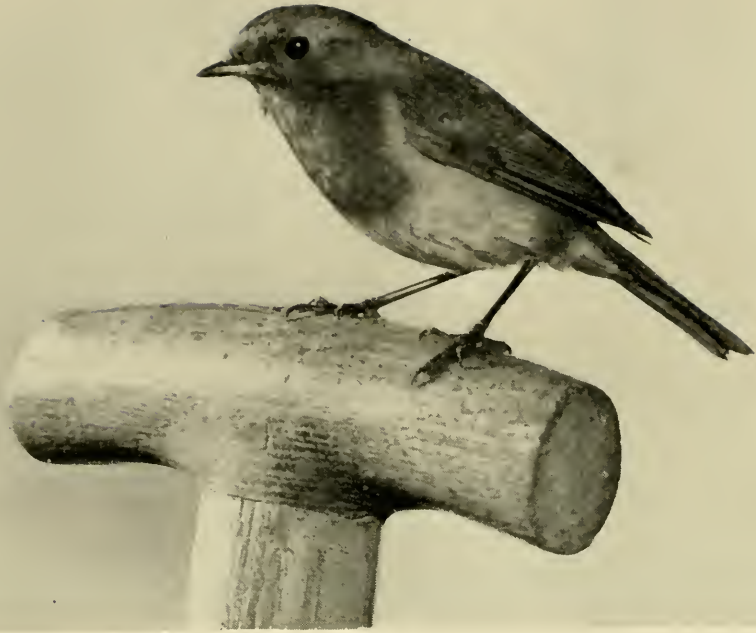
In various parts of the world small birds habitually build in close proximity to some bigger bird, generally a bird of prey. Thus, for example, the white wagtail regularly inhabits the nests of the osprey and white-tailed sea-eagle on the coasts of Sweden and Finland. The eyries of the prairie-falcon (*Falco mexicanus*) are frequently surrounded by the clustered nests of cliff-swallows (*Petrochelidon pyrrhonata*). In Africa some species of weaver-birds make a practice of grouping their nests near that of an eagle, vulture or buzzard. A colony of nests of the slender-billed weavers (*Teteropsis pelzelni*) may be found actually hanging from the sticks on the underside of a kite's nest. Among British birds a rare vagrant, the red-breasted goose, and a winter visitor, the barnacle-



Plate III

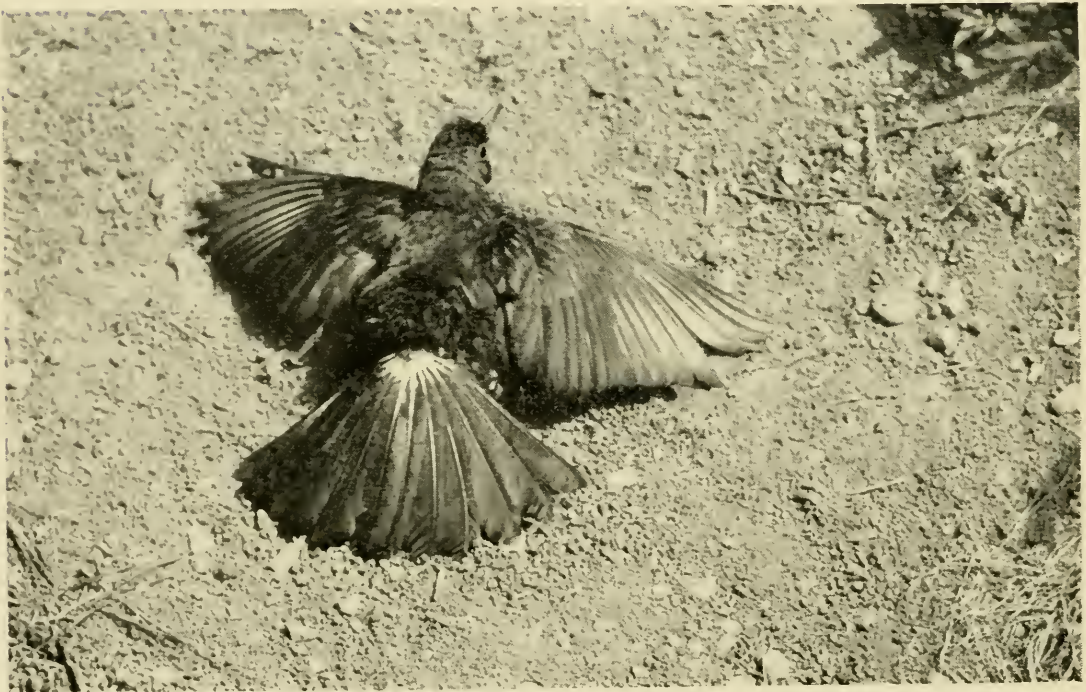
Great tit removing cap from milk-bottle; the feeding of tits from milk-bottles is an example

V. L. Breeze



Ronald Thompson

a. Robin perched on spade: this bird is a commensal partner of man



C. W. Teager

b. Hen blackbird sunning: this habit may lead to the curious practice of "anting"
Plate IV

goose, are known to seek the proximity of birds of prey at nesting time. In Siberia the former species places its nest under cliffs occupied by a pair of buzzards or falcons, which, it has been thought, assures the geese some protection from marauding foxes. Another British species, the red-necked phalarope, often seeks protection in its breeding haunts in Iceland by nesting in close proximity to a sitting ptarmigan. The ptarmigan is endowed with great courage and tenacity and drives off the arctic skuas which otherwise persistently rob the phalaropes of both their eggs and young. The wood-pigeon has also been observed on several occasions nesting in the proximity of a breeding kestrel, sparrowhawk, merlin or hobby.

The last four examples are incipient but true commensalism, as the benefits are clearly confined to the side of the defenceless bird. However, with colonial nesters such as the weavers it is rash to assume, as most observers have done hitherto, that no advantage accrues to the more powerful partner. It is possible that the weavers act as sentinels for the raptorial birds with which they associate during the breeding season. The rather curious biblical warning given to idle gossips may have been based on some acute ornithological observation in the field: "For a bird of the air shall carry the voice, and that which hath wings shall tell the matter."

When the white wagtail breeds in the eyries of ospreys and eagles, the association may also entail mutual benefit, for the wagtails have been frequently observed and photographed hunting the insects in the nests of their hosts.

Durango has collected numerous examples of birds which apparently seek protection by breeding in the middle of colonies of more aggressive species. In Sweden and Finland tufted duck and turnstone nest in gull and tern colonies—in fact there it is unusual to find a nest of these two birds in any other situation. They even follow the colonies if for some reason the gulls and terns change their breeding sites. In Britain tufted ducks nest alone in concealed situations on the edge of lakes and ponds. Long-tailed tits also frequently build in colonies of fieldfares. On Fårö in the Baltic, although typical and suitable nesting sites in the form of sandy beaches are available, the little tern chooses to nest in colonies of arctic terns on stony ground. In Sweden, France and America the black-necked grebe breeds in colonies of black-headed gulls, whiskered terns and Franklin's gull (*Larus pipixcan*). The white wagtail is a regular inhabitant of gull colonies on the coast of Finland.

Although these associations have not been adequately studied, probably all of them will, in time, be recognised as commensal relationships.

There is another type of nesting association in which birds play a popular and very prominent role in Britain. The erection of buildings with cliff-like façades, overhanging roofs and convenient eaves and beams, has enticed swallows, martins and swifts away from rocky caves and mountain precipices. It has brought them to live and breed in close proximity to man himself. In Africa certain swifts and swallows normally confined to breeding in cliffs which are by no means common, have taken to nesting on buildings of European type—not only on houses but also under bridges and similar structures. Their numbers have since greatly increased. It seems likely that a similar course of events occurred in Britain. Probably at some remote period both man and martins shared the same caves and cliffs around the coast, and the birds eventually followed man and made use of his new and self-made habitations.

The poets have described the difference in the nesting habits of the various members of the swallow tribe. In England “the temple-haunting martlet” seeks out the purely human dwelling more persistently than the swallow. It favours baronial halls, castles, small towns and villages where it “builds in the weather on the outward wall.” On the other hand the swallow “twitt’ring from the straw-built shed” prefers the company of domestic animals. The arrangement of beams and roofing inside farm buildings is better suited to its nesting requirements.

Swallows show a slight preference for certain domestic animals. Their prime favourites are cows. Other things being equal they will build in an occupied cowshed rather than a stable or a pigsty, although their love of pigs and horses is also great. Sheep are not so acceptable as companions.

Human beings obtain great delight from the presence of swallows and martins which nest on their barns and houses. They are not only intrinsically beautiful and graceful birds, but since they arrive in March and April they have become the symbol of spring flowers and sunshine, and the nostalgic hope of better times to come. Man, however, is forever seeking utilitarian motives for his actions. We find, therefore, that various “reasons” are put forward why the birds should be actively encouraged. It is frequently asserted, for example, that swallows rid the cowshed of noxious and irritant flies. There is also a widespread

superstition in Britain that if the swallows' nests are robbed of eggs the cows give bloody milk. So far there is no evidence that man benefits, either indirectly through the well-being of his stock or directly, except aesthetically, from the close proximity of the birds, and any advantages appear entirely on the side of the martins and swallows. Nevertheless, if we admit the psychological element it is evident that the relationship entails mutual benefit.

Much the same may be said of the curious ties that link the robin and man in Britain. The bird receives all the tangible advantages, which chiefly consists of food deliberately or accidentally provided during the critical winter months. Man, on the other hand, obtains great aesthetic satisfaction and pleasure from the bird's song and appearance, but most of all from its tameness.

*“But what gives me most joy is when I see
Snow on my doorstep printed by their feet.”*

In many other regions of Europe the robin is a shy woodland species which shuns human habitations and is ruthlessly trapped, persecuted and eaten by man. Fairly reliable figures show, for example, that twenty thousand robins were killed for the table in one season near Toulon in France. In England to-day a man known to eat robins would risk social ostracism. Here we have the interesting phenomenon of two species exhibiting a commensal relationship in one part of their geographical range and a predatory relationship in another.

There are several birds in Britain which enjoy less well marked commensal relationships with man. Thus, jackdaws, rooks and gulls regularly follow the plough, and sparrows, wood-pigeons, and stock-doves obtain a considerable proportion of their food from agricultural crops. In British seas and on the Newfoundland Banks the fulmar and great shearwater follow the trawlers, and round the coasts where the fishing vessels discharge their catches, various species of gulls are commensals of fishermen. During the last sixty years many black-headed gulls, herring-gulls and common gulls have changed their habits in the winter. When the cold weather sets in they move up the rivers into the large towns where they obtain food in the parks and along the water fronts from the passers-by. These movements are diurnal and towards evening the gulls can be seen flying away to roost in quieter surroundings.

One of the most curious and unusual types of commensalism is demonstrated by tits which have recently developed the habit of stealing milk from the bottles left by the milkman on his rounds (See Plate III). This remarkable phenomenon was first noticed about thirty years ago in England and it has since spread rapidly through many parts of Britain. Mainly great tits and blue tits, but also several other species, rob the bottles and they systematically remove paper or metal caps to get at the milk. Although this habit has undoubtedly arisen spontaneously and independently in different parts of Britain there is no reason to doubt that its spread has been greatly accelerated by the tits learning from their parents and by mimicking one another. It is a good illustration of Elton's transmission of new ideas and new behaviour which does not involve "any organic inheritance or mutation in the ordinary sense." The kea's behaviour (see p. 23) is probably another example of the same type of learning.

The word "phoresy" was coined to describe the passive transport of one insect by another, but the term is now used to indicate any regular association of this type, not necessarily between insects. Occasionally phoresy and commensalism are difficult to distinguish and almost merge into one another. In the case of remoras we know that the small fish are not mere hitch-hikers but get free meals during their travels. The larvae of certain mites (hypopus stage, Plate V), on the other hand, which are carried about by a great variety of insects, and have like the remoras developed special suckers for the sole purpose of clinging to their transport hosts, have no mouth parts. Therefore we can assume their journeys are no mere joy rides, but entail long fasts. This is the classical type of phoresy—a highly specialised method of dispersal with the object of finding new hosts. It is more difficult for instance to define the relationships between those mites which destroy the eggs and larvae of certain insects, and the adult insects upon which the mites hitch-hike. The unsuspecting female carries them around until she lays, whereupon the mites quickly terminate their trip and transfer to the eggs, which they eventually consume. Certain curious nest-dwellers, the pseudo-scorpions (p. 248) are great hitch-hikers and use birds as well as insects as a means of transport.

There are a few curious records of snails being found in the plumage—especially under the wings—of newly arrived migrant birds. Several plover have been found with the same species of bladder snail (*Physa*) both in the crop and among the feathers. It was suggested that these

birds might deliberately place snails in their plumage (see also p. 127 for a description of "anting") before starting on a long voyage in order to provide themselves with at least one meal on the trip. Whether the presence of these snails is accidental or not, it is certainly a method by which their range can be extended—even to remote oceanic islands. Even more extraordinary, and reminiscent of the ancient fable of the eagle and the wren, is the record of a migrating short-eared owl transporting a live goldcrest.

So far we have considered only those commensal relationships in which the bird plays the active role, seeking either food, protection or suitable nesting sites, or perhaps all three, from an indifferent or at any rate acquiescent partner. The greater number of so-called commensal relationships involving birds, however, are those in which arthropods are the active partners (see Chap. 14). Birds' nests form an ideal environment for these animals and within them insects and mites teem in thousands. The chief benefit which the majority of these nest-dwellers enjoy is no doubt the relative dryness and warmth of the habitat. They have solved a very ancient problem: "Again, if two lie together, then they have heat: but how can one be warm alone?"



Moth, *Tinea lapella*,
a commensal from birds' nests (x 4.5)

CHAPTER 3

SYMBIOSIS

Now for as much as the Crocodile sojourneth in the water, he hath his mouth all full of leeches within. Whensoever he goeth up out of the water on the land, and thereafter yawneeth (which he is wont commonly to do when the west wind bloweth) then entereth the Sandpiper into his mouth and swalloweth down the leeches, and the Crocodile is pleased at the help which he receiveth and hurteth not the Sandpiper at all.

HERODOTUS

WHEN TWO different species of animal or plant live in close association, from which they derive mutual benefit, the relationship is known as symbiosis. A few biologists hold that the term implies dependence and that its use should be restricted to those rare cases in which neither partner can survive without the other. An assassin-bug, (*Rhodnius prolixus*) and its symbiotic fungus (*Actinomyces rhodnii*) provide a good example of this relationship. The fungus lives in the intestine of the bug and is passed from generation to generation on the eggshells and in its faeces which are then eaten by the nymphs when they hatch. Without the fungus the insects' development only proceeds normally until the fourth or fifth moult, and the majority fail to become adult. The few which complete their metamorphosis are sterile and do not reproduce. It is thought that the fungus provides a source of vitamin B for the bug, essential to its proper development. At any rate the two organisms are entirely dependent on one another for survival. The majority of biologists, however, believe that the word "symbiosis" should not be interpreted too rigidly and can, therefore, be used to describe any regular, though not necessarily obligatory, association in which benefits are enjoyed by both partners. Thus, the world-wide relationship between man and the cow is clearly symbiotic, although

there is considerable difference in the advantages which accrue to a sacred cow of the Hindus and a British dual-purpose shorthorn.

A bird which may, with justification, be considered a symbiotic partner of man is the barn-owl (Plate VI). It regularly makes use of sheds, out-houses and barns during the breeding season and also frequently roosts in buildings. In return it renders an invaluable service by destroying large numbers of vermin which infest stacks and farmyards. "It is as useful in clearing these places from mice," remarked Pennant, "as the congenial cat."

There is one family of birds, the starlings (*Sturnidae*), of which several species have, independently in different parts of the world, developed symbiotic relationships with the large grass-eating mammals. The common starling in Britain supplements its diet by paying periodical visits to flocks of grazing sheep and cows and feeding upon the insects which they stir up in the grass, or by actually picking parasites off the animals' backs.

There are few prettier sights than a flock of starlings whirling out of the frosty air—their wings transparent against a low winter sun—and settling among folded sheep, or a herd of cows. They work carefully and painstakingly over the ground which has been disturbed by the footsteps of the farm animals, and perform an extremely useful service by destroying the disease-carrying ecto-parasites of domestic animals and removing grass-eating insects and parasitic worms from their pastures. The relationship is certainly of mutual benefit, but although quite regular, it is essentially casual and each party can do quite well without the other. The African ox-peckers (*Buphagus*), on the other hand, obtain their entire food supply and much of their nesting material from the bodies of the large herbivores and are thus wholly dependent on wild and domestic animals. They have developed a very close relationship with their partners, especially the rhinoceros, for which animal in particular they act as sentinel. Big game hunters were the first to appreciate this fact, for the birds frequently spoiled their chances of a fine bag. "On many occasions," wrote Andersson, "has this watchful bird prevented me getting a good shot at that beast; the moment it suspects danger it flies up into the air uttering sharp shrill notes that never fail to attract the attention of the rhinoceros, which, without waiting to ascertain the cause, almost instantly seeks safety in precipitate flight." Moreau has noted that the ox-peckers, on occasions, stick very close to their "hosts", even clinging to

the flanks of the greater kudu antelope (*Strepsiceros kudu*) galloping at full speed !

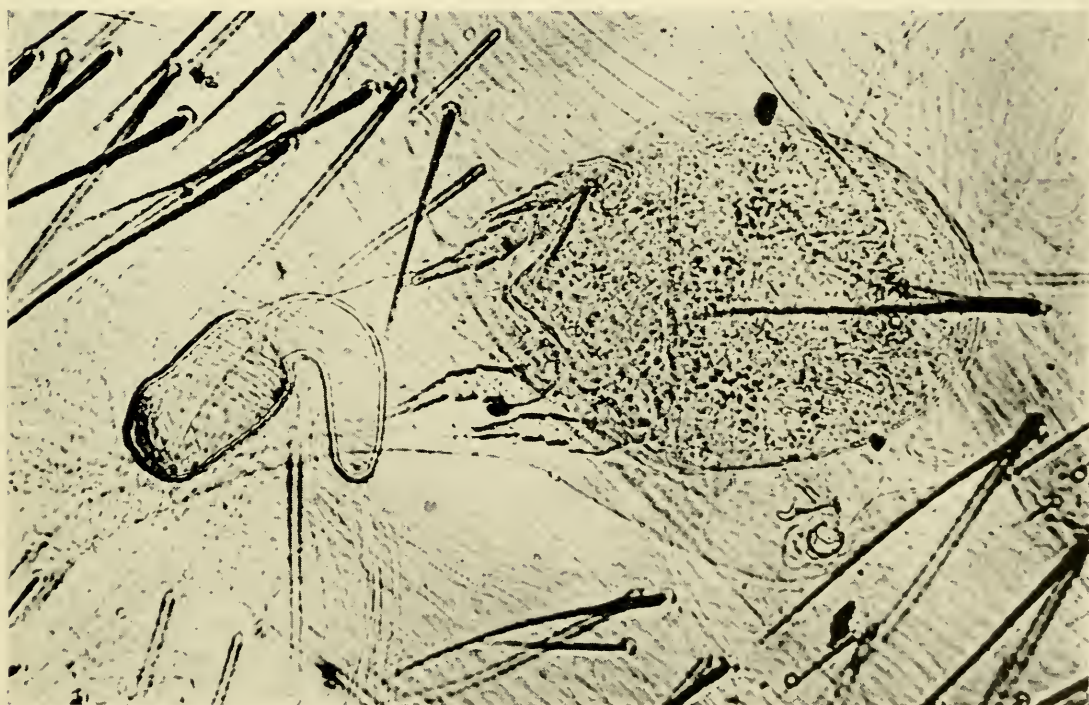
It is a remarkable but not altogether agreeable sight to see ox-peckers "working" over the bodies of large mammals. In some ways they remind one of nuthatches or tree-creepers searching a tree trunk for insects, for they flatten themselves against any perpendicular surface and use their tails and feet in much the same manner. On the other hand the ease with which they move backwards and forwards is distinctly reminiscent of certain feather lice. They run and hop about the beast they are "de-lousing" in a very lively fashion, diligently searching every portion of its body, and we are told, "They often make long drops downwards from the shoulder to the foreleg or down the side of the animal whose coat they are engaged upon . . . If alarmed when at work on a giraffe's long neck they descend rapidly like a rat or a mouse down the whole length of the anatomy of the beast and finally come to earth by way of its legs ! If endangered by the sweep of the host's tail they flatten themselves still more and allow it to brush lightly over them, or jump nimbly out of the way." This habit of continually rising and resettling on the host's body was also observed by Moreau who was reminded unpleasantly of blow-flies round a carcass. However, their attentions appear welcome to these large animals who, far from being irritated by the birds' fidgety behaviour, even tolerate them clinging and crawling about their faces and heads. Most observers have been impressed with the apparent understanding which exists between the two partners, for the bird's presence appears to convey a sense of well-being to the mammals.

The crop contents of ox-peckers have been examined and their food is found to consist mainly of ticks (an average of about forty ticks per bird) and biting flies, although lice are also taken in smaller numbers. In addition to ecto-parasites, clots of blood are frequently encountered in the crops of ox-peckers, for they have developed the sinister habit of eating the flesh and blood from the sores of cattle which they are de-lousing. It is said that the birds do not inflict the wounds but merely enlarge those which may already be present. They have, nevertheless, in this way, become a nuisance to domestic cattle, particularly herds which are in poor condition. The same tendencies are displayed by the European starling in certain parts of the United States. Recently, during an exceptionally cold spell of weather, when other sources of food became scarce, the birds likewise began to eat the flesh wounds on



a. (× 264)

J. G. Bradbury



b. (× 230)

Arthur L. E. Barron

PHORESIS: THE HYPOPUS LARVAE OF MITES BENEATH THE SCLERITES
OF BIRD FLEAS



Plate VI

Barn-owl feeding rat to young: owls are frequently infested with rodent fleas, and this photograph illustrates how the transfer from mammal to bird can occur

Eric Hosking

the backs of cattle. In this case the initial puncture was said to be made by the starlings themselves while enucleating the cysts of bot flies and warbles which are located beneath the hide. In any case it is a short step from enlarging an old wound to inflicting a new one. The keas of New Zealand (*Nestor notabilis*) learned the bad habit of eating flesh off the backs of sheep by the innocent practice of collecting wool for nesting material. The situation is obviously fraught with great danger for both the ox-peckers and starlings and should the balance tip towards parasitism, the starlings' days, at least in the United States, are numbered.

Apart from this bird there are several common British species which feed fairly regularly if casually among domestic animals. Magpies, jackdaws and rooks are not infrequently seen perched on the backs of sheep, pecking off ecto-parasites and fly-larvae (see tail-piece Chapter 11) which are often located just beneath the skin. They also work the grazing land for insects and parasitic worms.

An unusual type of "de-lousing" is carried out by the grey phalarope, a tame, delicate little wader, which is a passage-migrant in Britain. It frequently accompanies surface shoals of large fish and whales, periodically alighting on their backs and removing and eating their ecto-parasites. Aquatic animals are entirely at the mercy of these gruesome creatures, which they acquire in the water and are incapable of dislodging. Pliny noticed with sorrow that "when fishers twitch up their hooks they see a number of these skippers and creepers settled thick about their baits . . . And this vermin is thought to trouble the poor fish in their sleep by night within the sea." Most of us who have witnessed large fish landed in trawls or nets experience a thrill of horror at the sight of the "lice" (Copepoda) and worms plastered on their gills, around their sexual aperture and anus and other tender and vulnerable areas of their bodies. The phalarope's activities must be particularly welcome to whales and one wonders if these animals deliberately rest on the surface with the object of attracting their attention.

Historically the association between the crocodile bird and the crocodile is the most famous symbiotic relationship ever recorded. A translation of the well-known passage by Herodotus is quoted at the head of this chapter. To-day there is no known bird which habitually enters the mouth of the crocodile to de-leech its gums, although Meinertzhagen has seen the Egyptian plover do so on more than one

occasion. For all we know the species referred to by Herodotus as the "Trochilus" may now be extinct. However, it is generally believed that the Egyptian plover (*Pluvianus aegyptius*) is the species concerned and it is to-day referred to as the crocodile-bird. It certainly possesses many of the attributes generally associated with birds manifesting this type of symbiotic behaviour. Its plumage is conspicuous, it is unusually tame and according to at least one observer its flesh is extremely unpalatable. All birds which habitually "de-louse" large animals show a certain degree of tameness and boldness. This is equally true of starlings, ox-peckers, phalaropes, mynahs, weavers and magpies in the old world and grackles, tickbirds and cowbirds in America. Moreover, the majority of birds which "de-louse" cattle or associate with them on pastures are gregarious and go about in flocks or small parties. One is inclined to think that only species which are in some way protected against predators can afford to expose themselves continuously and blatantly in the middle of open country on the backs of cows or buffaloes. The flock definitely affords them some protection, for birds of prey will often attack certain species if they happen to come across a single individual but would not dare to do so if they are present in numbers. Cott's recent work on the unpalatability of certain birds suggests that the "de-lousers" are evil-tasting species which consequently do not fear raptorial.

The buff-backed heron is a scarce wanderer in Britain, only two specimens having been recorded with certainty from this country. In its native haunts in southern Europe, Asia and Africa it is known as the cattle-egret. This bird has developed a close relationship with cattle, with which it associates in the fields, feeding on the ectoparasites which drop off them and the insects which the animals disturb in the grass as they wander through the pastures. One of the most interesting points about this partnership is the egret's predilection for domestic animals and the way in which it has modified its habits to fit in with theirs. In Africa in certain districts during the rainy season, the cattle are concentrated in fly-free areas north of latitude 10 and the buff-backed heron moves up with them. In the dry season large numbers of both animals again move southwards—the birds' local migration being entirely dependent upon the cattle. At sunset the domestic animals are confined in a compound and the egrets then repair in a flock to a nearby swamp or lake. After drinking and bathing they return to the village or cattle camp where they roost communally

in an adjacent tree. Unlike most herons they do not leave the roost at sunrise but wait until cattle are released from the compound. As many as sixty-eight cattle ticks have been taken from the egret's crop, but they are by no means confined to this type of diet. Frogs and other aquatic animals are taken freely if they come across them.

The only British breeding bird which takes advantage of the winged insects swarming on domestic animals is the yellow wagtail which hawks for blood-sucking horse-flies and clegs (*Tabanidae*) round cattle grazing in the fields. Its vernacular name in France means "little herdsman" and at least two African tribes designate it as "goatherd." The degree with which these species of birds associate with cattle seems to vary in different districts and even with different individuals. De-lousers will often take advantage of any unusual circumstance which disturbs insects from their hiding places. Thus cattle-egrets keep just ahead of bush fires and mynahs follow sudden inrushes of water—intercepting the insects which are disturbed by the flood and flames. One species of ani or tick-bird (*Crotophaga*) has developed the interesting and curious habit of following columns of the dreaded legionary ants (*Dorylinae*) and feeding upon the insects which are "flushed" by the ants as they drive relentlessly through the forest.

In south-east Africa Swynnerton has made a long and careful study of mixed bird parties and has come to the conclusion that although sociability and the protection of the weaker species concerned may account in part for these flocks, their principal function is co-operative hunting. They are in all probability *drives*. He has watched, for instance, the different species in a mixed party searching the vegetation at various levels, while others again such as drongos (*Dicruridae*) and flycatchers moved along with them and only took insects on the wing which were disturbed by the "beaters." The role of the drongos was apparently that of clepto-parasites but Swynnerton surmised that their aggressive nature and readiness to attack made them very welcome additions, and no doubt greatly added to the "mobbing" force of the whole party.

Little is known about the function—if indeed there is one—of the various winter flocks of birds in Britain. It is not infrequent to meet mixed parties of tits numbering a hundred or more. Recently it has been shown that blue tits search trees and bushes at higher levels than great tits, and it is quite possible that co-operative hunting is one of the objects of these flocks. The association of feeding starlings and lapwings

may also have some similar function. In any case it is a subject worthy of further investigation in this country.

In the previous chapter we have described birds which seek protection by building in or near nests of termites and ants. We must now consider an even more interesting nesting association between certain birds and Hymenoptera in which both partners are thought to receive protection. In South America, to take one example, the yellow-backed orioles (*Cacicus cela*)—brilliant yellow birds, very conspicuous in every way—build in colonies around one of the great wasp nests. They place their nests so close to the wasps that when the tree sways the homes of the insects and the bird rattle against each other in the wind. Their presence keeps off the principal enemies of the orioles, such as egg-thieving opossums, tree-snakes and monkeys. It was Myers who first pointed out that the birds in a lesser degree also protect the insects. Any accidental damage suffered by wasp nests is likely to be by animals which have failed to notice their presence until too late. The intruder, needless to say, regrets the episode just as keenly as the wasps themselves. Brightly coloured birds grouped about the nest serve as an advertisement which warns all and sundry from a safe distance that the wasps are there. In other words once the birds become well-known recognition-marks of the *ensemble* they serve as an additional warning mechanism. Moreover, most, if not all, colonial nesting birds—of which rooks are a fair example—keep a sort of permanent lookout or watch, and at the first intimation of danger the whole colony is in an uproar. It is probable that the unusual noise and movement also disturbs the wasps. To be forewarned is to be forearmed, and it is no doubt of great value to the insects to be made aware of danger before it is at close quarters. This gives them the opportunity of driving off the enemies before they are within reach of the nest itself. In Africa, as well as in South America, some of the birds—although by no means all of them—which are concerned in similar associations are both colonial nesters and very conspicuous.

It is only in fairly recent years that the nesting associations between insects and birds have attracted much attention. The subject is exceptionally interesting and complicated and the reader is referred to the original papers by Moreau and Myers listed in the bibliography. A question which naturally occurs is this—do nesting associations of this type, between wasps, bees and birds exist in Britain, which have hitherto been overlooked? The obvious place to search for such an incipient

relationship is near bee-hives in gardens. Birds which normally nest around human habitations are gregarious and as we have already noted, several species of birds and families of birds which manifest general gregarious tendencies, seek protection from bees and other social insects.

There are a few British records of birds nesting and rearing young in close proximity to Hymenoptera.

- (1) A jackdaw nesting two years running in a hollow tree with wild bees—both birds and insects using the same entrance hole.
- (2) A jackdaw nesting in a hollow ash tree with hornets—using the same cavity but different entrance holes.
- (3) A swallow and wasps nesting under the same eave, with the nests touching each other.
- (4) A sparrow and hornets nesting under a thatched roof situated about one foot apart.
- (5) A wren and wasps nesting within six inches of each other in an attic.

All five birds reared their young successfully, which, in two instances, were known to be second broods. These particular associations may well have been accidental and due to a predilection for the same type of nesting site. But this fact in no way detracts from the interest of such records. Chance must play a very considerable part in first bringing symbiotic or commensal partners together. Once such a partnership between species has been firmly established, it is on the whole, fairly obvious, although in the case of birds, recognition by naturalists in the literature, came surprisingly late. On the other hand, in the early stages before the relationship has become fixed as a specific habit, individual cases are generally dismissed as coincidences. It is however, unwise to disregard such isolated observations or dismiss them lightly. Nothing is really known about the origins and evolution of nesting associations between birds and aggressive insects or other species of birds. Some workers believe it is merely a question of identical habitat preference, or that the main element involved is the sociability of birds. Others again consider that nesting sites close to an aggressive species are less disturbed by predators and are therefore more attractive to the birds. It is quite possible that all these factors play a part and may wholly explain some of the cases concerned. Never-

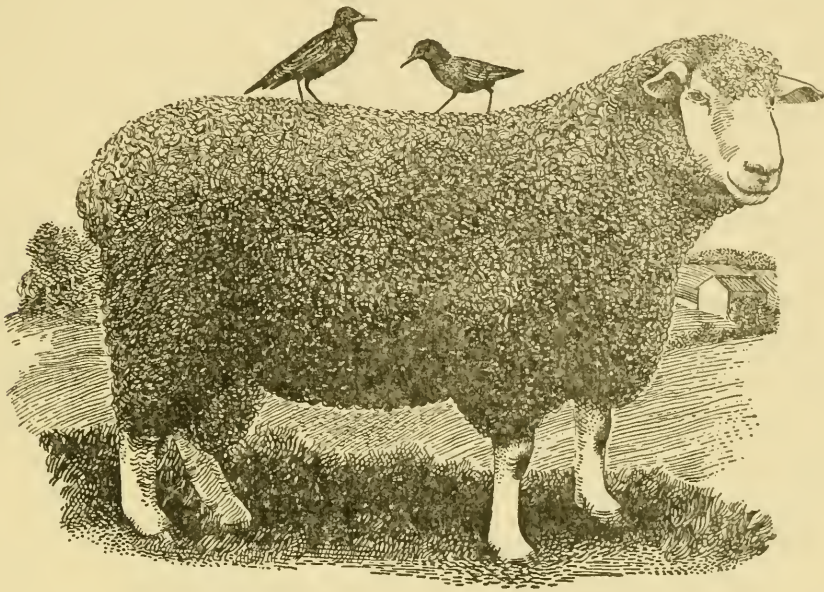
theless no really adequate theory has been produced to cover all the facts relating to the close association between nesting birds and vicious insects.

We have described how starlings destroy the ecto-parasites of cattle : there are some mites and insects which perform a similar task for the starlings. Foremost among these minute "de-lousers" is a group of predacious mites, the Cheyletidae, which live permanently on the body of birds and prey on feather mites (Analgesidae) and possibly also eat the eggs of feather lice (Mallophaga).

In the previous chapter attention has been drawn to the fact that many of the insect inhabitants of birds' nests are beneficial to their hosts. Many rove beetles (Staphylinidae), some species of which are host specific, are regular inhabitants of birds' nests and mostly prey on insects or mites, including ecto-parasites. Certain fly-larvae and mites, and a few moth larvae found in nests are coprophagous and feed on the birds' excrement.

In tropical countries a true symbiotic relationship has been developed between birds and certain flowering plants. Thus, humming-birds (Trochilidae) with their long slender bills and tube-shaped tongues imbibe nectar and pollinate and fertilise the flowers as they pass from bloom to bloom. Various species show a marked preference for flowers of certain colours, especially scarlet, and the ruby-throated humming-bird (*Archilochus colubris*) migrates northwards across America and Canada as different red flowers open in succession. The Honey Eaters (Meliphagidae) have an elaborate brush on the tip of the tongue which acts as an efficient pollen-collecting device. In Britain red berries attract birds and a much more casual and ill-defined relationship exists between berry-eating thrushes, for instance, and plants like the hawthorn and yew. The berries are eaten and the fleshy portions digested, while the seeds which they contain pass through the birds' bodies and are disseminated in a condition in which germination can take place. In the plant world however, there are copious examples of very strict dependence among symbionts. A classical relationship is that between fungi and orchids. The seeds of the latter cannot germinate without certain chemical substances which are supplied by the former. The fungi on the other hand can only live on the plants from which they derive their own nourishment. Hence the relationship takes the form of a close and powerful alliance, but there are rather similar associations in which the situation

can be better described as an armed truce. This state of affairs is also encountered in the various commensal and symbiotic relationships between vertebrate hosts and bacteria and Protozoa. As we have seen, the host frequently tolerates the presence of commensals. Tolerance in the opinion of Goodrich, is merely a stage between immunity and disease. Symbiosis, Bernard has declared, is the frontier of disease.



CHAPTER 4

THE EFFECT OF PARASITES ON THE HOST

If you join two lives, there is oft a scar

ROBERT BROWNING

“THE PEARLS of Britain,” records Pliny, “be small, dim of colour and nothing orient.” But Julius Caesar openly admitted that the breast plate which he dedicated to the Venus Genetrix was made of English pearls. This may have been part of a Come-to-Britain campaign designed to boost the Empire, but Pliny insinuates that the great conqueror was mean and deliberately foisted second-rate pearls on the Venus Mother.

These pearls were found in the shells of fresh water mussels. Scotland enjoyed quite a flourishing pearl trade as late as the reign of Charles II and the rivers Tay, Don and Spey were particularly famous in this respect. It is said that one very large pearl from Wales is mounted in the British Crown. If so it forms a fitting monument to the extreme hazards of the trematode worm’s life-cycle.

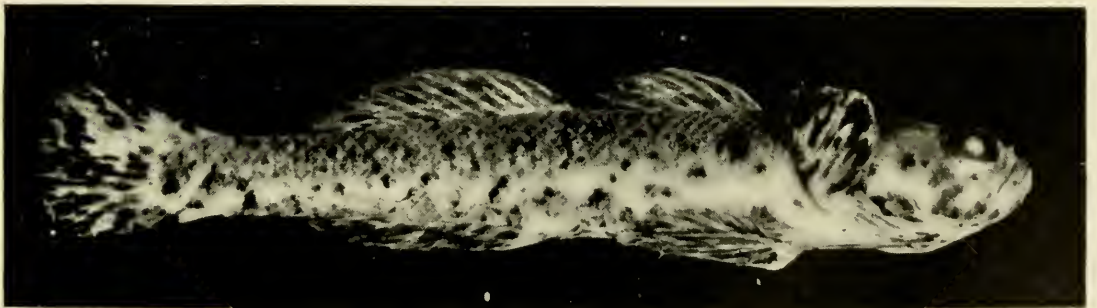
Pearls in Britain to-day are found chiefly in the marine mussel (*Mytilus edulis*) and not in the fresh water species (*Unio* and *Anodonta*). They are usually formed round the body of a bird-parasite—a worm which uses the mussel as an intermediate host and is found, in the adult stage, in the reproductive organs of maritime ducks such as the eiders and scoters.

The mantle of the mollusc, a flap of skin which envelops the soft part of the body, secretes a hard substance popularly known as mother-of-pearl, with which it forms the lining of the shell. If the parasites become accidentally attached to the outside of the mantle, they are quickly enveloped in a covering of epithelial cells. These cells continue to secrete and to envelop the worms in fine alternating concentric



J. G. Bradbury

a. Section of pearl from freshwater mussel, River Tay ($\times 20$)



J. G. Bradbury

b. Goby infected with metacercariae of the herring-gull fluke, *Cryptocotyle lingua* ($\times 1.3$)

Plate VII

EFFECT OF PARASITE ON HOST



Plate VIII

Young starling preening: the host itself is the ectoparasite's greatest enemy

C. W. Teager

layers of aragonite and conchiolin, thus forming the iridescent and highly prized pearls. These rhythmical lines of growth are well illustrated in the photograph of a section of pearl from the River Tay in Plate VIIa. Other intruders, such as mites or larval tapeworms or inorganic matter, may also serve as the centre round which pearls are formed.

Pearls and tuberculosis are both manifestations of the host's response to parasites. They represent two extremes. The single lustrous sphere in which the duck fluke lies entombed is the mussel's successful solution of a relatively simple problem. The extreme emaciation, suppurating liver and other gruesome symptoms of an owl or a rook suffering from tuberculosis are, on the other hand, the bird's desperate and ineffectual reactions to bacterial toxins which eventually prove fatal.

The results of parasitism upon a bird are varied but generally the harmful effects are brought about in a limited number of ways. The parasites may consume the body tissues or body fluids of the bird, or produce substances which are poisons or irritants. They may inflict grievous bodily wounds or cause mechanical injury by pressure or obstruction. They may bring about changes in both metabolism and behaviour and, lastly, introduce other more deadly parasites into the bird's body.

Sometimes one parasite can, at different times, affect the host in all these ways. Leeches, for example, eat the blood of their bird host. Their saliva is poisonous and may inflame the body tissues and even kill the bird. The wounds they inflict while feeding do not heal easily and severe haemorrhages frequently ensue. They also occasionally suffocate the bird by crowding together and obstructing the air passages. They are carriers of spirochaetes and fowl-pox.

Apart from the obvious consequences of these attacks by parasites, obscure and indirect reactions are also involved. For example, the herring-gull fluke, in its first larval stage, infests the common periwinkle (Plate XXVIIIa) and feeds upon its sex organs. It castrates the host, thus first of all making further reproduction impossible for the snail and also causing it to grow in size. The host is thus turned into a giant eunuch. From a cursory glance at the outside of the shell a practised eye can pick out any one of these sadly afflicted winkles. They are specially favoured by fishmongers who, innocent of the reason for their large size, display them prominently on their slabs and

counters. Fortunately, in this stage both worms and winkles are digested by the equally innocent customer.

The second intermediate hosts of the herring-gull fluke are various kinds of inshore fish. The larvae penetrate beneath the scales and into the superficial layers of the skin and there become encapsuled. The tissues of the host react by producing a concentration of pigment round the cysts. The whole fish then appears to be covered in an unsightly rash of black spots. The common goby photographed on Plate VIIb has been heavily infected with these larval trematodes. Such a heavy attack as this, which results from a chance meeting with a dense swarm of larvae, frequently kills the fish. The cercariae pour out a secretion from the penetration glands to facilitate their entry through the skin. This secretion is highly toxic if injected by thousands of larvae simultaneously. To get some idea of what the fish experiences we may imagine walking into a swarm of flying ants on a hot summer afternoon and suddenly, all too late, realising that the ants have settled, cast off their wings and are quickly boring into the skin. When parasites attack human beings in swarms they are generally microscopic organisms which are drawn passively into the body with air or swallowed with food or water. Even those trematodes which will attack a swimmer and actively penetrate the skin are so small compared with their victim that at the time of invasion he is unconscious of the event. Sometimes he may experience a mild prickling sensation of the skin and a faint rash appears and almost as quickly disappears. Fortunately we are spared the knowledge of what we are calmly breathing in and out in the bus or the theatre. Because we have a limited range of eyesight and are lacking in imagination we do not lynch the man sitting beside us who spits on the floor.

The harmfulness of parasites largely depends on their numbers. The adult stage of the herring-gull fluke which browses in the bird's intestine does not seem to cause any inconvenience when only one or two specimens are present. If the gull is unfortunate and catches a very heavily infected fish similar to the specimen shown on Plate VIIb and many thousands of flukes are liberated simultaneously in the intestine, severe inflammatory conditions and even death may ensue. It is true that single individuals of some parasites are dangerous. One tick can provoke a mortal paralysis owing to its toxic saliva. On the whole, however, such cases are rare. Broadly speaking, providing the numbers of parasites are low the effects are slight. But accident or

circumstance may expose the host to a very high infection or permit the uncontrollable multiplication of the parasites within the body which generally spells disaster. In order to soften Pharaoh's heart no new parasites were created but the numbers of existing ones were temporarily increased. When the dust turned to lice the importance of this fact was no doubt appreciated by the Egyptians—"Then the magicians said unto Pharaoh, This is the finger of God." It is this problem of numbers upon which the host concentrates most of its efforts and which it strives desperately to solve. Birds have developed fidgeting, preening, dust-bathing, blinking and, in certain species, "anting" (see p. 127) to such a fine art that ecto-parasites are generally kept within reasonable bounds. Temporarily, at the end of the nesting season, or if the host falls sick, their numbers may increase until they assume menacing proportions, but this is unusual. The host has also developed two main types of resistance to internal parasites. In some cases, where small organisms are concerned, it imposes a sort of birth-control on the invader and in other cases a curb on overcrowding, like the housing act, and thus prohibits the development and establishment of any further individuals of the same species in the same individual host. This is a particularly effective method where helminths are concerned. In fact, in many cases it is the early worm—and often only the early worm—which gets the bird.

Both types of resistance can be demonstrated in the case of avian malaria. During the ten days following infection the parasites are found to accumulate very rapidly in the bird's blood. Then the host falls ill and displays symptoms characteristic of the disease. During this crisis the number of parasites in the peripheral blood stream increases to a peak, but after about five days the bird recovers and the parasites apparently disappear. However, a few are able to hang on in the bone-marrow and the spleen where they continue to reproduce but only in a very discreet manner. Then suddenly, for some reason which remains obscure, the host's power of imposing birth-control on the parasite seems to fail and there is a sudden increase in its numbers and the sufferer has a so-called relapse. This feature is also characteristic of malaria in man.

The reason for the sudden initial fall in the number of parasites is principally due to their destruction by certain other blood cells of the bird known as the phagocytes. A curious sort of armament race takes place within the bird's veins and arteries. The phagocytes begin to

increase in numbers soon after the malaria parasite is inoculated into the bird. So do the parasites. Both increase more and more rapidly. Sometimes the parasites occur in vast numbers—one infected corpuscle to every ten healthy red blood cells is not uncommon. A desperate running fight ensues—the phagocytes killing and ingesting the parasites as quickly as they appear in the blood. Sometimes the parasites win and their uncontrolled reproduction kills the host, but generally, in the case of avian malaria, the phagocytes are victorious. The parasites are destroyed—except, as we have pointed out, for a few isolated pockets of resistance in the bone-marrow and the spleen. When the emergency is over and the parasites have vanished from the outer peripheral stream the number of phagocytes returns to normal. The standing army which remains appears sufficient to cope with the ordinary situation. But if the resistance of the host is lowered and the parasites again temporarily get the upper hand, wholesale mobilisation of the phagocytes occurs all over again. For the continuation of their life-cycle it is of vital importance that *Plasmodium* should appear periodically in large numbers near the surface of the host's body. Without these occasional outbursts of reproductive activity they would never find their way into the proboscis of the insect carrier. On the other hand it is not in their interest to kill the host outright.

A great number of unknown factors may be involved in the so-called lowered resistance of birds. The weather, particularly humidity and low barometric pressure, the phases of the moon, the amount of sugar present in the blood, exposure to ultra-violet rays, have all been implicated and may be the direct or indirect cause of a relapse. In the case of many parasites a bird's resistance varies with age. Tuberculosis is pathological chiefly in old birds, whereas only young birds fall victims to the attacks of certain worms.

In addition to phagocytosis the birds react to the presence of *Plasmodium* by developing certain specific substances known as antibodies in the blood serum and other body fluids. Their presence renders the environment difficult or unsuitable for the parasite. This keeps the numbers down after the initial reduction by the phagocytes—at any rate any new infection by the same species is destroyed or unable to develop. This phenomenon is known as partial immunity. Immunity is the most widely studied of all the effects which parasites produce on their host, for it has a wide practical application in medicine. In the case of certain virus diseases such as small-pox in man and fowl-pox in



J. G. Bradbury

a. Common louse-fly, *Ornithomya avicularia*, with fully developed wings ($\times 9.9$)



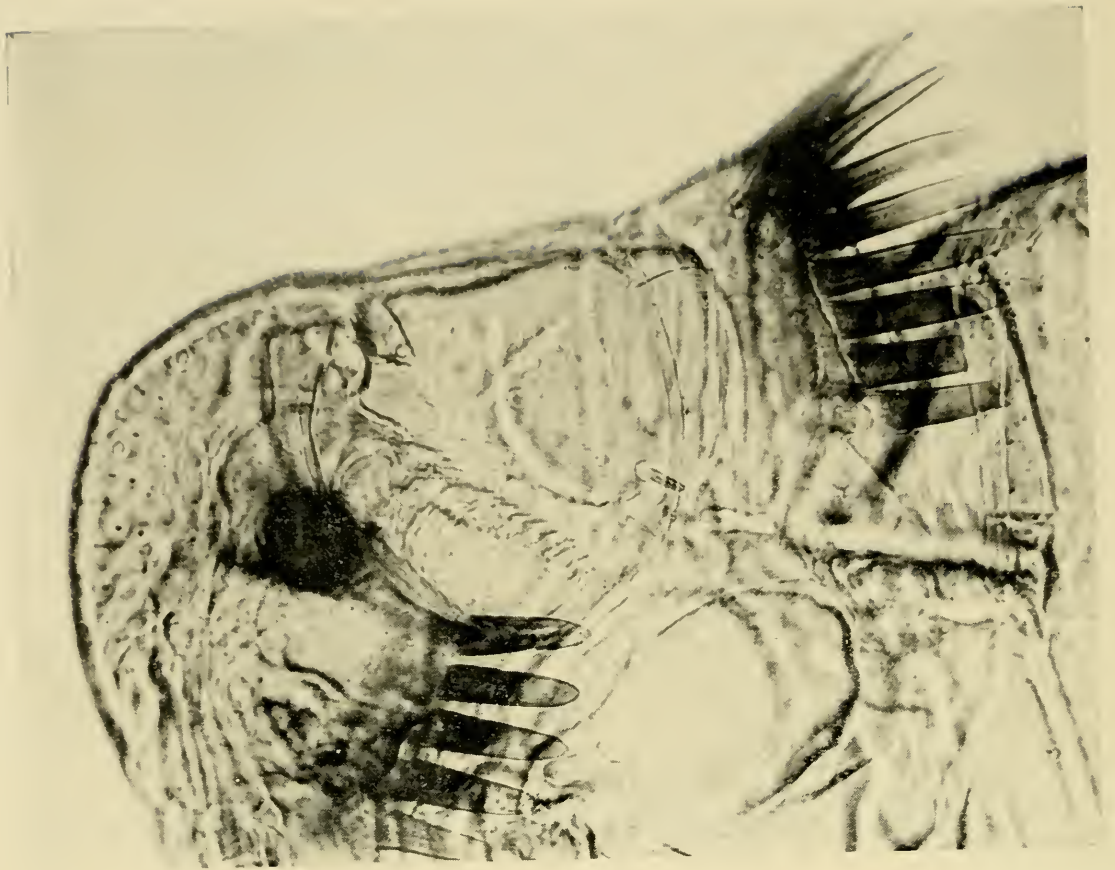
Arthur L. E. Barron

b. Swallow louse-fly, *Stenopteryx hirundinis*, with non-functional wings ($\times 5.1$)



J. G. Bradbury

c. Sheep ked, *Melophagus ovinus*, entirely devoid of wings ($\times 7$)



A. E. Botting

a



A. E. Botting

b
Pronotal combs of, a, mammal flea, *Spilopsyllus cuniculi* ($\times 180$), and
b, bird flea, *Ceratophyllus gallinae* ($\times 212$)

Plate X

birds, one attack confers a lifelong resistance or immunity against that particular organism. Generally, in the case of the larger parasites immunity is such that it prevents reinfection of the same species but only while the infective organisms are still in the body of the bird. Thus complete recovery—that is to say the death of the parasites—exposes it to a fresh invasion. This state of affairs is so advantageous for the worm or protozoan concerned that it might well be considered an adaptation of the parasite rather than the host. In other words, the host protects the parasite for life from intra-specific competition and offers itself once again for spoliation by some other member of the race if death removes the intruder. Simultaneously, of course, it also protects itself from the crushing, possibly fatal, burden of over-population.

In the case of many endo-parasites of insects, superparasitism frequently results in a battle between the larvae, only one surviving per host. Thus intra-specific competition limits the number of parasites and in this way achieves much the same results as the temporary immunity developed by the host itself. In the case of birds, if a heavy initial infection occurs, and many larval worms are ingested simultaneously, intra-specific competition may also occur between the developing adult worms.

This balance of power or mutual adjustment of parasite and host is regarded as the hallmark of successful parasitism. Caullery considers that in the case of such an infection the parasite and host together form a functional balanced system which is placed in opposition to the external environment. In other words both parties make the best of a bad job. The host's reactions—the result of selection—tend to reduce the inconvenience to a minimum and the parasite has to live as unobtrusively as possible in a hostile environment. Together they must face the dangers and hazards of the outside world.

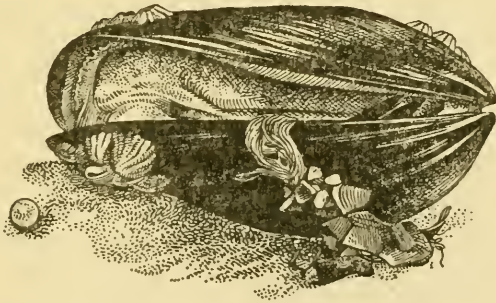
In the case of larval flukes it is worth remembering that there can be no gradual adaptation between host and parasite. Selection is entirely one-sided. The parasite castrates the host, or in the case of young snail hosts inhibits the growth of the gonads, and therefore the more susceptible snails, and even those which survive infection the most successfully, do not reproduce themselves and are eliminated from the population. Consequently adaptation can only be on the side of the parasite. In the case of larval flukes this situation is very obvious, but it probably exists in many other cases of parasitism, when it is wrongly assumed that adaptation is mutual.

It is of course a well known fact that micro-parasites such as bacteria and the viruses can, under certain circumstances, show an increase or decrease in the pathological or poisonous effect they exert on their host. The same phenomenon can be observed in various parasitic Protozoa. For example, if the spirochaete which causes relapsing fever in man is inoculated into mice, and passed rapidly through a series of these animals, the organism loses its power to infect man at the end of a few years. It is also noticeable how in many epidemics, such as the influenza epidemic of 1948-49, the virus increases in virulence as it passes from host to host. By the spring the disease was far more serious than at the beginning of the winter. Certain trypanosomes, such as the species which attack the big game of Africa, exert no ill effects on those animals which are considered to be their normal hosts, but prove virulent and fatal if they are passed to domestic cattle. In other cases, such as pigeon-pox, the effect on unusual hosts like the chicken is negligible in comparison with the effect on the normal host. Again the introduction of other parasites may lower or raise the virulence of an infection. Thus mild and chronic avian malaria in canaries can be stimulated by the presence of spirochaetes, and develop virulence and toxigenicity which soon kills the host. These variations are often considered to be the result of selection acting upon certain types already present in the infection or developed by mutations. In bacteria they are frequently associated with morphological changes. Such evolutionary trends can be observed in the case of unicellular organisms owing to the numerous generations which follow one another in rapid succession. The phenomenon is one of great interest and practical importance but despite an immense amount of research it is still not properly understood.

Turning now to brood parasites, such as the European cuckoo, the attack on the host is relatively easy to observe. In the first place the female destroys at least one egg of the host which she replaces by her own. Subsequently, if the egg is accepted and incubated, the young cuckoo, on hatching, destroys all the other eggs or nestlings which may be present. Henceforth the entire efforts of the foster parents are directed towards feeding and rearing the intruder chick. Frequently birds desert their nests after a visit from the cuckoo, but even such cases entail a considerable loss of time and effort on the part of the victim. It must be remembered that a female cuckoo can, under favourable conditions, lay over twenty eggs in different nests during a single

breeding season. One species of bird is generally parasitised in a particular district and the cuckoo's attentions can result, over a period of years, in a serious reduction in the numbers of the host. Some very careful observations have been made on the reed-warbler in a circumscribed area in Germany. The first year in which counts were made fourteen nests were present of which four contained cuckoos' eggs. Six years later, in the same area, only eight were found and of these no less than seven contained cuckoos' eggs. It seems quite possible that a favoured host can be exterminated in certain districts by over-parasitisation by the cuckoo.

It cannot be too strongly emphasised that the effect of all types of parasites on the host is detrimental. If we find that a bird seems little, if at all, inconvenienced by the presence of Protozoa or worms or lice, or a cuckoo in the nest, we can nevertheless assume that it would be better off without them. There are, for example, certain worms which live in the oviduct of birds and are known to inhibit egg-laying. There are others which are likewise located in the oviduct, yet apparently produce no symptoms of any kind. Over a long period, however, they may well reduce the total numbers of eggs laid. Small effects such as lack of vitality, loss of voice, excessive blinking, or perverted habits like dirt eating are extremely difficult to gauge. Nevertheless, it is only a question of degree. Potentially all parasites are harmful.



Mussel, *Mytilus edulis*, with a pearl

CHAPTER 5

THE EFFECT OF PARASITISM ON
THE PARASITE

Ruinous inheritance !

GAIUS

A PARASITE's life is an impressive gamble. Indeed it is difficult to envisage insecurity on such a scale. The chances of a grouse roundworm finding a grouse are far less than the reader's chances of becoming the parent of quads, or a cabinet minister.

Most free-living animals do not die of old age—they are killed and eaten. The majority of parasites, on the other hand, die a lingering death from hunger or exhaustion because they fail to find a host. As Shipley pointed out, the eggs of the grouse roundworm lie scattered all over Scotland, but millions and millions of their young, which hatch out and wriggle up the sprigs of heather around them perish because their particular plant is never eaten by a grouse. Similarly, vast numbers of immature ticks cling hopefully to blades of grass, waiting for the millionth chance which will bring an animal brushing through the vegetation within reach of their waving forelegs.

Owing to the difficulty of finding a host—a difficulty which is superimposed on the more familiar hazards of life—the mortality among most parasites is enormous. A vast number of eggs or larvae have to be produced in order that the species can survive at all. Consequently a characteristic feature of most parasites is a relatively enormous development of the reproductive organs, which frequently come to dominate the body. Intestinal worms produce eggs by the million and even brood-parasites like the cuckoo lay four or five times as many eggs as their hosts. The difficulty of host-finding can often be estimated by the number of eggs laid. Female ticks of the

family Argasidae which live in the nests and burrows of their hosts lay a few hundred eggs, whereas those of the family Ixodidae, which generally have to depend on a chance meeting with their host in the open, lay in thousands. There are also various peculiar asexual forms of reproduction which help to increase the progeny of certain parasites. Thus, each fertilised trematode egg, say of the herring-gull fluke (*Cryptocotyle lingua*), by fragmenting inside the first intermediate host (see p. 200), gives rise to several million larvae. Certain bird tapeworms multiply by budding in the larval stage and by the production of chains of individuals—strobilisation—in the adult stage. Parasitic Protozoa, of which the malaria group is the best known example, have the power of splitting up into several individuals once they have been introduced into the blood stream of the bird.

The difficulty of finding a host is in itself a major issue but, added to this, parasites experience great difficulty in finding a sexual partner. Consider the position of two blood flukes which by the greatest possible good fortune penetrate into the veins of the same duck. Consider the further good fortune of these flukes if they happen to meet in their progress through the interminable labyrinth of the host's blood vessels. After two such coincidences they cannot possibly risk parting again. It is, therefore, not surprising to find that devices for ensuring permanent contact between such fortunate individuals are commonly met with among parasites. The male of the duck blood-fluke (*Bilharziella palonica*) has a flap of skin (the gynaecophorus canal) down the ventral side of its body, in which it envelops the female. Henceforth the two progress in a permanent embrace along the blood vessels of the duck and the fertilisation of the eggs is assured. In the case of *Collyriculum faba*, a fluke from the sparrow and other wild birds, and *Balfouria monogama*, from the marabou stork, a male and female worm are snugly enclosed together in a cyst, the formation of which they induce in the tissues of the host. In the case of the sparrow fluke the cyst is situated beneath the skin in the region of the cloaca and in the stork is an invagination of the wall of the stomach. The gape-worm (*Syngamus trachea*), which is a familiar pest in the farmyard as well as a parasite of many wild birds, lives joined together in pairs (Plate XXVIIb) in the trachea and bronchial tubes of the host. Male and female are attached permanently to one another by their sexual apertures.

In the case of some parasites the male is dwarfed and permanently attached to the female. This is a curious phenomenon more frequent

among animals which live in the sea than on land. There is one famous example of a male roundworm which lives as a parasite inside the vagina of the female. There is no doubt that this is a certain way of ensuring that sperms are available when the eggs are ready for fertilisation, but like so many other devices to which parasites resort, it is rather an exaggerated form of the more usual relationship between the sexes. Among some ticks which also attack birds there are cases of dwarf males parasitising the females to which they become permanently attached (see tail-piece, Chapter 12). They pierce the skin of their mates and gorge themselves on blood recently extracted from the body of the host. Many internal parasites, however, have solved the problem of fertilising their eggs in another way. Both male and female organs are found in the same individual. Such two-sexed animals are known as *hermaphrodites* and in many cases they are capable of self-fertilisation and are completely independent. Marital worries are unknown as far as tapeworms are concerned, for they can produce millions of offspring in complete peace and solitude. Some hermaphrodites—for instance quite a large proportion of trematodes—do, nevertheless, copulate with another individual if the two should happen to meet in the heaving darkness of the bird's intestines. There is no question of waiting for the right sex—as copulation can take place between any two mature individuals, a mutual penetration by the male organs occurs and cross fertilisation results. Each partner then lays eggs.

Various parasites, for instance some ticks and nematodes, have found yet another solution to the same problem. They resort to virgin birth and in such cases their eggs develop without being fertilised. Sometimes this form of procreation, which is known as *parthenogenesis*, goes on for several generations, but when a male happens to be available the female returns once again to the more usual form of reproduction. In some species, however, only females have been found and it is believed that the male sex has been dispensed with altogether.

In this way parasites are forced to adopt a dangerous procedure, for asexual reproduction reduces the variability of the species concerned. New combinations of mutations by sexual cross-fertilising cannot occur, and such characters will remain isolated in each asexually produced line or population. Huxley has stressed that the sexual process confers a greater plasticity in evolution, and the parasite is forced to sacrifice evolutionary potentialities by adopting parthenogenesis, polyembryony and strobilisation in its efforts to reproduce

itself. It may have no alternative as a short term policy, but in the long run such a procedure may prove fatal to the race.

Apart from the modifications connected with reproduction, there are certain morphological features which recur persistently in parasites. Organs of locomotion are partially or totally lost. Intestinal worms and leeches have no ambulatory processes. Parasitic insects which live on the bodies of birds, such as feather lice, fleas and bugs and certain flies, are wingless or have mere vestiges of wings which for the purpose of flight are useless. On the other hand, they have developed very varied and efficient organs of attachment, such as hooks, suckers, anchor-like protuberances and prehensile lips—"for their strength is to sit still." In the case of ticks, fleas and some fly-larvae the mouth-parts, which are embedded in the host's flesh, are armed with re-curved spines (see Plate XII). Leeches, on the other hand, have cup-like suckers at both ends of the body, some flukes cling grimly from the rear only, whereas lice hang on by their claws. It is quite obvious that once a parasite has reached a suitable host it must make every effort to remain with it. To be sneezed out of the nasal cavity of a duck or blown out of an elephant's trunk are very great dangers which leeches must guard against. Birds with the "gapes" are racked by coughing—a sort of recurrent earthquake for the worms in their throats—and it is, therefore, scarcely surprising that these nematodes live with their anterior ends embedded in the mucous membrane of the bird's trachea. In a way, parasites are caught between the devil and the deep sea, for often organs of locomotion would be extremely useful for finding their host, but a distinct disadvantage once they have achieved this object. The parasitic fly *Carnus hemapterus*, directly the bird host is found, quickly creeps between the feathers, but first casts off its own wings. This is an unusual case. Generally parasites lose their own organs of locomotion and employ other transport animals (see p. 18 and tail-piece of Chapter 8) in order to reach their host.

Many internal parasites absorb food through the surface of the body. There is a tendency to lose their mouths and part, or all, of the digestive organs. This modification is found in some Protozoa as well as in worms and various other parasites. In ticks and leeches, which frequently have to endure long fasts between their meals, portions of the alimentary canal are extended in the form of pouches and branches in which the blood is stored and from which it can be absorbed slowly.

Almost all the blood suckers—insects and worms, as well as leeches and ticks—have developed a special sort of saliva which mixes with the blood as it issues from the wounds they have inflicted and prevents it clotting, both at its source and within the proboscis or gut of the parasite. Many parasites also lack the sensory organs which normally keep animals in touch with the external world. Eyes and ears would be useless to a fluke in the liver of a bird, or to a feather mite in a curlew's quill and, indeed, they possess neither. Instead they have developed other senses or tropisms by which they are guided to small circumscribed areas of the host's body or on long migrations through the tissues of the host.

The difficulty of finding their host has imposed upon many parasites a fantastically complicated life-cycle. Moreover most endo-parasites, in order to reach their goal, must pass from a highly specialised but stable environment into the strikingly different and fluctuating conditions of the outside world. No man can leave an air-conditioned hotel, say in Toronto, in mid-winter without putting on an overcoat, but a parasite must face even more violent changes without any artificial protection.

A few parasitic Protozoa pass from host to host during contact between individuals—by licking, kissing, sexual intercourse or feeding of young by the parents—but many form resistant cysts or spores which pass into the outside world, where they are carried hither and thither by the elements and possibly reach another host by the medium of air or water or contaminated food. Some Protozoa are entirely dependent on invertebrate vectors. The malarial parasites are permanent prisoners in the circulatory system of their vertebrate host and doomed to perish with it, unless they are rescued by a blood-sucking insect. Only the sexual stage is passed in the mosquito and it seems likely that the insect carrier has been secondarily interpolated in the cycle. The opposite is probably true in the case of trypanosomes which were primitively insect parasites.

The majority of worms have become involved with a complicated series of intermediate hosts. Many bird flukes, for instance, have seven stages : egg, free-swimming miracidium, sporocyst and redia within a snail host, a free-swimming cercaria, an encapsuled metacercaria in a second intermediate host (which can belong to almost any group of animals ranging from mammals and frogs to leeches and jelly-fish) and finally the sexually mature individual in the bird (Fig. 4). Sometimes an extra

host is added or one cut out. The life-cycle of tapeworms is characterised by the absence of free-swimming larvae but in many cases up to four different intermediate hosts are used. Roundworms also frequently depend on intermediate and transport hosts, and the filarias are taken up from one host and put back on another one by blood-sucking insects.

Complicated life-cycles are unquestionably characteristic of internal parasites. On the other hand extremely simple life-cycles are met with among external parasites, particularly those like feather lice, mites, and the sheep ked, which pass generation after generation on the same individual animal. Parasites, it is true, develop many features in common but free-living organisms become adapted to a specialised environment in the same way, and we find for instance that cave-dwelling animals all over the world are often characterised by blindness and pallor. Parasitism merely provides a particular habitat and mode of life which calls forth certain equally distinctive adaptations.

Some parasites are able to live on a wide range of hosts belonging to different orders or even classes of animals, but it is more usual for a parasite species to be confined to a relatively small group of hosts. These may embrace a whole order such as the ducks, geese and swans (*Anseriformes*) or two or three related species like the swallow and house-martin, or even a single species or even subspecies of bird. Parasites which are confined to one particular host, or to a group of related hosts, are said to be host specific.

Host specificity is the result of the parasite adapting itself to life in a certain environment, and if the adaptation is very close it is unlikely that it will be able to survive on, or in, any other host. Many free-living animals have become adapted to particular environments or highly specialised diets, and are therefore unable to live elsewhere. The crested tit in Scotland is restricted to areas where there are old rotten pine stumps in which it nests. The marsh fritillary butterfly (*Euphydryas aurinia*) in Britain is confined to an environment where the devil's-bit scabious is found—the only plant upon which the female will lay her eggs, although the larva will feed on honeysuckle, snowberry and certain other leaves. The koala bear can only survive on a diet of fresh eucalyptus shoots and is therefore restricted to places where the plant grows. Such examples could be multiplied indefinitely. It may originally be a single attribute which links a parasite to one particular animal but once the association has begun all the characteristics of the host, morphological and physiological, as well as biological, play their

part in guiding the parasite along certain well defined lines of development. The permanent ecto-parasite becomes adapted to the external covering of the host—the feathers or hair and the skin texture. Such characters affect the mouth-parts of the parasite, its integument, and claws. Certain feather lice in which adaptation has become very close cannot lay their eggs on feathers of a different structure from that of their normal hosts. In other cases ovulation and hatching can only take place within very narrow ranges of temperature. The fertility of the eggs may also depend on whether the parasite has fed on the right host. Many ecto-parasites seem to be closely adapted to the chemical composition of the blood and feathers of their host. In a carefully controlled experiment Wilson has shown that one of the chicken lice would feed on feathers of an American heron, but the nymphs did not complete their moults and the adults died within three to sixteen days. Some bloodsuckers placed on an abnormal host will often refuse to feed, others attempt to do so without enthusiasm or success, while others again will imbibe the strange blood but die shortly afterwards. As Lucretius remarked, “What is food to one man may be fierce poison to others.”

Most lice are strongly host-specific, but a notable exception is the species from pig and man. The human louse will feed and breed on swine, and the pig louse is equally at home on man. There is an obvious resemblance between the near naked skin of the domesticated pig and man, and again, the chemical composition of their blood must have a lot in common—at any rate neither proves lethal to the lice in question. There are other parasites which normally feed on these two hosts: the human flea (*Pulex irritans*) and the jigger (*Tunga penetrans*); a tick (*Ornithodoros moubata*); certain of the floor maggots (*Aucheromyia*), a nematode worm (*Ascaris lumbricoides*) and the influenza virus.

In some cases, when a parasite appears to live normally on a strange host some part of the biological cycle is nevertheless disturbed. The human louse breeding on the pig produces an abnormally high proportion of females—a factor which could lead ultimately to the extinction of the race.

Where endo-parasites are concerned the chemical composition of the various body fluids is probably of much importance, and also the composition of the gut contents, and the physical structure of all the internal surfaces which the parasite pierces or clings to during the course of its life-cycle. The rapidity with which food passes through an

animal's body, for instance, can determine which cysts have time to hatch before they are eliminated.

In all types of parasites there is a close adaptation to the habits of the host. Sand-martins dig long burrows in sand quarries, place their nests in the excavations, and return to them year after year, and thus expose many of their ecto-parasites to peculiar and unusual conditions, combined with severe isolation—which is also a factor conducive to speciation. It is therefore significant but not surprising to find that sand-martins have at least two fleas, a tick, mite, fly and beetle, all of which are host-specific.

The feeding habits of certain animals expose them to infection by worms which use their prey as transport hosts. This frequently results in a sort of pseudo-host-specificity. Thus certain flukes which are found in nature in a few species of fish-eating gulls will develop successfully in a wide range of hosts in the laboratory, including dogs and rats. The distribution of adult flukes is chiefly governed by the feeding habits of the final host and has been called ethological specificity by Baer. He contrasts this with the type demonstrated by the tapeworms of birds, which he designates as phylogenetic specificity. In their case specificity is strongly developed, a fact which he suggests is due to their very ancient association with their hosts.

It is of great interest that, unlike the adults, the first larval stages of trematodes are markedly host-specific. This fact has led many people to suggest that flukes were primitively parasites of molluscs and that the adult stage in vertebrates is a relatively recent development. This might account for their lack of specificity in the adult stage. Tapeworms on the other hand are rarely host-specific in their larval stages.

In the case of permanent obligate parasites, such as feather lice and mites, which pass several generations upon the same bird, there are few disadvantages and many advantages in host specificity. They may be compared to the fauna of oceanic islands, which have few opportunities for extending their range to other lands and relatively little competition from invading species, and can consequently adapt themselves more and more closely to the specialised conditions of their own particular habitat. This enhances further the prospects of the individual, enabling it to live and breed more efficiently and to achieve a relatively harmonious personal relationship with the host, without endangering the survival of the species.

The fauna of an oceanic island is also subjected to intense isolation over long periods of time, circumstances which, as we have already mentioned, are known to favour the formation of distinct species. The same factors operate in the case of permanent bird parasites. The obligatory restriction of the feather louse population to a particular bird host enables it to form distinct species and to develop characters which make it impossible for it to live on other species of birds; the more distinct the species the greater the ensuing isolation, consequently the process is cumulative and host-specificity becomes both its own cause and effect.

In the case of temporary parasites which only visit the host at intervals to partake of a blood meal, host-specificity is fraught with great danger, for the chances of finding one species of host after long periods of separation are often remote. On the whole, parasites like ticks, mosquitoes and leeches are not host-specific, although with a combination of special circumstances like those we have mentioned for the sand-martin strict specificity can develop.

In the present state of our knowledge, however, it is often impossible to recognise, let alone explain, the various adaptations which limit parasites to single hosts. The common hen flea (*Ceratophyllus gallinae*) for example is an insect with remarkably catholic tastes. It has been found (see p. 111) on over a hundred different species of bird host. A closely related species (*C. rossittensis*), almost indistinguishable morphologically is, on the other hand, closely confined to the carrion-crow. Such cases are not understood and for the time being must remain a mystery.

A strictly host-specific parasite like the crow flea is closely adapted to a dependent condition—a situation which is fraught with great danger. Even in the case of free-living animals restriction to a single source of food can lead to disaster. If some unforeseen event, such as a sudden change in climate or the spread of some rare disease, destroys the hitherto plentiful food supply the species of animal in question cannot survive. In recent years large numbers of brent geese perished during the sudden worldwide famine of eel grass. As a few individual birds still retained the possibility of changing their feeding habits the species was enabled to weather the crisis. One of the great ironies of life is that the most spectacular and successful specialisations of to-day frequently spell doom and destruction for to-morrow.

CHAPTER 6

THE ORIGINS OF PARASITISM AND THE EVOLUTION OF PARASITES

How Mutability in them doth play
Her cruel sports . . .

EDMUND SPENSER

THERE ARE no parasitic starfish or lampshells but in all the other large groups we find animals which have abandoned a free life in favour of parasitism. Zoologists have little, if any doubt that all parasites have evolved from free-living animals. Many such organisms are, of course, at different stages of evolution, some being much farther removed structurally from their ancestral stock than others and consequently resembling them less and less. Before the larval stages of these animals were known their origins in many cases remained obscure. Now that the life-cycles have been worked out their past has been revealed. Thus, for example, the dog whelk has a free-swimming larva known as a veliger and so has the worm-like, shell-less, footless, colourless, toothless gastropod mollusc (*Entoconcha mirabilis*) which lives as an internal parasite of sea cucumbers (Holothurians). Fish-lice, too, some of which as adults resemble little bags of blood fixed to the gills of fish, have an active swimming larva very similar to the larva of the free-living copepods, which swarm in the sea. An endo-parasite (*Sacculina*) which resembles a mass of roots ramifying through the internal organs of crabs, has a free-swimming larva which instantly reveals its true nature and places it among the barnacles (Cirripedia).

These are extreme cases. Most parasites are not modified beyond recognition. As we have seen in the foregoing chapter certain structural alterations are associated with the parasitic mode of life, but we can still find in most of them a well-marked resemblance to their free-living relatives. There are, however, no free-living tapeworms or

flukes in existence but although their origins are obscure the larvae reveal traces of an independent past. In many groups of animals parasitism has arisen anew several times over, a fact which is confusing and irritating for zoologists as it seriously interferes with their desire for orderly pigeon-holing.

Parasitism can develop gradually or suddenly. It can be the outcome of a long series of complicated interactions or the result of isolated accidents which occurred a million years ago or only this morning. A long established and widespread habit, such as the wanderlust shown by mites, together with their inclination to creep into cracks and crevices, may be the starting point. On the other hand some unusual occurrence such as the accidental introduction of a number of unicellular organisms into a bird's inside, with its food or water, or with the air it breathes, may provide exactly the right conditions and circumstances required to induce them to begin the parasitic mode of life.

Many animals are saprophagous, that is to say they feed on dead and decaying matter, such as dung or putrefying corpses. It is a short step from a dead nestling to a decomposing flesh wound on a living bird, and the fly-larvae, which occasionally try the latter as an alternative meal, are following one of the well-trodden paths to parasitism.

Many of the arthropod parasites of birds, such as bugs, mosquitoes, and ticks, were originally suckers of plant juices. As the geological record proves, these groups evolved before birds and mammals and, no doubt, in the past were essentially vegetarians. It is a relatively easy matter for them to pierce the skin of an animal either accidentally, in error, or deliberately if no other food is available, and to extract its body fluids. These accidental and casual drinks of blood which no doubt originally took the form of an occasional meal might easily become a habit, and then a necessity. Blood appears to be a somewhat dangerous beverage, for like alcohol, it can convey certain immediate advantages, yet carries with it the dreaded seeds of dependence. In the case of careless blood drinkers the sins of the parents may be visited upon the children in dramatic fashion—even unto the millionth generation or more.

Competition for living space is very keen in nature. Even such unattractive milieus as vinegar, gall and crude petroleum have been successfully populated by certain species of worms and fly-larvae. Sometimes an ecto-parasite finds competition too intense on the surface of the host's body and creeps into a convenient orifice, a step which

can eventually result in a change to an endo-parasitic mode of life. It is not, of course, suggested that all internal parasites have passed through an ecto-parasitic stage.

The females of many animals are predisposed to take this route, for they frequently seek sheltered nooks and crannies in which to breed. We find that the females of the roe-deer flea (*Dorcadia dorcadia*), for example, are fixed permanently inside the nostrils of their host, but the males are free and wander about over the whole body.

One species of black-fly (Simuliidae), of which the males are not parasitic at all, mates in the ears of its host—for where the female leads the male follows and in due course both sexes may take to an endo-parasitic life.

Numbers of temporary insect parasites are only parasitic in the female sex—the males feeding romantically on dew and nectar. In many cases the development of fertile eggs has become dependent on a blood meal and so tied the species to a vertebrate host.

There are multiple ways in which parasitism can arise and in fact there is only one vital element in the genesis of a parasitic relationship and that is opportunity. Flies are continually, although unwillingly, brought into contact with spiders and it comes as no surprise to find a group of flies (Cyrtidae), which in the larval stage parasitises spiders. Ducks eat leeches with extreme relish and there is one case on record when some of these birds arrived overnight at a leech farm and by breakfast time had devoured the entire stock of 20,000 leeches. Nevertheless we find that at least one species of leech parasitises ducks. There is an even more curious situation existing between certain birds and mosquitoes. Swallows, for example, devour them by day and by night are devoured by the insects.

The most favourable condition, therefore, for the dawn and development of dependence is a social environment and it is in crowded communities, whether of birds or ants or men, that one finds parasitic relationships developed most consistently. Here the scene is set, the dangerous opportunity is ever present, and it is merely a question of time before one of the organisms concerned exploits the situation. It may thereby obtain some advantage, however transitory, which starts it upon a course of irreversible specialisation—the risky road to dependence.

A commensal relationship is potentially even more dangerous than a merely social tie, for by nature it is more intimate. The closer the

association, the more easily is the balance upset. One partner can then suddenly take a mean advantage of the other. Thus we have already seen that certain *débris* feeding fly-larvae which find shelter in birds' nests will sometimes return their hospitality by surreptitiously eating the fledgelings alive. Some of the predatory mites, which live permanently on birds and hunt other small arthropods in the forests of feather and down, have abandoned the chase and turned parasitic themselves. They have lost their powerful jaws and now chew the pith of feathers or the various layers of the bird's integument. Although commensals obviously expose themselves to treachery of this sort, it would be entirely wrong to imagine that commensalism is an inevitable step in the development of the parasitic habit. It merely represents one of a number of ways in which parasitism can arise.

In the cases we have cited the prey is a small animal, which has occasionally been able to turn the tables on the predator by becoming a parasite. The more usual course of events is for the predator itself to find the prey too large to kill but nevertheless it can feed upon it and become permanently attached to it. This is undoubtedly one of the commonest ways in which the parasitic habit has originated. Some leeches, which have not developed a specialised taste for one particular food, will kill any small animal they come across in their wanderings in ponds and streams. They attach themselves to their unfortunate victims and suck them dry. If, however, a leech finds an elephant taking a casual bathe in the river and can creep into its anus, the days of precarious wanderings are over. However successfully and however long a leech maintains this position it will certainly never suck the elephant dry. Large size is fundamentally a bar to the parasitic habit. An elephant's trunk, like the leech's sucker, may pre-adapt it to ectoparasitism, but it is clearly impossible for any large mammal to secure a life of ease and plenty in such a manner.

The rove beetles (*Staphylinidae*) have developed a wide range of habits. The majority are saprophagous and swarm where there is dead and decaying organic matter such as dung and corpses, but many are predacious, both as adults and larvae. A large number of these beetles are found exclusively in the homes of other animals. We can guess that they were first attracted to this habitat by the concentration of animal life or animal excrement and later became adapted to, and possibly largely dependent on, the higher temperature characteristic of nests. In the case of the species which favour the homes of birds and mammals



a



b



c



d

Photographs by Arthur L. E. Barron

The shearwater flea, a, *Ornithopsylla laetitiae* (male, $\times 17$), is related to the rabbit flea, b, *Spilopsyllus cuniculi* (male, $\times 22$), whereas the hen flea, c, *Ceratophyllus gallinae* (male, $\times 19$), is probably derived from a rodent flea similar to d, *Ceratophyllus anisus* (male, $\times 20$)



J. G. Bradbury
 a. Blow-fly, *Calliphora* sp. ($\times 24$)



Arthur L. E. Barron
 b. Hen stick-tight flea, *Echinophaga*
gallinacea (female, $\times 136$)



Martin Duncan
 c. House-gnat, *Culex pipiens*, (female, $\times 57$)



Arthur L. E. Barron
 d. Sheep tick, *Ixodes ricinus* (female, $\times 101$)

MOUTHPARTS SHOWING ADAPTATIONS TO SPECIALISED
 METHODS OF FEEDING

they have retained the more primitive predacious habits and are gainfully employed, as far as the host is concerned, killing and eating their flea parasites. In the intensely social environment of a termitary or ant hill the behaviour of the staphylinid beetles has radiated out along several different lines. Firstly, the predatory habit has developed into straightforward parasitism and the larvae of some species are parasitic upon the nidicolous pupae of certain flies. Secondly, there are species which are commensals of the ants. They live as tolerated guests and, for example, accompany the foraging expeditions of the legionary ants, picking up some of the food captured on the way. They have come to resemble their hosts to a remarkable degree. Thirdly, there are scavengers and corpse eaters. Towards this category the ants show a certain degree of hostility—with good reason, because in the case of diseased and disabled workers, the beetles sometimes reduce them prematurely to the status of a corpse. Fourthly, there are the symbiotics which, like those from birds' nests, prey on certain enemies of the ants, such as parasitic mites and the larvae of certain flies. Finally, we have the true guests (symphiles) which are housed, fed and even reared by the ants and, in return for their hospitality and solicitude, eat their eggs and young. To encourage their ministrations the beetles exude a glandular liquid which the ants find madly attractive and lick up with intense eagerness. It is not known if the liquid exuded by the beetles confers any benefit on the ants. It appears more probable that they are merely sacrificing their brood in order to indulge an irresistible craving for the exudation—a situation which the beetles have learned to exploit. Such curious behaviour is also found in human communities where men will sacrifice their own health and the welfare of their families in order to indulge in drugs and drink.

Thus it will be seen that, once established in a communal environment, the rove beetles have exploited the situation in a variety of ways. They have launched out into different kinds and different degrees of commensalism, symbiosis and parasitism.

There are certain features (see p. 38), both morphological and biological, which appear to be characteristic of parasites. These attributes are useful and adapt them to the parasitic mode of life, in the same way that the streamlined shape of whales and sharks adapts them to a wandering life in the sea. How these modifications have come about is the subject of much discussion. Parasites themselves are very varied organisms, pertaining to widely separated groups of animals, and it is

highly improbable that in their case every kind of evolutionary change is brought about in the same way. Mites and feather lice, for example, pass generation after generation on the same individual host and, where they are concerned, one can expect to find evolution working in much the same way as it does on the fauna of a small oceanic island. Competition between members of the same species of lice and the same species of mites, both for food and accommodation, must be intense. On the other hand, certain intestinal worms battle in solitude with the host, the elements and space—for them intra-specific competition plays a minor role.

Some zoologists believe that natural selection, acting upon chance mutations, gradually alters parasites and adapts them to their special mode of life. In experimental breeding of the small fruit fly (*Drosophila*) several mutations are known to occur producing wingless flies, or flies with sickle-shaped or greatly reduced wings, which are reminiscent of some of the types found in nature in the various species of parasitic louse-fly. Such mutations may be advantageous for a parasite and consequently on certain hosts the wingless type would stand a better chance of surviving and reproducing itself. It is also thought possible that certain features of a parasite's environment, for example, the ecto-parasite's contact with the constant heat of the bird's body, or the fact that many worms and Protozoa are permanently immersed in their food, act in such a way that some types of mutations are favoured or even induced; natural selection would subsequently determine their survival value. This theory may apply especially where minor adaptations are concerned—such as the similar comb-like structures found on the bodies of very dissimilar insect ecto-parasites like certain flies, fleas, beetles, lice and bugs.

On the other hand some biologists argue that in order to start on this peculiar form of existence an animal must be *pre-adapted* to parasitism. Baer surmises that the louse-flies possessed a tendency to regression of the wings, blood-sucking habits and viviparity which *destined* the group to a parasitic life. In support of this theory it must be pointed out that the features which are characteristic of parasites are by no means peculiar to them. Thus, some tapeworms will lay one hundred and fifty million eggs a year, whereas the estimated annual output of a free-living starfish is upwards of two hundred million. Animals such as the limpet and the common goby have efficient suckers with which they cling to wave-swept rocks. Some female deep-sea

fish have dwarf males which live on them as parasites and many molluscs are hermaphrodites. Snakes and earthworms have lost their legs or ambulatory processes and certain jelly-fish are capable of absorbing nourishment through their skins. In these cases the factors which determine a vast output of eggs, the development of suckers, the loss of organs of locomotion and so forth, obviously have nothing to do with a parasitic environment. It is easy to see that any animal might already possess one or several of these specialisations *before* it took to the parasitic mode of life. Furthermore, the difficulty experienced, say, in reaching a new host is obviously so great that it is hard to conceive how such an animal could become established as a parasite unless it already possessed immense powers of reproduction. The theory of pre-adaptation is, therefore, undoubtedly attractive in the case of species which are introduced suddenly and violently into an entirely new environment.

It is as well to remember that if individuals vary at all pre-adaptation must exist. Some of our friends seem to enjoy heat waves, while others become inactive and sit around sighing and mopping their brows. It is permissible to claim that the former are pre-adapted to a hotter climate. Professor J. B. S. Haldane once demonstrated at a Royal Society *Conversazione* that he is immune to the bite of bed bugs. So was his father. The Haldane family are therefore pre-adapted to survive a bug-borne epidemic, should one occur. To say that plants and animals may be pre-adapted is really only another way of saying they are not all alike, for every variation is potentially both adaptive and pre-adaptive. On the other hand, as Bodenheimer has pointed out, in one sense no real adaptation to a new environment ever takes place. No matter how different life may be, say, in the sea, or in the gall-bladder of a bird, an animal's response cannot surpass the hereditary base of reactions. Theoretically evolutionary possibilities are endless, but certain lines are mutually exclusive, and once an animal has started along one of these evolutionary paths, others are automatically barred. The more highly specialised an animal becomes the less are its chances of being able to break away, and certain lines are thus self-directing and self-restricting. Therefore, although *Sacculina* develops root-like extensions of the body which ramify throughout the host's tissues, it cannot turn into a plant—although such a transformation might have definite advantages.

There are also some very interesting examples of direct modifications which have been produced merely by a change of host. For

instance, the sexual form of certain roundworms develops directly from the egg in sheep, but in rabbits the same worm produces an asexual generation. In a few abnormal hosts worms are dwarfed, or only one sex—the male—may achieve development. Again, variable strains of trypanosomes are known which are dependent upon and produced as a response to the environment in a particular vertebrate host.

Whatever theory is favoured, from the point of view of the biologist, parasites remain a particularly interesting and fruitful study. For, although there are no fossils with which to compare parasites, free-living forms from which they must have been derived are often available and the two can be examined *alive* side by side. The zoologist can look at an active free-swimming copepod dashing about in the water with its antennules twitching and its swimmerets beating, and he can also examine the parasitic fish louse, attached like a small sack of blood and eggs to the host—and stare in amazement at the results of evolution.

It is probable that parasitic animals exceed non-parasitic forms, both in the number of existing species and in the number of actual individuals. For example, from man—not counting bacteria and fungi—over five hundred different species of parasites are recorded. This mode of life consequently appears, at first sight, to be highly profitable. However, the evolution and progressive transformation in the direction of successful parasitism clearly reduces and circumscribes the possibility of future readjustments. Huxley has defined biological progress in its broadest sense as “control over the environment and independence from it.” The evolutionary trend of parasites is in the opposite direction—towards dependence.

We have already called attention to the fact (p. 7) that many animals can be parasitic for some period of their lives and yet show no trace of this particular mode of existence, either in form or function, during other stages of their life-cycle. There are also those cases in which one sex is parasitic and the other is not, and the free sex displays no modifications which can be attributed to the strikingly different way of life chosen by its mate. Furthermore, whether we are dealing with a coot or a cuckoo, a butterfly or a bed-bug, an earthworm or a lungworm, we find that the eggs and sperm of both free-living and parasitic animals are remarkably alike.

It would certainly appear that a parasitic existence during the larval stages of an animal's life-cycle is neither so harmful nor so irrevocable as in the adult stages. Many entomologists believe that the

Hymenoptera, including the most highly developed of all insects, the social bees and ants, are descended from ancestors which were parasitic in their larval stages. Keilin has put forward strong evidence to show that the Cyclorrhapha flies, which include the house-flies, bluebottles and their allies, are likewise descended from ancestors all of which had parasitic larvae, although at the present time only a small proportion have retained this habit.

It is perhaps obvious that the benefits bestowed on an organism by the parasitic mode of life would be most marked in its immature stages. During the period of maximum growth it is sheltered from the rigours of the outside world and protected from violent changes in the environment. It is also provided with an abundant and constant food supply. Moreover, its close relationship with the host is for a limited period only, which does not involve the permanent sacrifice of independence, nor the loss of those sense organs which constitute its link with life in the outside world.

The French zoologist, Giard, gave the name of "placental parasite" to the mammalian foetus. Many biologists strongly object to the term "parasite" used in this sense and consider that it cannot be employed to indicate a relationship between individuals of the same species. Nevertheless, the fact remains that during foetal life the mammalian young obtains food, water and oxygen from the body of the mother and through the organ of attachment—the placenta—excretes the waste products of metabolism. Various reactions, not always beneficial, set up by the presence of the foetus, are singularly reminiscent of those brought about by an alien organism feeding at the expense of the host. In fact, placental parasitism represents the supremely successful example of this mode of life. It seems possible that a fundamental distinction can be drawn between the parasitic adult and the parasitic young, the full significance of which has not hitherto been fully appreciated. In the former, parasitism appears to lead to dependence and a loss of evolutionary potential, whereas in the immature stages, it may, on the contrary, prove to be a successful and progressive step.

PART TWO

Bird Fleas and Feather Lice

INTRODUCTION

Sir, there is no settling the point of precedency
between a louse and a flea.

DR. JOHNSON

BIRD FLEAS and feather lice do not sing. Nor do they fly about flashing brilliantly coloured wings in the sunshine. It is scarcely surprising that in Britain bird and butterfly enthusiasts number thousands, but the collectors of fleas and lice can be counted on the fingers of one hand.

The Mallophaga and Aphaniptera are small, drab insects of insignificant appearance and without obvious aesthetic appeal. In the mind of ordinary men and women they have loathsome associations of dirt, disease and furtive scratching. Moreover, they are too small to study with the naked eye and the finer structures on which their classifications are based have to be examined with the aid of a microscope. From the scientific aspect however, they are of great interest, not only as carriers of deadly disease but as insects closely adapted to the parasitic mode of life.

Both bird fleas and feather lice prey upon avian hosts, and their mode of life has imposed upon them certain well known features associated with parasitism. Thus both are wingless, both have failing or poorly developed eyesight, and both have claws adapted to clinging. In addition they have developed a very resistant integument, and can consequently survive a nip from the host that would squash or fatally injure many insects of similar size. The Ceratophyllid bird fleas and a certain number of species of Mallophaga also share a rather curious

adaptation. The males have antennae especially modified for grasping the female during copulation.

Despite these features which they have in common, the two orders present a profound contrast.

First of all the feather louse undergoes no metamorphosis. When it hatches from the egg, a feat it accomplishes by pushing up the cap which opens like a lid, the nymph or young louse which emerges is more or less a miniature edition of the adult—minus the sexual organs.

It reaches maturity by a series of three moults, that is to say it periodically casts off its integument for which it has grown too big. Each time it changes its skin in this manner it becomes a little more like the perfect insect. Its whole life-history from egg onwards is passed upon the host, and from the day it hatches it can chew feathers. The feather louse's world is the hot, fidgeting body of the bird, with which its fate is indissolubly linked. The reproduction of the host means a future for the louse and the death of the host spells its inevitable doom.

Fleas on the otherhand, have a complete metamorphosis (Plate XVIII). The larva, which develops inside the egg, hatches by ripping up the egg-shell with a special spine situated on the front of the head. The sort of legless caterpillar which emerges does not remotely resemble a flea, and at this stage chews its food rather like a feather louse. After a series of moults it changes into a pupa, or resting stage, from which, in due course, the perfect insect emerges. Unlike the larval stages of the feather louse, those of the flea are free and are generally passed in the host's nest.

In many cases fleas themselves only spend a limited amount of time on the body of the host, and should the bird die they can survive for days, weeks, or even months, hiding in the nest or some appropriate crack or crevice. They can also live for a long period after emerging without food, but ultimately they are compelled to partake of a blood meal or perish without reproducing themselves.

Structurally the adult insect also presents a considerable contrast. Fleas are flattened from side to side, essentially an adaptation to life in fur. Only a very fat man who has once been thin can appreciate the advantage of not having to turn sideways to get through a gap, especially if he happens to be in a hurry. On the host, fleas are nearly always in a hurry.

Feather lice on the other hand are flattened from above downwards. Their life depends on being able to cling closely to the feathers, or,

in other words, to protrude as little as possible above the surface of the host.

Fleas are, generally speaking, much more active insects than lice. They have more need to be. The feather lice can run, but they generally confine themselves to sudden short rushes which enable them to move quickly out of sight if they are momentarily uncovered by the bird's preening.

Species restricted to the head or neck, out of reach of the host's beak, can sacrifice speed and become more closely adapted to the feathers. Fleas, except for one or two rare exceptions such as the stick-tight flea of poultry (see p. 62), not only have to move rapidly on the host, but they need to jump on and off at very short notice. Hence they are provided with long powerful legs, whereas those of the feather lice are short and weak.

It is perhaps unnecessary to stress the fact that the feather lice bite and chew their food, while the fleas suck it up in liquid form through tube-like mouth-parts (Plate XII). Expressed differently, the latter cannot eat, they can only drink.

It is when we come to regard these two groups of insects as a whole that we realise how great the contrast is between the two.

Ornithologists calculate that there are approximately 8,500 species of birds in the world to-day. Louse experts estimate that there are more than three times as many feather lice, making a total of approximately 25,500 species. Of bird fleas about 60 are known and named. Possibly the total is somewhere around a hundred.

The feather lice show great diversity in form and structure, whereas the fleas, at least to the naked eye, present a very homogeneous appearance. Again, each order of birds has its own characteristic feather lice—just as it has its own Cyclophyllid tapeworms—whereas the bird fleas show no such restriction to a group of hosts. Moreover, many species of feather lice are host-specific, that is, confined to a single species of bird, whereas most of the fleas are not. Finally many feather lice have specialised habitats upon the bird's body—some are confined to the head, others to the wing feathers, others again live inside the quills. Except for the two or three species in which the females are sedentary and therefore obliged to congregate on the head (see p. 76), fleas have no special location on the host's body.

Thus an immense gap divides these two orders. The feather lice, one can deduce, are a very ancient group. They are also a highly

successful group on birds, less so on mammals. Fleas, on the other hand, are not successful as bird parasites. They primarily prey upon mammals and only a few have succeeded in changing over to bird hosts. Up to date no one can say it has been an advantageous step and so far the order has failed to expand on birds.

Perhaps the greatest interest of the feather lice arises from the fact that they have, through the ages, been saved many hardships and violent changes of environment which the birds themselves have experienced. For this reason and also perhaps because their evolution proceeds, fundamentally, at a slower tempo, they have evolved and differentiated less rapidly. Thus the feather lice have not diverged so widely from the parent stock and by their resemblance to one another they can reveal the original but now hidden relationship of the birds themselves. The parasites' environment has remained comparatively stable. For example, the temperature of a bird's body is relatively constant whether it is living in the Alps or in the Sahara. The composition of the feathers and blood on which the parasites feed is also relatively stable, whether the bird is living on a diet of wire-worms, berries, fish, green leaves, carrion or grain. The hosts themselves have had to contend with great geological and climatic changes, and also new habitats into which they are forced by competition, which in turn have involved changes in their mode of life and diet. In such circumstances the birds respond by physiological and morphological changes which often conceal their true descent.

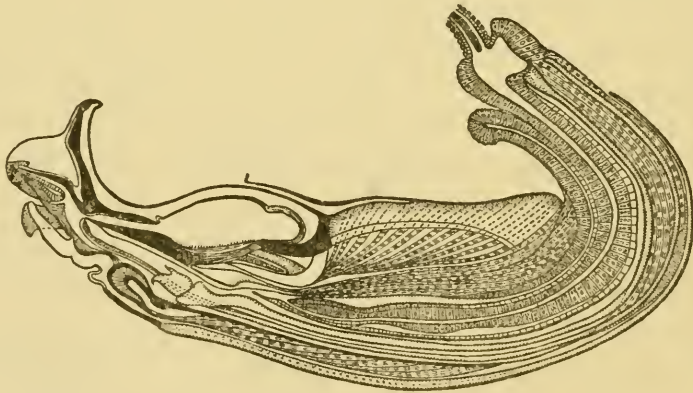
There are many groups of birds which are a puzzle to the systematists and which are difficult to place in any scheme of classification. What is the rightful place of the flamingoes—with the ducks or with the storks? Are the humming-birds related to the swifts or passerine birds? Are woodpeckers correctly placed in a separate order? In Chapter 8 we shall consider the evidence provided by the feather lice which infest birds, and see what light these throw on the classification of their hosts.

Strong criticism is sometimes levelled at parasitologists regarding the evidence of host relationship drawn from a study of parasites. It is argued that a mistake can as well be made regarding the systematic position, say of feather louse or a tapeworm, as of the bird itself. With this we entirely agree, and we would not therefore accept as strong evidence of relationship, the sharing of say one genus of parasites by two hosts. However, when a bird of doubtful position harbours three

genera of feather lice common to some possibly related group of birds, we consider the evidence of relationship strong—for three major errors in the interpretation of louse morphology would be improbable. In all cases, however, the evidence presented by both host and parasite has to be carefully examined and sifted because of other factors (see p. 141) which may be involved. As yet there is little co-operation between one type of specialist and another. There is a natural tendency for the ornithologist to place more reliance on the work of his fellow bird specialists, which at least he can appraise, than on that of the entomologist and helminthologist, and frequently he rejects out of hand the valuable evidence provided by the parasitologists.

The fleas, unlike the feather lice, have only been associated with birds for a few hundred thousand years (see p. 90), and through them we can study quite another aspect of parasitism—namely the effect on the parasite of the change to a new type of host.

In the following account of the Mallophaga and the Aphaniptera we have concentrated on the British fauna, but it must be realised that numerically the two groups are not comparable, for the former contains about 1,500 species in Britain, and the latter about a baker's dozen. Consequently, while it is quite possible to give a very brief account of the various species of bird fleas, the feather lice have to be treated in a more general manner.



“ The intromittent organ of fleas is probably the most complex genital apparatus to be found in all insects.”

CHAPTER 7

FLEAS (APHANIPTERA*)

(ἀφανής=NOT APPARENT, πτερόν=WING)

Though this little Creature is almost universally known to be a small brown skipping Animal, very few are acquainted with its real Shape and Figure, with the Structure, Strength, Beauty of its Limbs and Parts, or with the Manner of its Generation and Increase.

DR. HOOKE

STRUCTURE, LIFE-HISTORY AND HABITS

THE SIMPLEST way to collect bird fleas is to take a nest from which the fledgelings have recently flown and to keep it in a cardboard box or linen bag. Providing the nest is damped periodically, the larval or pupal fleas continue to develop in the debris or rubbish in the bottom, and in due course hatch out. It is a more lengthy process to collect them off the bodies of their host. Less than one bird in ten harbours fleas, and then generally only one or two specimens at a time. Moreover the host has to be enclosed in a receptacle immediately after being shot or captured, otherwise the fleas hop off and escape. The maximum number recovered from a bird is 25 specimens from a house-martin. On the other hand, no less than 4,000 have been bred out of a single martin's nest.

On opening the collecting bag the fleas can often be observed sitting at rest on the sides (Plate XXXIII). In profile they are faintly reminiscent of miniature brown pigs—"bunch backed like a hog." This effect is produced by the absence of a well defined neck, for the head appears to pass broadly into the thorax. Moreover the flea is devoid of a "waist," which is such a characteristic feature of wasps and many flies.

The largest British flea is the mole flea (*Hystrihopsylla talpae*) which measures about 5 to 6 mm. in length. The British bird fleas vary from

* Also known as Siphonaptera

1 $\frac{3}{4}$ to 4 mm., the largest being the rock-dove flea (*Ceratophyllus columbae*), although both the sand-martin flea (*Ceratophyllus styx*) and the moorhen flea (*Dasypsyllus gallinulae*) come very near it in size. At the other end of the scale we have one of the house-martin fleas (*Ceratophyllus rusticus*) and the house-sparrow flea (*Ceratophyllus fringillae*).

Fleas vary in colour from almost black to pale brown. Their integument is extremely tough and slippery, as anyone knows who has tried to squash a flea in his fingers. The insect generally manages to squeeze under a nail and make good its escape with a disconcertingly sudden jump which the eye cannot follow.

It is, of course, well known that the hard part of an insect is external. In other words the skeleton consists of a chitinous outer covering to the body similar to that of a crab or a lobster instead of an internal scaffolding like the bones of mammals and birds. This hardening and toughening of the cuticle is most pronounced, on the whole, in parasitic insects.

If a flea is examined under the microscope it is found to be covered with strong, rather widely spaced bristles, arranged in definite rows or groups, varying in length and thickness, and lying close to the body. This greatly adds to the general streamlined effect. Each of these bristles is set in a socket (Plate XXXIIIc) and articulates with the cuticle. They are very valuable characters when it comes to classifying the fleas.

On certain segments the hardened exo-skeleton is produced into a series of spine-like backwardly projecting teeth, which form combs (Plate X). These combs greatly facilitate the animal's progress through fur and feathers and protect vulnerable areas of their bodies. Parasitic insects from quite unrelated groups which live in the fur of mammals, such as modified flies (*Nycteribiidae*) and bugs (*Polyctenidae*) parasitising bats, and the beetle (*Platypsyllus castoris*) from the beaver have also developed comb-like structures. A few of the feather lice have somewhat similar devices formed from expansions of the cuticle. This type of comb is only found on parasitic insects. The genal comb (Plate Xb) which protects the mouth, and the pronotal comb situated on the first segment of the thorax are generally the most conspicuous in fleas.

The head of the flea, as in all insects, encloses the brain and bears the mouth parts, eyes and antennae. It varies considerably in shape, and in the fleas which have become "fixed" such as the hen stick-tight flea (*Echidnophaga gallinaceus*) and the parrot stick-tight flea (*Hectopsylla psittaci*) the front of the head is sharply angled. This

facilitates their close, and in the case of the female, permanent attachment to the host by their mouth-parts. A similar modification (Plate XI), but less pronounced, can also be observed in the common rabbit flea (*Spilopsyllus cuniculi*) which is partly sedentary, and in the related shearwater flea (*Ornithopsylla laetitiae*).

Fleas are descended from winged ancestors (see p. 73) and the thorax still bears a strong resemblance to the thorax of flying insects. It has become secondarily adapted to support the jumping legs of the flea. It consists of three segments which are broken up externally into different sized chitinous plates thus giving it the appearance of a sort of crazy pavement. In the hen stick-tight flea, and the parrot stick-tight flea, the thorax is greatly reduced and the three segments are narrow and crowded together. These fleas have lost the power of jumping and consequently there is a corresponding reduction in the huge muscles of the thorax.

The respiratory organs of a flea consist of a network of tubes, which end blindly, known as the tracheal system. The air enters through the external openings, the spiracles, which are conspicuous features along the sides of the body, and is carried to all the tissues by the ramifications of the tracheae.

In certain sedentary fleas, the spiracles on the thorax have been lost and are now represented by mere pin-point depressions in the cuticle, while those on the abdomen are greatly enlarged.

The chitinous external portions of the spiracles are, of course, rigid, but just below the surface is a complicated apparatus whereby the tubes may be shut. A rhythmical opening and closing of the spiracles can generally be observed, which is associated with the inflation or deflation of the main trunks of the tracheal system. Sometimes when the flea takes a lot of exercise, or is ripening eggs, the first and eighth abdominal spiracles, which are much larger than the rest, remain open continuously.

This type of respiration is obviously quite different from that of vertebrate animals such as birds or mammals. Human beings are apt to regard their own personal structure as "normal" and everything that differs from it as distinctly humorous. It is difficult for them to realise that fleas breathe through holes in their sides, have a nerve cord below their stomachs and a heart in their backs; or that certain other arthropods lay eggs through their elbows, urinate through their heads and regularly practise virgin birth.

The abdomen of the flea consists of a series of segments each of which is protected, externally, by a dorsal and ventral overlapping chitinous plate known respectively as the *tergum* and *sternum* (Plate XVII). The first sternum is missing, and the three last segments are highly modified in connection with the sexual organs and form a series of flaps and levers and struts of peculiar complexity.

The abdomen contains the digestive and excretory organs, the heart and circulatory system and also the ovaries and testes. The main nerve cord runs along the ventral side of the body and has, in addition to the brain, a series of swellings at intervals along its length. These swellings (see Plate XVII) are nerve centres known as ganglia. In the male flea there are eight such nerve centres and in the female only seven. This fact does not suggest that the male is the more gifted of the two—on the contrary, a fusion of the ganglia indicates a more highly specialised or “advanced” condition. Apart from this curious form of sexual dimorphism the internal structure of a flea is rather generalised and presents no very unusual features. For further details the reader is referred to the excellent descriptions of the anatomy of insects which can be found in Ford’s and Imms’ books in the *New Naturalist* series.

In many insects the male can be described as the weaker sex and this is certainly true in the case of fleas. The female is larger, lives longer, weighs twice as much and is hardier and more resistant if conditions deteriorate. It is also said to assume the active role in mating. This last point is difficult to prove and indeed is probably a subjective impression due to the greater size of the female which in mating adopts a position covering the male. When a male bird flea approaches a female it can be seen to cock its antennae out of their grooves, and in view of the important role these organs play in mating this might well be described as taking the initiative. The ancient writers thought the antennae of fleas were ears and it is of course quite possible that with them the flea perceives vibrations. They may also serve as organs of smell and touch. In bird fleas and their allies they are much larger in the male sex and when cocked are held aloft like a pair of horns (Plate XI*d*). During copulation the male takes up a position beneath the female and uses the antennae to grasp her firmly from below. At other times they are folded back neatly into the grooves along the sides of the head, thus adding to the general streamlined effect of the body (Plate XI).

In the case of the hen stick-tight flea, which is sedentary, copulation often takes place between adjacent individuals, without either of them detaching themselves from the skin of their host—although the male is not permanently fixed like the female. The process may last twenty-five minutes or longer.

It is easy to tell the sexes apart even without the aid of a hand lens, as the end of the body of the male has a rather rakish upward tilt—somewhat reminiscent of a drake's tail—whereas the female's body merely narrows terminally. The external sexual organs or *genitalia* are of primary importance in distinguishing between closely related kinds, or species, of fleas. In fact among the bird fleas it is sometimes the only practical way of telling them apart. These organs in the male are fantastically complicated. The terminal segments are modified for grasping the female, and the penis with its guiding rods is itself a structure of extraordinary complexity—in fact it is the most complex genital organ to be found in any insect. The more one considers it, the more difficult it is to understand how such a structure can have been evolved either by a series of mutations or by natural selection, or by means of both. We have tried to understand the way in which this apparatus worked from studying permanent preparations of copulating martin fleas, and we have puzzled over the slides for hours. An American morphologist attempted the same study with another species of bird flea. Although he elucidated many obscure points much remained a mystery; he concluded his description with a sentence which exactly expresses our views. "Truly," he wrote, "the thing does not make sense."

The genitalia of the females are much less complicated but they also afford a most important clue to classification and relationship. The female flea has the capacity of storing the male sperm, and releasing it at intervals as her eggs ripen. This enables her to lay fertilised eggs as long as two months after copulation. The internal organ which receives and stores the sperm from the male, the *receptaculum seminis* or spermatheca (unpaired in all British bird fleas) is chitinised and thus visible from the outside in cleared and mounted specimens (Plate XVII). In outline it roughly resembles a barrel-shaped flask with a thick neck. The subtle difference in the proportions of these two parts affords the simplest character for distinguishing between the females of closely related species (Plates XIII and XIV). In Britain where one is concerned with relatively few fleas, it is easy

RECEPTACULUM SEMINIS OF BRITISH BIRD FLEAS
AND MAMMAL FLEAS
(x 165)

a

Ceratophyllus garei
(from carrion-crow)

b

Ceratophyllus borealis
(from rock-pipit)

c

Monopsyllus sciurorum
(from red squirrel, for
comparison with *a* and *b*)

d

Ceratophyllus columbae
(from rock-dove)

e

Hoplopyllus glacialis
(from Artic hare; not British,
for comparison with *f*)

f

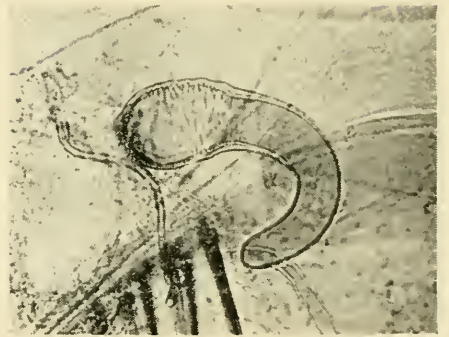
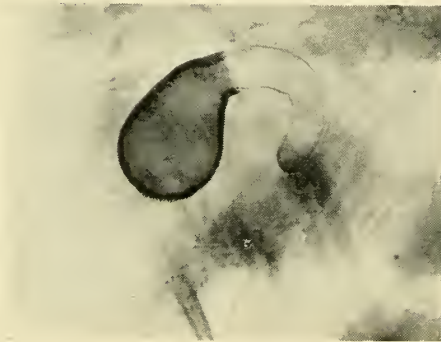
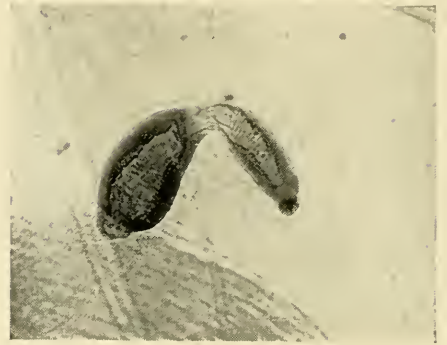
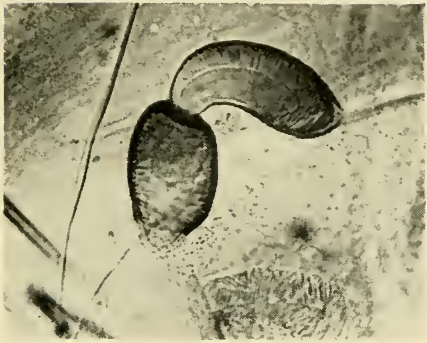
Ornithopsylla laetitiae
(from puffin)

g

Dasyopsyllus gallinulae
(from skylark)

h

Orneacus rothschildi
(from house-martin)



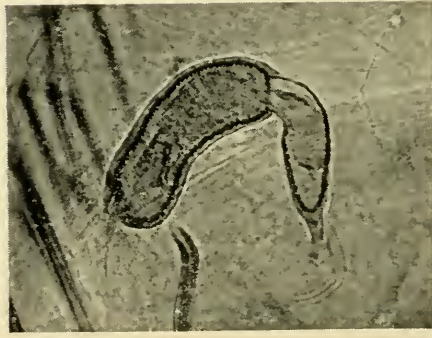
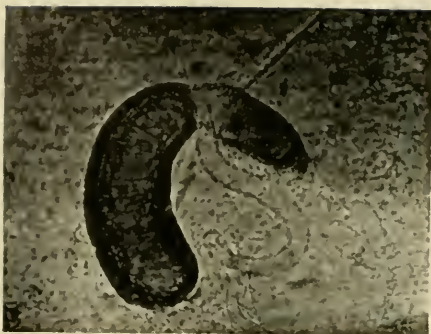


Plate XIV

Arthur L. E. Barron

RECEPTACULUM SEMINIS OF BRITISH BIRD FLEAS
AND MAMMAL FLEAS

(x 165)

a

Ceratophyllus gallinae
(from blue tit)

b

Ceratophyllus fringillae
(from house-sparrow)

c

Ceratophyllus farreni
(from house-martin)

d

Ceratophyllus rusticus
(from house-martin)

e

Ceratophyllus hirundinis
(from house-martin)

f

Ceratophyllus styx
(from sand-martin)

g

Monopsyllus anisus
(from brown rat; not British,
for comparison with a-h)

h

Ceratophyllus vagabunda
(from herring gull)

enough to carry these differences in one's head and, once under the microscope, there is little more difficulty in "spotting" species of fleas than species of butterflies.

In nature bird fleas probably copulate when the host is incubating eggs or when the young are in the nest or on the host itself, for they seem to require not only a blood meal but a certain degree of warmth to stimulate their interest in the opposite sex. In a glass tube they remain completely indifferent until the tube is heated in the palm of the hand. They will then mate readily enough.

Some fleas seem to require a meal from their true host before they will copulate. In the laboratory the common rat flea (*Nosopsyllus fasciatus*) will feed more readily on man than on rats but according to Strickland this does not provide an adequate stimulus. The common hen flea (*Ceratophyllus gallinae*) however, which is very hardy and less particular in more ways than one, will breed successfully on mammalian blood, man or rat. Some of the house-martin fleas copulate without a feed at all—a fact which we have observed ourselves.

Many male fleas die soon after mating, but the female survives, not only to deposit her eggs but to supply an important element in the diet of her offspring. It has been proved that she requires a blood meal before laying fertile eggs and therefore in the absence of the host breeding is impossible. Blood appears to have a stimulating effect upon the reproductive organs of the female, for she generally lays within twenty-four hours of feeding even if she has been starved for weeks previously.

In countries with well defined seasons, most phases of an insect's life-cycle are restricted to certain periods of the year. For example the purple emperor butterfly is only seen on the wing in June and July, and wasps are not troublesome round the Christmas tree. Fleas are also more in evidence at certain seasons. For example, in temperate climates such as our own, the number of fleas per rat rises in the summer and falls off sharply in the winter, whereas in parts of tropical India the opposite is true and the flea population is at its height in the so called cold season. In Texas the hen stick-tight flea almost vanishes after the spring rains, but is again plentiful in dry cool periods in the autumn. Pliny, many hundreds of years ago, remarked upon these seasonal fluctuations and drew attention to the "fleas which skip merrily in summer time in victualling houses and inns, and bite so shrewdly."

Frequently both adult and larval fleas are found pullulating in the nests of hibernating mammals. Brumpt states that a certain *Ceratophyllus* found in the nests of hibernating voles, lays eggs and breeds right through the winter. If this is true the host's long sleep must be troubled by bad dreams. Certainly during the period in which the hedgehog is torpid, its fleas are quite active. It has been shown however that the rhythmical inflation and deflation of the tracheal tubes—in other words the flea's breathing—is considerably slowed up during the hibernation of the host. The quickest rhythms are found in gravid females in summertime and therefore it seems likely that this species at any rate does not breed in winter.

Bird fleas have a more sharply defined breeding season than mammal fleas. Although in all species seasonal changes in climate affect the number of eggs laid, the proportion which hatch and undergo metamorphosis, the duration of each larval stage and so forth, yet broadly speaking, if conditions are reasonably favourable, rat fleas and many other mammal fleas are known to lay eggs, even if reduced in number, and breed all the year round. But the conditions such as plentiful blood meals and a raised temperature which induce the common rat flea and the stick-tight marsupial flea (*Echidnophaga myrmecobii*) to breed in mid-winter in the laboratory, have no effect on the common hen flea which will only lay eggs in the spring or early summer. This indicates that the parasite is well adapted to its particular hosts. It is vital that the flea's life-cycle coincides with that of birds, for it is only during a brief period in the spring that the host occupies a nest.

In India the native jungle fowl (*Gallus gallus*) is not infested with *Ceratophyllus gallinae*. This flea is undoubtedly a parasite of European wild birds which has only fairly recently developed a marked predilection for the domestic fowl. Although birds are present all the year round in hen houses *Ceratophyllus gallinae* still retains a definite spring breeding season. In time this may be modified to suit the new conditions. Here the stage is set for the evolution of a new physiological race and possibly a new species.

Some permanent parasites like the feather lice, pass their entire life-cycle on their host. It is of supreme importance to them that their eggs should not fall off after they are laid. To ensure against this misfortune the female glues them individually and with extreme efficiency to the feathers (Plate XXIV). In the case of the flea, which has a free larval and pupal stage generally spent in the nest, the reverse is

true, and if the eggs are laid on the host it is preferable that they subsequently roll off.

Like birds themselves, different species of fleas lay differently shaped eggs. The human flea (*Pulex irritans*) has a nearly spherical egg, but those of the common hen flea are elliptical. The eggs of the tropical rat flea (*Xenopsylla cheopis*) are midway between the two. In colour they are pearly white and relatively smooth with rather soft shells which are easily dented. They are devoid of the elaborate sculpture and ornamentation which adorn the eggs of butterflies and many feather lice but under a high power magnification the surface is seen to be finely pitted. When the host scratches and preens itself they roll off and are conveniently scattered. A keen entomologist once collected a spoonful off the lap of a visitor who, during tea, was affectionately fondling his kitten. Often the eggs are deposited directly in the nest of the host. They are just visible to the naked eye and are faintly reminiscent of a fine dusting of castor sugar. A female flea, at intervals, deposits a total of between 300 and 500 eggs. Except in the case of a sedentary species they are laid singly or in small batches—during the day and night—either on the host or on dried twigs and leaves in the nest. The sedentary species sometimes lay small egg masses, in which the individual eggs are glued together.

The hen stick-tight flea expels her eggs forcibly and they fall well clear of the head of the host on which this species congregates. According to the temperature and humidity they hatch in 2 to 14 days.

All but five of our sixteen bird fleas belong to the genus *Ceratophyllus* and these are essentially fleas of temperate climates. Especially in the early stages of their life-cycle they require a cool humid atmosphere.

The eggs of the common rat flea, which is fairly closely related to the bird fleas and until recently was included in the genus *Ceratophyllus*, hatch at a temperature of 41°F. The eggs of the tropical rat flea, however, require temperatures above 54°F. before the larvae can emerge. Hirst, discussing the problem of bubonic plague and its flea vectors, remarked that in all probability each species of rat flea has adapted itself to some particular range of climatic conditions. This is also undoubtedly true of bird fleas and it of course includes adaptation to the ranges of humidity and temperature found in the various types of nest they infest. It is obvious that conditions in a gannet's nest, a sand-martin's nest and a starling's nest are very different. The

hen stick-tight flea dies in the larval stages if the temperature falls below 50°F. Our poultry is thus saved in this country from a serious scourge.

The flea larvae rip up the egg shell, which generally cracks longitudinally, with a spine situated on the front of the head. When they emerge after about ten minutes' wriggling they are minute cylindrical semi-transparent maggots adorned with a few hairs but without eyes and with merely a pair of anal struts on the last segment to serve as appendages (Plate XVIII). Some species are very much more hairy than others. They twist about actively in the nest débris and sometimes curl themselves up sharply like a watch spring. It is especially in this stage that fleas require a humid atmosphere. Even the sweat and urine from the host's body play a large part in keeping the larvae alive. They cannot survive dry heat. Feather lice which pass their early stages on their hosts are independent of external climatic changes and their situation in this respect is singularly secure compared with fleas.

Buxton once measured the relative temperature and humidity in a Palestine cow-shed and two rat holes opening into it. The temperature recorded was the same in all three spots, but the greater humidity in the holes was sufficient to make the development of the flea larvae possible within them. No doubt it is the moisture requirements of the larvae which has imposed one of the greatest barriers to the infestation of birds by fleas. For insects such as these the change from a mammal's humid nest or lair to the dry aerial home of birds is revolutionary. It is significant that most of the existing bird fleas are found on species which breed on the ground and in banks, or use mud freely in the construction of their nests.

According to the temperature and humidity, which may speed up or delay metamorphosis during all its phases, the larval stage of a flea may last from one to twenty-four weeks. During this period it moults three times. (There are a few exceptions among the sedentary species which have only two moults.)

It is an undisputed fact that the mouth-parts of the larvae of fleas are adapted to gnawing but their diet has been the source of endless discussion. Leeuwenhoek as far back as 1694 noticed larvae of the pigeon flea "red with blood" but subsequent writers maintained that this element did not form part of their normal food. On the contrary, they were said to maintain themselves on organic refuse such as the dung of their host, dead flies, the bodies of adult fleas and the sawdust

in used spittoons. Aristotle was quite ignorant of the life-history of the flea but he had observed that dung was a contributing factor to their welfare. He wrote, "Fleas are the result of putrefaction of smaller bodies, for example where dried dung is, there you find fleas." One early naturalist reared the larvae on "the bran like substance which sticks in the comb when puppies are combed." It appears that this unattractive diet is adequate for the larvae of the tropical rat flea and the human flea but not for all species. Sharif proved that in addition to organic refuse which forms a necessary part of its diet it is essential for the larvae of the common rat flea to eat small quantities of blood. In nature this is provided by the female flea which, during her interminable meals, squirts out quantities of undigested blood through the anus, and thus amply justifies her Gargantuan appetite.

It was also proved experimentally that it is impossible to rear larvae successfully if the iron content has been extracted from the blood fed to them. One wonders if, in some cases, the blood-sucking habit of insects was acquired in connection with a lack of iron in their diet. This substance is essential to their normal growth and development, and a new source of supply may have conferred an immeasurable advantage on the pioneers who first tapped it accidentally.

It is, however, most unusual for an insect to require blood during more than one phase of its life-cycle and in this way, as in so many others, fleas are peculiar and exceptionally interesting. "Her young ones also suck up blood." In the case of the common house-martin flea (*Ceratophyllus hirundinis*) and the common hen flea it is known that their larvae thrive best on food which contains excrement and blood droppings of their parents, but it appears that at a pinch they can be reared successfully on broken down feather sheaths and epidermal scales.

The larvae of fleas sometimes swarm in thousands in one nest. It is therefore not surprising that they are occasionally found on the bodies of nestlings. Twenty per cent. of sand-martins are said to be infested during the nesting season. No doubt if they could evolve a closer relationship with the host at the larval stage their lives would be less hazardous and bird fleas as a whole might, like the feather lice, become more successful in the walk of life they have chosen.

The larva spins itself a cocoon before pupating. This is attached to twigs in the nest, and since grains of sand and dirt adhere to the outside, the camouflage is most effective. There is a certain amount of specific variation in the structure of cocoons. Those of the common hen flea

are pure silk, very strong, densely woven yet soft, and pale brown in colour.

The pupa itself vaguely resembles the adult in shape. Its head, body and legs, held close to its sides, can be made out, and in fact it suggests a wax model of a flea made by a rather indifferent artist. One of its most fascinating features, clearly visible in the pupa of the common hen flea though not in all species, is the vestigial wing buds on the thorax. They represent the only concrete evidence that fleas are descended from winged ancestors—a fact most entomologists inferred years before these structures were demonstrated by Sharif.

This stage of the life-cycle may last two weeks or more than a year. Long after the flea is fully developed it can lie dormant within the cocoon (Plate XVIII) waiting for some outside stimulus to precipitate hatching. It then bursts out within a split second. The vibration caused by the footfall of a passing animal may be sufficient.

After emerging from its cocoon a flea can live for a considerable time without feeding. In this stage both sexes survive for about the same period. Providing they are kept in rubbish, adults of the common rat flea can live without food for seventeen months in captivity. In the case of well fed fleas which are subsequently starved the females live nearly twice as long as the males. On a full diet of human blood the human flea has survived 513 days and the common hen flea 345 days. A Russian Ceratophyllid, however—a true hero of the Soviet Union—is said to have lived 1,487 days ! In captivity, however, fleas, like their hosts, probably survive much longer than in nature. It is not unusual, for example, for an adult robin to attain 10-12 years in an aviary, whereas only about one year is the average expectation of life in the wild. Hirst found that in solitary confinement a flea lived twice as long as in the company of others and it seems probable that in nature they have a short life and a merry one.

The food of an adult flea is blood. Accordingly the mouth-parts have been transformed into a piercing and sucking apparatus (Plate XII). In Ford's book in the *New Naturalist* series there is a very fine description of the mouth-parts of a relatively primitive insect (a cockroach) which shows how these have been modified in butterflies to form an apparatus for imbibing nectar from the centres of flowers. In fleas, however, it is no easy matter to decide which portions are homologous with those of the primitive biting types, and the experts are by no means agreed upon this question.

The wound in the host's skin and flesh is inflicted by the *maxillary lacinia* (Plate XII b)—a pair of sword-like blades which bear four rows of upwardly projecting teeth on their outer surface. Running along the middle of the inner surface is a gutter or channel. Down this, saliva, containing an enzyme which inhibits clotting of the host's blood, flows into the wound. While feeding, a thin median unpaired rapier-like blade, the *epipharynx*, lies squeezed between the two maxillary blades—all three together forming a tube up which the blood is drawn by the pumping mechanism in the head. The *labium* serves to protect the lacinia and bears the *labial palps* which are apparently organs of touch and are used as such when the flea is selecting a good spot on the host's skin through which to drive the blades. When a flea is feeding the mouth parts become fully embedded in the flesh, the head is drawn down on to the skin of the host, the front legs are tucked back or sometimes flexed and held above the body (see Plate XXXIII), and the flea supports itself with the middle and back pair, or only the latter. It is thus tilted sharply forward and appears to be standing on its head or in the early stages of turning a somersault. In the case of the hen stick-tight flea the feeding position is somewhat different. The maxillae stick out in front rather like the proboscis of a tick only not so straight—no doubt a more suitable attitude for a sedentary species to adopt.

Fleas have a voracious appetite and they have been known to feed for four consecutive hours without a pause. The tropical rat flea which is a particularly fierce feeder, weighs only 0.6 milligrams (or 1/40,000 of an ounce) and the capacity of its stomach is 0.5 cubic millimetres. Only a mere fraction of the blood imbibed is digested. Most of it passes through the flea unchanged and is squirted out drop by drop at the hind end or anus.

Many beginners, when first examining a mounted and cleared specimen of a flea, have been puzzled by what appears to be a strange patch of bristles in the forepart of the abdomen (Plate XVII). These are in reality a mass of about 800 spines in the inside of the crop or *proventriculus*—the only highly specialised portion of the alimentary canal of a flea—which help to crush up the blood corpuscles of the host.

It is not known if the non-sedentary species of bird fleas have any favourite feeding spots on the host's body. Rat fleas generally try to get a hold between the shoulder blades or on the back of the neck where it is more difficult for the host to kill them. Many wild rodents such as marmots are more frequently bitten on the rump. There is also a

great variety in the feeding habits of even closely related species of fleas. Some tend to take short frequent meals, others long feeds at considerable intervals. Some, like human beings, lose their appetites in hot weather. Again, one species will bite immediately it comes into contact with the host, and another will wander about trying here and there before it finally settles down to feed.

The tropical rat flea is a wary flea and is easily disturbed, but on the other hand it will try again and again to get going, whereas *Xenopsylla astia*, a closely related species, if once put off or distracted, temporarily refuses to bite.

It is true that most fleas are not so closely bound to their host as are the feather lice, but although they are in a sense free they have little or no possibility of actively searching for a bird, and luck must often play a considerable part in finding one. It is therefore fortunate for the flea that it is endowed with the power of fasting for considerable periods. Nevertheless, it must be the fate of a large proportion of bird fleas to hatch out in a nest long after the birds have gone, and to perish miserably without the hope of ever tasting blood.

Little is really known about the senses of fleas, but it appears that where the response to a host is involved they only function when the animal is at close quarters. For example, if hungry rat fleas are introduced into a cage with a rat, they do not, as would be expected, make a bee line for it. Instead they wander about in an aimless manner until their random movements bring them within a few inches of the host. Only then will they make directed efforts to reach the animal. Nevertheless in practice this method is evidently rather effective, for if the cage is opened after a few hours, most if not all of the fleas will be found on the rat.

During the Plague Commission's investigations in India and Egypt, guinea-pigs were sometimes liberated in plague infested buildings where rats had been known to die of the disease. Within several hours they had collected scores of rat fleas, and in turn became infected with the plague. As many as 988 fleas were caught off one guinea-pig. All investigators, however, have not recorded similar successes with these living traps. Some unknown factor, such as weather or temperature, seems to affect the appetite of the fleas or their capacity or inclination to wander about and find a new host in this manner, and sometimes the guinea-pig did not collect a single specimen.

The females of several species of fleas are sedentary and after finding a suitable host, they collect on its head, either on the ears or in the

nostrils of mammals, or round the eyes and wattles of poultry. They then fix themselves by means of their mouth-parts, which become embedded in the skin. When these fleas, male or female, first reach their host they begin to travel *against* the lie of the fur or feathers. Sooner or later this inevitably leads them to the head (occasionally they take a wrong turn down a leg and finish up between the toes), and when the ears or wattles are reached the shortness of the hair or paucity of feathers no longer produce the feeling of resistance to which the fleas apparently respond, and the females stop moving and fix themselves. It would be interesting to see if shaving a small ring of feathers, say at the base of the bird's neck, would trap the fleas into settling within easy reach of the host's beak.

It seems highly probable that smell exerts a strong influence on the flea's choice of hosts. It is a well-known fact that not only are horses immune to their bites, but also the grooms who look after them. Apparently no attempt has been made to exploit their dislike of horse smell, and there does not appear to be a commercial insecticide or deterrent with the attractive odour of stables.

Russian workers claim that fleas have a strong sense of smell and that at a distance of 8 cm. (about 3 inches) they can distinguish between the effluvia of a hedgehog and a mouse, and are also guided back to the host's nest by its odour.

The field-mouse flea (*Ctenophthalmus agyrtes*) even when starving, will only bite man with the greatest reluctance. There is obviously something repellent about him, as far as this flea is concerned, which exerts its influence long before the question of taste comes into play. It is probably smell.

Fleas are attracted to warmth, and there is a certain temperature, generally around that of the host's body, which they prefer and consequently seek. Once a cat flea has found a cat it has also found the conditions in which it is most comfortable and its wanderlust vanishes. It therefore remains on the host. Certain parasites, such as ticks, only feel an urge towards high temperatures when they are hungry. Once gorged they drop off the host's body. Bird fleas (which, unlike cat fleas, spend most of their time in the nest) may also find the warmth of the host unattractive after they are fully fed and so withdraw into the nests. However, no experiments have been performed to test this theory.

Many fleas are blind but all the British bird fleas have eyes placed

on either side of the head near the anterior edge of the antennal grooves. Although the eyes of the fleas are situated laterally, they are in fact displaced dorsal ocelli. These relatively simple organs probably do little more than enable their owners to perceive the difference between light and darkness and thus would only assist them in finding a host if it were in their immediate vicinity. Bird fleas are photonegative, that is to say, other things being equal, they move away from light. If, however, a collecting box or container is opened suddenly, the fleas inside often begin to crawl towards the aperture, for their attraction to the source of air currents is very marked and is apparently stronger than their aversion to light. As Strickland pointed out they become greatly agitated if blown upon. This reaction no doubt considerably assists them in finding a host which may be moving about or breathing in their vicinity. It has been suggested that the *pygidium* (Plate XIX) or sensillum, is an organ connected with this particular reaction. This is an extraordinary saddle-shaped structure which is present in both sexes, situated on the dorsal surface near the terminal end of the body. Its surface is densely clothed with spicules, and honeycombed with widely spaced pits, from the centre of which arises a single long sensory bristle. From above these pits appear like small rosettes (Plate XIX). A few experiments have been performed in Russia and Germany to test whether the *pygidium* is in fact connected with any particular sense. It is claimed that if this organ is painted over or cauterised the fleas cannot perceive air currents and consequently fail to find a host. An American entomologist once tried tickling the *pygidium* of feeding fleas and he recorded that they showed no visible response. This, however, is scarcely a fair test, since fleas, like some of their mammalian hosts, seem marvellously insensitive to outside stimuli once their attention is focused upon a hearty meal.

It has already been pointed out that the adult flea is totally devoid of wings. Therefore unlike certain other parasites, for example the mosquito, it cannot fly in pursuit of its host. The jumping legs of the flea are, however, very powerful and to a certain extent are good substitutes for wings.

In 1910, Mitzmain, an American naturalist, measured the leap of a flea and found it could cover a distance of thirteen inches horizontally. This was believed to equal a 300 yard jump by a six foot man. At the end of the last century Rothschild observed "performing" fleas at a circus moving objects many times their own weight, and was greatly

impressed by their enormous strength. He considered the feat equivalent to a man dragging two full sized elephants round a cricket ground. The modern physiologists, as Imms has pointed out, take another view. They hold that as the body of an animal becomes smaller so the *relative* (not the absolute) power of a muscle increases. The great strength of a flea is therefore more apparent than real, and according to present day calculations the feat of the performing fleas would be compared with greater accuracy to a man pulling two *sheep* round a cricket ground.

The structure of the legs has been especially studied in fleas from the sand-martin. There is a broad flat *coxa* (hip) joined by a small joint called the *trochanter*, to a short stout *femur* (thigh) and *tibia* (shin), and an elongated five-jointed *tarsus* (foot). The pair of claws on the fifth tarsal segment do not, at first sight, appear to be particularly powerful, but they are nevertheless marvellously well adapted to clinging.

As we have already pointed out, the bristles and spines lie close to the flea's body, almost like scales on a fish. Those on the feet, however, stick out at an acute angle (Plate XXXIIIc) and act as grappling irons. Anyone who has attempted to transfer fleas from one tube of alcohol to another with the aid of a paint brush, cannot fail to be impressed by the manner in which even a dead flea hangs on to hair or bristles.

Fleas can also climb up a vertical glass plate as long as the surface is moist. On a dry, clean, glass surface they cannot keep a foothold and fall off after reaching a height of a few inches. All fleas seem to show a desire to climb upwards, away from the ground. This reaction, which is called negative geotropism, may also help them in finding a host.

The human eye is not sufficiently quick to see the action of a flea's leg when it actually jumps. Some writers believe that the only movement is a sudden straightening of the leg, and its extraordinary force is due to the simultaneous extension of both the femora and tibia. Possibly owing to the fact that the hind end of the body is heavier than the head, a flea turns over in mid-air and lands facing the way from which it came. It is the back legs which touch the ground first and take the impact of landing.

Anyone who has bred fleas and watched them, knows that they react to various stimuli, such as air currents, vibrations or touch, by apparently random leaps. In this way they no doubt escape from certain enemies and also in other cases may reach a passing host. As

Waterston remarked, "It is more than likely in a life so precarious as a flea's speculative jumping plays a very large part."

In many insects one sex, generally the male, hatches out before the other, but in the case of fleas it is the female which emerges first. The period it spends in the cocoon is shorter than that of the male. As it also outlives the male by many months and can withstand spells of adverse conditions to which the male promptly succumbs, there are times when a breeding population of fleas consists almost entirely of females. Most large collections in the past were made off mammals themselves and the large excess of female fleas sometimes observed was attributed not only to the greater agility of males which more often escaped capture, but to a deep seated divergence in the habits of the sexes—the females supposed to cling to the body of the host and the males to remain in the nest. Indeed there is some experimental evidence to suggest that the females are more closely bound to the host's body. Quite recently it has been shown that the proportion of male and female fleas on rats in certain cities in the U.S.A. varies according to the weather. On hot days males predominate and on cold days females. In the case of bird fleas, however, some excess of females is also found when specimens are taken direct from the nests. Waterston recorded 2,368 (or 56 per cent.) females to 1,672 (or 44 per cent.) males of *C. farreni* from house-martins' nests and Rothschild found out of a total of 1,218 fleas (five species were represented) from house-martins' and swallows' nests that 732 (60 per cent.) were females. In many parasitic insects there is a very marked tendency for the sex ratio to tip more and more sharply in favour of the females. The reason for this is obscure. Thus the males of certain lice have so far never been found. Although female fleas lay many unfertilised eggs, these do not develop. However, as one male flea has been known to fertilise thirteen females their activity makes up to a certain extent for their numerical inferiority.

Because relatively few fleas are found on the bodies of the birds themselves it is assumed that they spend the greater part of their time in the nest or hiding in débris and only visit the host periodically when they require a meal. There can be little doubt that the greatest danger to a flea is the active and efficient defence put up by the host. It is no mere coincidence that the hen stick-tight flea is only found round the eyes and wattle of poultry—where the birds cannot preen themselves effectively.

In the course of several experiments Buxton showed that out of 50 fleas placed on a captive mouse only approximately 14 survived on the seventh day—the rest having presumably been eaten or killed by the host. Undoubtedly birds destroy many fleas and their remains are sometimes found in the host's crop. On the other hand there is no evidence that they form part of the normal diet of any insectivorous bird. Another point brought out by Buxton was the higher proportion of fleas which survived on captive baby mice as opposed to those on adult mice. Fledgelings are also relatively helpless in the face of attacks by parasites and the various species which pullulate in their nests must greatly reduce their strength and vitality.

By far the most uncomfortable nests are those of the sand-martin. *Ceratophyllus styx*, which teems in thousands in their burrows, over-winters either as an adult or as a pupa which hatches in the spring. It is sad to think that when the sand-martin reaches its breeding haunts in April, having successfully endured the hardships and hazards of migration, it is met by a reception committee in the form of thousands of ravenous fleas which can be seen waiting round the entrance to the nests.

It is perhaps obvious that one of the reasons why martins are generally so heavily infested with fleas, both with regard to actual numbers and variety of species, is because of this habit of returning again and again to the same nesting site. Holes in mud banks or quarries (Plate XXXV), and mud nests provide a favourable habitat for the early stages in the life-cycle, but this reason alone is insufficient to account for the numbers concerned. Compared with a house-martin flea such as *C. farreni*, the species infecting warblers, finches and thrushes have an extremely precarious existence. The temperature in a bird's nest during the incubation period and the rearing of the young fledgelings is sufficiently high to speed up metamorphosis of the flea to a maximum degree. The number of blood feeds, temperature, copulation and fertile egg laying are intimately linked and in the spring the flea population must be seething with activity within the nest. These palmy days are all too brief and at the end of 1-2 months the young birds are fledged and leave the nest never to return. Maybe one or two fleas, busy feeding on their host at the time, are carried away on each fledgeling. The great majority, whatever stage they have reached in their development, are left to perish miserably in the deserted nest.

On several occasions fleas have been observed leaving birds' nests in large swarms, and in Russia migration from abandoned mammals'

lair is considered the rule. Although these mass movements have only been noted rarely in Britain it seems likely that this type of migration plays an important part in overcoming the hopeless situation of fleas left in nests to which the hosts do not return. Scattered over a wider area and able to fast for long periods, their chances of coming into contact with a passing bird would be greatly increased. Fleas are frequently noted in isolated situations apparently far removed from either nest or host. For example there are records of two common bird fleas, the hen flea and duck flea, collected from under stones, on palings, under the bark of trees, among dried leaves, in hedge clippings, in a pile of reeds, in moss, on rocks, in caves, in barns and even swept from grass and flowers.

Up till now no observations have been made regarding bird fleas' preference—if any—for either sex of the host. Collectors rarely take the trouble to record the necessary data. Linnaeus declared that women harboured more fleas than men, but male squirrels on the other hand seem more heavily parasitised than females. Where only the hen bird incubates the eggs, the opportunity of becoming infested with fleas is obviously greater in her case.

In the butterfly collection varieties take a prominent place. Individual fleas sometimes display variations which are just as remarkable as, say, the black variety of the swallowtail, but so far they have not attracted much attention. There are certain characters of fleas which seem to vary more than others and in these—for example the shape of the seventh sternite of the females—the arrangement of the bristles is also variable. In fleas, as well as human beings, no two individuals are exactly alike. The bristle formula on the abdominal segments of a flea was worked out by Jordan who calculated that he would require 14,482,000,000,000 specimens in order to be sure that he had another one with the same arrangement on the sternites alone! Varieties, however, are well worth studying, for in them one often catches a glimpse of the future evolutionary tendencies in the species or even the family concerned.

THE DISTRIBUTION OF BIRD FLEAS

Any attempt at discussing the distribution of bird fleas must to a certain extent prove futile, because of the general lack of collecting.

THE 8th STERNITE AND TERMINAL PORTION
OF BRITISH BIRD FLEAS
(x 75)

a
Ceratophyllus rossittensis
(from carrion-crow)

b
C. gallinae
(from goldfinch)

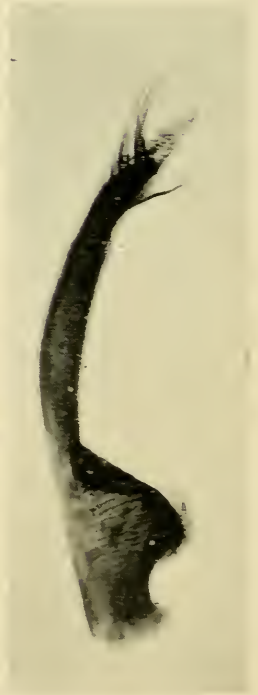
c
Ceratophyllus fringillae
(from house-sparrow)

d
Ceratophyllus borealis
(from Arctic tern)

e
C. columbae
(from rock-dove)

f
Ceratophyllus garei
(from duck)





THE 8th STERNITE AND TERMINAL PORTION
OF BRITISH BIRD FLEAS

(x 75)

a
Orneacus rothschildi
(from house-martin)

b
Ceratophyllus hirundinis
(from house-martin)

c
Ornithopsylla laetitiae
(from Manx shearwater)

d
C. rusticus
(from house-martin)

e
C. vagabunda
(from jackdaw)

C. farreni
(from house-martin)

g
C. styx
(from sand-martin)

Therefore, all the suggestions which follow should be regarded as tentative. Despite the relatively large numbers of specimens taken from Ashton Wold and Tring Park, these two places are not particularly good spots for fleas. In this case, as in so many others, the distribution shown is that of the collectors rather than that of the fleas (see Map 3). Bat fleas apparently show a strong predilection for cathedral cities but this does not reflect their sectarian views; it merely demonstrates the fact that their hosts are more numerous and thus easier to catch in large belfries than in small ones.

In studying the distribution of the fleas we are confronted with a much more complicated problem than in the case of the feather lice. Mallophaga pass their entire life-cycle on the bird and are so closely linked to it that their own distribution closely parallels that of the host. Whatever limits the range of the bird, whether it is climate (past or present), or food, or scarcity of nesting sites, or competition with other birds, or geological history, these same factors limit the range of the feather lice. They do not however exert a direct influence upon them. The bird, not the external habitat, is their environment. In the case of the adult fleas they are also closely linked to the host, which therefore must play an important role in determining their distribution. However, the larval stages are free and are therefore influenced by all the elements which affect a free living organism. There are many striking examples which illustrate this fact. The range of the hen stick-tight flea, despite the wide distribution of the host, is restricted to areas with a tropical or sub-tropical climate. The common rat flea is rare or absent in the tropics and more or less confined to Europe. Unlike its host it does not thrive in hot climates and has failed to spread all over the inhabited portions of the globe with man and his four-footed hangers-on. The rock-dove flea which is also a parasite of the domestic pigeon, has not spread beyond Europe. The dovecots of the United States harbour only hen fleas. In these cases the fleas fall short of the distribution of their host because the requirements of the larvae limit them to certain ranges of temperature and humidity.

It has already been pointed out that many fleas are not host specific and are found on a wide variety of birds. Nevertheless there is often a preference for certain birds with similar habits, and thus the fleas in question are distributed according to the conditions, or *microclimes*, found in different types of nest. Let us take for example three of the commonest bird fleas in Britain, the hen flea (*C. gallinae*) the moorhen

flea (*D. gallinulae*) and the duck flea (*C. garei*) (Maps 2, 3, 4). The hen flea is apparently much more tolerant of the dry conditions found in hen-houses and also in dry, loosely built nests placed in elevated situations. It is found more frequently than any other flea in the nests of the sparrow, starling, sparrow-hawk, swallow and so forth. *D. gallinulae*, however, prefers nests situated in relatively low positions such as those of the robin and warblers. It also seems partial to the closely built nests of finches, and in those of blackbirds and song-thrushes the relative frequency of these two fleas is about the same. *C. garei* on the other hand is essentially a ground flea, and can survive in wet swampy situations which prove fatal to the other two mentioned above. Thus it is the only one of these three fleas met with in the nests of ducks and geese, and certain waders and sea birds. No doubt this type of distribution reflects the larval adaptations of the fleas in question, and results in different horizontal zones of distribution within the same locality. Birds themselves show marked habitat preferences and we do not find rooks nesting on the ground or partridges in the tree tops.

There are certain cases where the distribution of the flea probably closely parallels that of the host, but collecting has been so inadequate that it is impossible to make any definite statement to that effect. The common house-martin flea (*C. hirundinis*) is found in Europe and the Himalayas and North Africa, and it seems likely that it accompanies the bird throughout its range.

The house-martin is divided up into several geographical races or subspecies. That is to say in certain areas where it is found the birds show marked variations common to the population of house-martins in that particular district. Thus an expert would be able to tell whether certain house-martins had bred in Algeria or the Himalayas or North Europe, by noting small differences in the colour, size, weight and so forth.

There are two house-martin fleas, *C. hirundinis* and *C. farreni*, which are known to extend their range beyond Europe. *C. hirundinis*, as we have already explained, is found on all three subspecies of the martin, but itself remains unchanged. At any rate there are no visible morphological changes connected with its geographical distribution. We have no method of estimating physiological differences which may be present. *C. farreni*, however, has split into two subspecies—one in Europe and one in North Africa. Only females are known from the latter region but these show constant differences in the arrangement of

the bristles and the shape of the seventh sternite. So far we know of no explanation of the fact that one insect displays geographical variation throughout its range and another, with the same host and the same distribution, does not. However, it will be seen from the section on the evolution of British bird fleas (p. 94) that these two species are not very nearly related and *C. hirundinis* may be a much more recent acquisition of the house-martin than *C. farreni*. Time, and a certain degree of isolation, is necessary for the establishment of subspecific differences in a population of either fleas or birds.

An exceedingly interesting case is that of the sand-martin and its fleas. These birds are found in Europe and the United States and specimens from both continents are indistinguishable. The martins as a group are considered to have originated in the Old World and to have spread to the New World in Pliocene times. On the grounds that the sand-martin in the U.S.A. is not sub-specifically distinct from the European bird, it is argued that it may well have invaded the New World at a much later date, possibly in post-Pleistocene times. When we come to consider its fleas a most surprising fact emerges. The European sand-martin flea (*C. styx*) and the American sand-martin flea (*C. riparius*) although very closely related are specifically distinct. It is irresistible to suppose that the American flea is an offshoot of the European flea, although it seems strange that it should have been more affected by the new environment than the host. It must be remembered that the main population has to over-winter in the nesting site whereas the host seeks more congenial quarters farther south. Therefore one can imagine that winter in the flea's new habitat might be strikingly different—say colder, or wetter, or more prolonged, than in the previous winter quarters. This might lead to a speedier evolution of the parasite.

Three important types of distribution are thus demonstrated by the martin fleas. First, fleas which infest the host right across its range of subspecies, but themselves show no geographical variation. Secondly, fleas which show subspecific variation paralleling that of the host. Thirdly, fleas which show either subspecific variation or specific differentiation while the host itself remains unchanged.

A fourth type of geographical variation is, however, illustrated by fleas. *D. gallinulae*, as we have already shown, is not host-specific and is found on a very great variety of birds. This species has diverged into sub-species without any reference to the hosts. Thus in the Western

United States we find one geographical race and in Europe another, no matter what birds the flea happens to infest.

So far we have considered certain bird fleas which parallel the host's range, and others which fall short of it. There are a few cases, probably, where a bird flea has extended its range *beyond* that of the true host, but these are, for obvious reasons, rather difficult to detect. *C. gallinae* is possibly an example. There is some reason to think that originally it was a tit flea, but on the domestic fowl it has invaded remote islands where the tits are absent.

There are other aspects of this problem which appear still more complicated and are more difficult to understand. We have for example the two very closely related species of bird fleas *C. garei* and *C. borealis*, which both favour ground nesting birds with a preference for wet or swampy nesting sites. The former is distributed throughout the mainland of Britain. The latter is confined to the outer western isles such as St. Kilda, Inishtrahull and the Scillies where *C. garei* is absent (Map 2). The explanation of such a distribution is obscure and one can but hazard a guess. Maybe the factors are inter-specific competition and *C. garei*, a late comer, may have ousted *C. borealis* throughout the mainland of Britain. The latter has only survived on outlying islands, and on the continent, in the Alpine fastnesses of Central Europe.

The distribution of *C. vagabunda* is also interesting although in view of the collecting lacunae little can be offered beyond a few tentative suggestions and speculations. This flea is rather rare and is apparently an ancient species, and it has broken up into geographical races one of which is peculiar to Britain. It is chiefly an inhabitant of nests of rock dwelling sea birds such as the herring-gull (*Larus argentatus*) and the shag (*Phalacrocorax aristotelis*). It has a Northern or Boreal distribution, and specimens are known chiefly from Spitsbergen, the Shetland Isles and Outer Hebrides, Northern Turkestan, Northern Siberia and Alaska. It is also found in the Alps of Central Europe. This is quite a well known type of distribution and is believed to be the result of the advance and subsequent retreat of arctic conditions during one of the glacial periods or ice ages. There are similar examples among many British plants and animals such as the small gentian (*Gentiana nivalis*), the star saxifrage (*Saxifraga stellaris*), a butterfly, the mountain ringlet (*Erebia epiphron*) and the alpine hare (*Lepus timidus*) and the ptarmigan (*Lagopus mutus*).



1



2



3



4

In the Alps the host of *C. vagabunda* is the alpine chough (*Pyrrhocorax graculus*) and one may hazard the guess that choughs were once its true hosts all over the Palaearctic region which they then occupied. When the ice began to retreat the choughs, which were adapted to the cold conditions were only able to survive in the extreme north or in the mountains where the climate suited them, and where they escaped the intense competition from certain other species better adapted to the warmer conditions. Our chough (*Pyrrhocorax pyrrhocorax*) which is not confined to mountains has managed to survive precariously in a few areas in Britain on remote cliffs. Its fleas are not known. The bird possibly responsible for the present decline of the chough is the jackdaw with which it comes into direct competition. This is the bird most likely to prove a suitable host for a chough flea and it is interesting to find *C. vagabunda* parasitising the jackdaw in Britain, even far inland. The number of records of this flea from all birds in the British Isles is twenty-four, no less than five of which are from the jackdaw. The next largest number of records from one host is from the herring-gull (4) and shag (4). It is possible that this boreal species of flea will once again spread gradually all over the Palaearctic region, having firmly established itself on the chough's successor.

ORIGINS AND EVOLUTION OF BRITISH BIRD FLEAS

There are approximately one thousand different species of mammal fleas known in the world to-day, but there are only between fifty and sixty bird fleas. It is thought that the bird fleas have been derived from the mammal fleas, in relatively recent times. This can be

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- MAP 1. Distribution of the three commonest fleas from the house-martin in Britain.
 ●: *Ceratophyllus hirundinis*; +: *C. farreni*; Δ: *C. rusticus*
- MAP 2. Distribution of the duck flea, *C. garei*, and boreal flea, *C. borealis*, in Britain.
 ●: *C. garei*; ⊙: *C. borealis*
- MAP 3. Distribution of the hen flea, *C. gallinae*, in Britain. (The concentrations of records denote the chief collecting areas of five well-known collectors, Rothschild, Waterston, Newstead, O'Mahony and Britten.)
- MAP 4. Distribution of the moorhen flea, *Dasypsyllus gallinulae*, and the shearwater flea, *Ornithopsylla laetitiae*, in Britain.
 ●: *D. gallinulae*; ✠: *O. laetitiae*

deduced from the following facts. Only a small number of species of fleas are involved and these are widely scattered throughout the families comprising the order as a whole. Host-specificity is less marked than in the mammal fleas, and there are relatively few cases in which geographical variation or the formation of subspecies has occurred. There is also a lack of specialisation in the fleas themselves. By this it is meant that bird fleas as a whole have not, from the structural point of view at any rate, diverged very far from the mammal fleas from which they are derived. In all cases except the genera *Dasypsyllus* and *Mioctenopsylla* one can point with confidence to the group of mammal fleas from which they originated. This is one reason why bird fleas are exceptionally interesting objects of study. The change over from mammals to birds seems a difficult one and few species have been able to take advantage of this large mass of potential hosts. There are certain conditions which appear particularly important if success is to be achieved in this direction. Out of the 55 or so bird fleas described 27 are from birds which return to the same nesting sites year after year, 19 are from ground- or hole-nesting birds, 9 are known only from islands, and of the remaining species a large proportion parasitise birds which use mud in the construction of their nests. A combination of the first three conditions is of course the most favourable. The opportunity for straggling from a mammal to a bird host, occurs more frequently on the ground (Plate XXXIVa) and the conditions in these nests are more suitable for the development of the larvae. Colonies of sea birds return year after year to the same site and thus give any fleas which may have succeeded in living on them for one season another chance, and again another chance, to consolidate their position and multiply. Islands—particularly oceanic islands—afford the degree of isolation which favours species formation. Thus we find that a rabbit flea has succeeded in establishing itself twice on sea birds, once on puffins and shearwaters on the rocky islands off the west coast of Britain (Plate XI and Map 4), and again on the other side of the world on an auklet (*Ptychorhamphus aleuticus*) on Coronados Isle, Gulf of California. On the mainland of Britain shelduck, for example, nest in burrows, and are frequently attacked by hungry rabbit fleas which may even be found attached to their heads, yet no shelduck flea has been evolved. The factor which is missing is almost certainly prolonged isolation in a relatively restricted area. On the Canary and Pityuse Isles a shearwater has acquired a flea of the genus *Xenopsylla*—the most

prevalent group of fleas on rats and mice on the mainland of North Africa. Similarly penguins and certain other sea birds nesting on the islands off South America, South Africa and Australia and on various islands in between such as Bird Island, the Falkland Isles, Kidney Isle and so forth, are infested with a genus of fleas clearly descended from South American rodent fleas. Originally they must have picked up these fleas in the Cape Horn area and carried them westwards and eastwards to their various breeding stations. On the Kerguelen Isles, in South Georgia and on Antipodes Isle, the diving petrel (*Pelecanoides urinatrix*), a gull (*Larus dominicanus*) and a burrow-nesting parrakeet (*Platycercus unicolor*) have each acquired a flea of the family Pygiopsyllidae, a group of primitive marsupial fleas which are the dominant Aphaniptera of the Australian region.

In Britain we have 16 species of bird fleas. Of these no less than 11 belong to the genus *Ceratophyllus*. The family in which these fleas are placed contains the majority of species from the north temperate climates of the world, and the genus in question claims 45 out of some 55 bird fleas known. These fleas have made the change over to birds along a slightly different evolutionary path from those mentioned above. They are clearly descended from the fleas of tree-climbing rodents such as squirrels and certain rats (Plate XIId), and have probably been evolved from this source twice or even more often. Both types of hosts have developed arboreal habits, and the fleas from squirrels are in a sense pre-adapted to the dry aerial environment of birds' nests. The mutual arboreal habit now ensures the necessary opportunity for straggling. *Ceratophyllus gallinae* has been recorded frequently from squirrels' dreys and the squirrel flea (*Monopsyllus sciurorum*) is repeatedly found in birds' nests. It has been collected from crows' nests in Northamptonshire in localities where the rightful host, the red squirrel, is no longer to be found.

There are two other genera of bird fleas represented in Britain which, although they may be included in the same family, are not closely related to *Ceratophyllus*. The first is *Dasypsyllus gallinulae*, a flea found on a wide variety of birds nesting on or near the ground. This is rather an ancient and obscure genus and it is only possible to hazard a guess as to the mammal fleas from which it is derived. The arrangement of bristles on the head is somewhat similar to that found on a prevalent genus of South American fleas, *Pleochaetis*, which may have given rise to *Dasypsyllus*. All the other known species, except one, are

found in South America on birds such as the cheu-can (*Pteroptochus rubecula*) and it is a group which certainly originated in the Neotropical Region. *D. gallinulae* is also found in British Columbia (North America) where it has developed into a distinct sub-species. Possibly this is the route by which Europe received this single representative of the South American fauna. The other genus is represented by one of the most interesting fleas in Britain, *Orneacus rothschildi*, of which nine specimens only are known*. These were taken from a house-martin's nest situated on the cliffs at Kinneff on the east coast of Scotland. A slightly different subspecies of the same flea was collected in the Swiss Alps by Jordan and Rothschild. The other known species of this genus was found in a martin's nest in Ladakh, Kashmir at 10,500 feet. These fleas are derived from quite another group of mammal fleas, the genus *Citellophilus*, parasitising ground squirrels (*Citellus*), and with these they show a striking affinity. It is difficult to guess the place whence the Scottish martins got these fleas. The fossil record proves that the mammal *Citellus* was present in Britain (Thames Valley) in the Pleistocene many thousands of years ago. The nearest species of *Citellophilus* to-day, however, is found in the Pyrenees. It is probable that the switch-over from ground squirrels to house-martins took place somewhere in the Palaeartic region, but the possibility cannot be ruled out that *Orneacus* was brought to east Scotland by migrating martins which had picked up the fleas on their travels.

The common house-martin flea (*Ceratophyllus hirundinis*) as we have seen has a very wide distribution and is also found on the martins breeding in Kashmir.

It has already been mentioned that among British bird fleas there is one representative of the family Pulicidae (to which the human flea *Pulex irritans* belongs). This is the shearwater flea, *Ornithopsylla laetitiae*, descended from one of the rabbit fleas of North America. In the Palaeartic region there is only one species of rabbit flea of this family found on the common rabbit and one (*Hoplopyllus glacialis*) on the arctic hare but in North America there are at least ten species and sub-species. Puffins and rabbits live in close proximity—even using each other's nesting burrows—on the rocky islands off the coast of Britain. In fact our rabbit flea has been taken off the puffin on Skomer Isle. The first idea that occurs is that the common rabbit flea at some remote period passed on to the puffins and shearwaters, and gradually

*Since re-discovered in Aberdeenshire (Allan 1950).

became modified into *Ornithopsylla laetitiae*. It would thus represent its direct ancestor. A detailed study of the morphology of these fleas, however, shows that this is extremely unlikely and the attractive theory has to be abandoned. Both, no doubt, originated from North American rabbit flea stock (*Hoplopsyllus*), but are not themselves very closely related. Curiously enough little or no collecting has been done from nests of sea birds on the eastern coast of North America but it is highly probable that some of these, too, harbour species descended from rabbit fleas. If and when such fleas turn up, they may give us a more direct clue to the immediate ancestry of *Ornithopsylla laetitiae*.

Along with the house-sparrow, the common hen flea of Europe was also introduced into the United States, where it has spread on to numerous wild birds as well as domestic poultry. Up to date there is no parallel case of a modern introduction of a bird flea from North America into Europe, but occasionally a rather weird flea, the South American parrot stick-tight flea, is taken off a variety of captive birds at the Zoo including tame pigeons. There is always a possibility that this species might spread to native birds via the ubiquitous sparrow which hops in and out of the aviaries at the Zoo. In South America it has a wide range of hosts, but was first recorded from a parrot. This flea is a relative of the jigger (*Tunga penetrans*) which burrows beneath the skin and heavily infests the feet of the natives in South America and Africa. It causes great irritation and abscesses develop at the spot where it is embedded as the result of secondary infections. Like the jigger the female of the parrot stick-tight flea is permanently fixed to the host but it remains attached to the surface of the skin. The modifications arising from the sedentary habit (see p. 63) can be studied in this and allied species of fleas.

It has already been pointed out (p. 68) that bird fleas—at least *C. gallinae*—can breed on mammals as well as on their true host. A relatively loose bond with the host was probably one of the characteristics necessary to allow the change from mammal to bird to occur in the first place. Consequently bird fleas are frequently found on mammals. When a cat catches a sparrow for example, it generally carries it about for a while and allows it to get cool. The fleas soon leave the bird, and at times change on to the cat and so in a small way avenge the death of their host. How long they survive and whether, outside the laboratory, they do in fact breed on a mammalian host is

not known. Such species as the sparrow flea and the hen flea have been taken off cats and many other predatory animals such as rats, stoats, weasels, and foxes. Conversely certain mammal fleas are not infrequently found as stragglers on birds of prey, especially owls (Plate VI), or on small birds which to a certain extent share their habitat. Thus the rabbit flea straggles on to burrow- and ground-nesting birds, and has been taken off ducks, puffins, shearwaters and partridges. The American and British squirrel fleas are found in a variety of arboreal nests, and occasionally on the bodies of birds themselves. Bat fleas have been found on the swift, the human flea on wild duck, and the hen flea and house-sparrow flea on man himself.

It is not difficult to imagine new species arising in this way, providing some accident supplies the necessary isolation. On Skomer Isle one can conceive our rabbit flea establishing itself permanently on the shearwaters, and thus giving rise to a situation which may puzzle and confuse future systematists.

Even among such closely related species as our eleven *Ceratophyllus* we can trace certain evolutionary trends and try to construct a phylogenetic "tree" by studying details of morphology. For example by grouping them according to the degree of thickening and hardening (sclerotisation) of certain internal organs of the female, and the shape of the receptaculum seminis (Plates XIII and XIV) we find they fall into two main groups. The first contains the three British species *C. garei*, *C. borealis* and *C. columbae* from the British fauna and one species from Turkestan and another from North America. This group shows the least sclerotisation and has a kidney shaped body to the receptaculum. It is descended from the *Monopsyllus sciurorum* group of squirrel fleas (Plate XIIIc). The second group, which falls into two distinct sub-groups, shows sclerotisation and a progressively more vermiform body to the receptaculum. These fleas represent a second evolution from the same genus of rodent fleas, this time from the *Monopsyllus anisus* group (Plate XIVg), which are found on rats and squirrels in the Pacific area of the Palaearctic region. Our bird fleas may have originated from that area via North America. The first of these sub-groups contains *C. hirundinis* and *C. rusticus* from our fauna. The second sub-group, with the most pronounced sclerotisation, includes all our other Ceratophyllid bird fleas and many foreign species, and incidentally all those which have become adapted to relatively dry nests.

In considering the evolution of a genus like these bird fleas which appear to have been derived at least twice from closely related mammal fleas—possibly at different times and in widely separated parts of the world, it must not be forgotten that certain characters from an ancestral flea may also re-appear in different branches of one stem.

One very interesting *Ceratophyllus* must be mentioned here. Although it has not yet turned up in Britain it seems to us there is quite a good chance that it will eventually be discovered on the stoat and marten in Northern Scotland. This is *C. lunatus*, a former bird flea recorded from the Alps, Alaska, North Sweden and Northern Russia, which has once again reverted to a life on mammal hosts. This return to its original type of host must have happened before or during the last Ice Age, judging from the familiar boreal-alpine distribution (see p. 87) of the flea. It also must have occurred fairly early in its history as a bird flea, for although it displays certain features typical of bird *Ceratophylli* the modifications of the receptaculum seminis usually associated with an avian host have been arrested at a relatively early stage.

The fact that there are several bird fleas with the boreal-alpine type of distribution proves that they had already changed on to avian hosts at any rate before the end of the last Ice Age in Europe.

THE EFFECT UPON THE FLEA OF A CHANGE TO A BIRD HOST

It has been pointed out (p. 90) that the change over to bird from mammal host must have taken place in relatively recent times. Nevertheless, this new environment which involves such great differences in food, temperature and habitat, has already left its mark upon the fleas.

A study of the *Ceratophyllidae* and the *Pulicidae* shows that the trends of evolution are different within the two main families or super-families. When a switch over to a bird host occurs it seems to speed up these family trends.

In the *Ceratophyllidae* there are four genera of bird fleas, *Ceratophyllus*, *Orneacus*, *Dasypsyllus* and *Mioctenopsylla*, and two species from the genus *Frontopsylla** (chough fleas) which have unquestionably been evolved from different groups of mammal fleas (p. 91). Nevertheless,

*Since the completion of this manuscript *Frontopsylla laetus* has been found by Allan (1950) in a house-martin's nest in Kincardineshire, Scotland.

despite their varied origins they all show a marked increase in the number of teeth in the pronotal comb (see Plate X). The mammal *Ceratophylli* in question rarely have more than 22 teeth in these combs, but the bird fleas all have from 26 to 40. Thus in all bird *Ceratophyllidae* we find without exception a combination of two facts (*a*) the environment "bird" (*b*) a larger number of spines in the pronotal comb. This structural modification, therefore, appears to be connected with, or possibly is the direct consequence of the change of host, and thus presents an example of convergent evolution.

In the family *Pulicidae* there is a general tendency towards a reduction and final loss of combs. The change to bird host has apparently accelerated the process. This phenomenon can be observed in the two genera of bird fleas derived from rabbit fleas (*Spilopsyllinae*). The rabbit fleas (Plate X) still possess pronotal and genal combs or at least a pronotal comb, but the shearwater and auklet fleas have neither one nor the other (Plate XI).

Thus the change of hosts has produced convergent evolution in both families, but leading in opposite directions. When a *Ceratophyllid* flea leaves a mammal and becomes permanently parasitic on birds the result is additional teeth in the pronotal comb, but if a *Pulicid* flea takes this same step, the reverse appears to happen and one must expect an increased rate of reduction and final loss of the combs. Therefore, when studying this type of evolution it must always be remembered that the effect of the change depends on the derivation and nature of the flea, as well as on the nature of the host and other environmental factors.

There is another morphological modification which can be observed in certain bird fleas, which is almost certainly associated with the change of host. This is a tendency towards a shift in position and ultimate reduction of the plantar bristles of the feet. The normal number of plantar bristles is five and this primitive condition is still found in the *Ceratophyllidae*. In the whole family *Pulicidae* there is a tendency towards reduction, and all the rabbit fleas for example, have only four pairs. Once again the condition is accentuated in the bird fleas, for both in the two species derived from rabbit fleas and the two derived from the tropical rat fleas, this reduction has developed farther than in any other allied fleas. The third pair of plantar bristles shows either a change of position—a shift upwards and inwards which Jordan describes as "crowding towards the apex"—or is lost altogether.

Despite the fact that this trend is not present in the family Ceratophyllidae as a whole, the kittiwake flea (*Mioctenopsylla arctica*) also shows a weakening and loss of tarsal bristles—at least in the hind tarsus. In this case the mysterious influence which produces these parallel changes in bird fleas seems to affect certain species of the whole order irrespective of family trends.

It has already been seen (p. 42) that among parasites there is often a tendency towards loss of eyes, and this is particularly marked in animals which live in the host's nest. In the case of fleas, however, the matter is by no means so simple. It is true that many nest dwelling species are blind but the bird fleas, which are nest dwellers *par excellence*, all have well developed eyes. There appears to be some connection between the life of the host and the degree of development of the flea's eyes. Thus broadly speaking nocturnal animals—for example bats—are parasitised by blind fleas and diurnal animals by fleas with eyes. It is remarkable nevertheless that all bird fleas, even the sand-martin and shearwater fleas which live in nests in burrows, should have retained their eyesight. The question is a complicated one and further research into the problem would be of great interest.

The changes referred to above are morphological ones and therefore relatively easy to detect. There must be many other changes linked with a parasitic life on birds, physiological ones for example, about which little or nothing is known. One such adaptation has already been mentioned, namely the development of a well defined breeding season in *C. gallinae* to coincide with that of the host. It is most probable that this feature is common to all the bird fleas of the temperate zones.

From time to time isolated observations are made on bird fleas which may bear some relation to their particular mode of life. As we have noted, one of the most vital problems which annually confronts the majority of bird fleas is the question of survival when the nest is deserted at the end of the breeding season. In this situation widespread scattering is an advantage. It is, therefore, not surprising that *C. gallinae* and *C. garei* are so frequently collected far removed from either host or nest (p. 81). This ability to hibernate or rest, fasting, under the bark of trees, among leaves, in cracks on fences or in piles of rubbish, there to wait for a passing host, seems especially well developed in bird fleas. As we have already suggested, the need for wide dissemination may also account for the mass migration of certain species. One of the

mammal fleas which has been noted in Russia for these periodical mass movements is closely related to the bird Ceratophyllids. In this case most of the fleas move out of the burrows at night, but on several occasions Waterson in Scotland witnessed large swarms of hungry fleas leaving birds' nests in broad daylight. They bit viciously at him when they landed on his outstretched arm. Possibly climatic changes or hunger initiate the exodus. In Finland one observer noted that the common hen flea migrates from open nests if the temperature falls below 14°C. However, little or no research has been done in this field, so we can only speculate.

As we have explained (p. 136) the Mallophaga have evolved the habit of "hitch-hiking" or phoresy, as it is called technically, as a means of reaching another host when their own dies; there are at least two records of them attaching themselves to fleas ! However, fleas, with their highly developed powers of leaping do not apparently make use of winged flies for transport. A few moments after the bird dies they come to the surface of the feathers and jump off into the blue. There is one known case, however, when a bird flea was found on a queen wasp and another in a wasp's nest. Wasps being carnivorous may have picked up the fleas when visiting corpses. This type of relationship often escapes notice and although these two occurrences are probably accidental, it is well worth looking out for further evidence of association between bird fleas and wasps.

EFFECT OF FLEAS ON THEIR BIRD HOSTS

Mammal fleas are notorious carriers of disease. As vectors of bubonic plague they have been directly responsible for the deaths of millions of rats and millions of men. A large number of less well known diseases are also spread by them. Thus they carry a roundworm (*Filaria*) which eats out the hearts of dogs, besides several of the common tapeworms, for which they serve as intermediate host. They spread at least two serious diseases among rabbits and hares, one of which, tularemia, can also affect other animals including man. They act as the intermediate host for a species of trypanosome (*T. lewisi*) parasitic in rats and another in rabbits, and they can also become infective for endemic typhus, *Salmonella* and possibly leprosy. So far, however, they are not known to be vectors of any serious disease of birds although bird

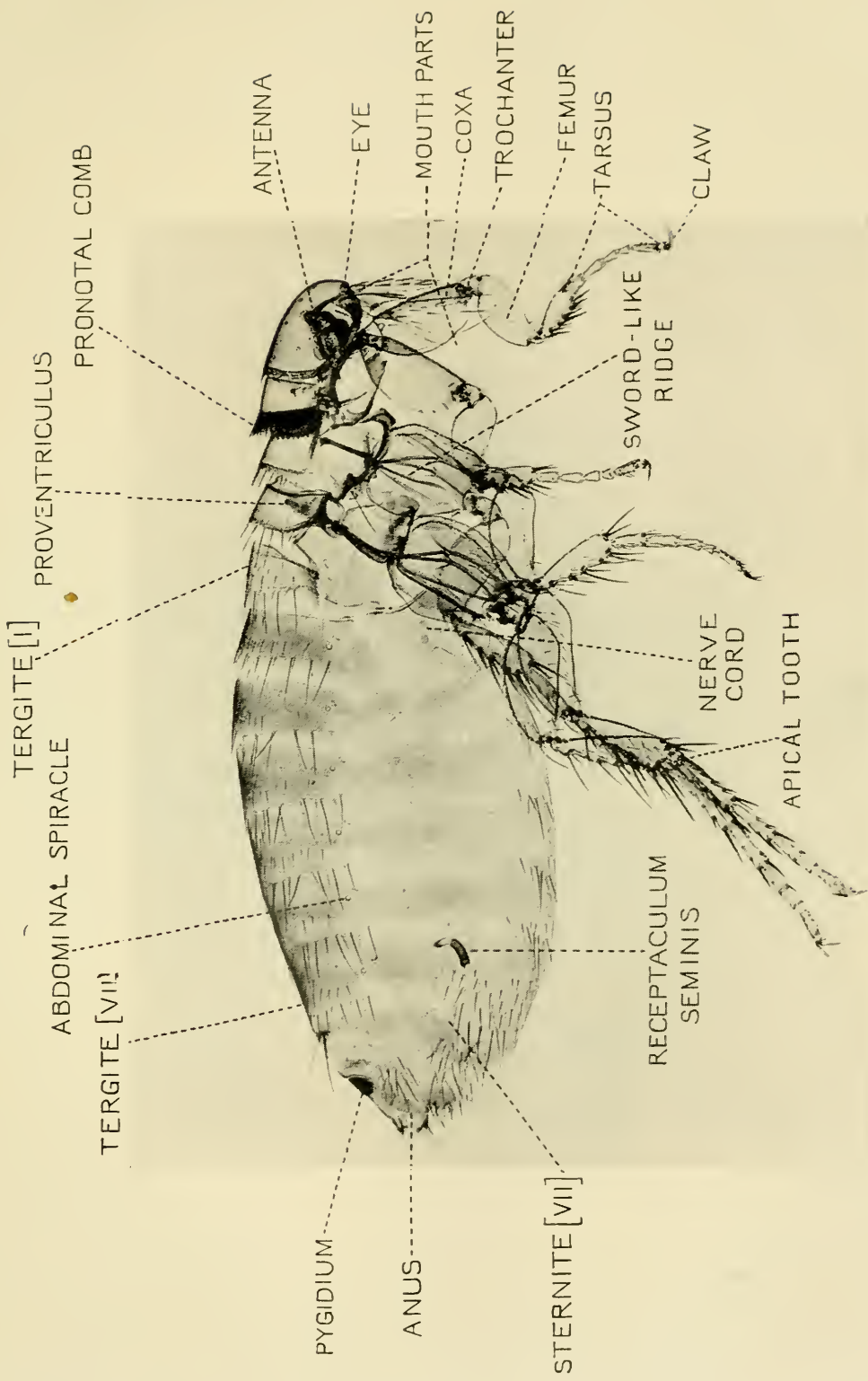


Plate XVII
 Common house-martin flea, *Ceratophyllus hirundinis* (female, x 36) showing important characters
 J. G. Bradbury



Arthur L. E. Barron
a. Eggs (× 29)



J. G. Bradbury
b. Larvae (× 19)



J. G. Bradbury
c. Pupa within cocoon (× 37)

fleas can transmit the trypanosomes referred to above. Their harmlessness in this respect may be more apparent than real, due to the fact that we are ignorant of the true rôle they play. However, fleas have only been closely associated with birds for a relatively short period, and therefore they may not have had time to become adapted as carriers or intermediate hosts of other bird parasites.

Occasionally plague-carrying mammal fleas straggle on to birds. Thus, in the Rothschild collection there is a specimen of the tropical rat flea taken off a bird. Certainly the hen stick-tight flea, which is also frequently a parasite of rodents, can carry plague from wild to domestic rats. Birds, when they nest or roost in rat-infested houses or chicken coops must be regarded as potential reservoirs of plague. On the other hand the Ceratophyllidae, which are the commonest and largest group of bird fleas, are not very effective vectors of plague.

In the case of the hen stick-tight flea, which is not a British species, the direct effect of an infection is very serious. Poultry lose weight, egg laying is reduced, and birds not infrequently succumb to heavy infestations.

The effect of a bite on a human being, in the case of non-sedentary species of fleas, varies considerably from one individual to another. The local swelling which causes a certain amount of irritation is probably due to the enzyme which entered the wound in the insect's saliva. As time goes on, a certain immunity is usually developed and elderly people hardly react at all to a flea's bite. Whether this is also the case in birds is not known.

In any case it is extremely difficult to gauge the direct effect of fleas on nestlings. The few specimens living on the bodies of adult birds can be of little or no importance but several thousand fleas in a nest full of young birds must present a serious menace. The mortality from all causes among nestlings is high, sometimes sixty-five per cent. of all those hatched in the case of small passerines. It seems reasonable to suppose that when a single population of fleas runs into four figures the constant drain of blood must be a contributing cause of death among the more delicate young birds.

BIRD FLEAS AND THE EVOLUTION OF BIRDS

In the Mallophaga as we have seen, these parasites have in many cases evolved at a somewhat slower rate than their hosts. The bird's

body has provided the feather lice with a more or less constant environment and one which has altered them less than the impact with the outside world has altered the host itself. Therefore, the relationships of the parasites often throw light on the relationships of the birds.

In mammal fleas, although they are altogether much less closely bound to their hosts than feather lice, and in the larval stages also have to cope with climatic and other outside influences, the same type of phenomenon can be observed. For example the extraordinary and unique group of fleas known as the helmet fleas of Australian marsupials are also found on the pouched mammals of South America, thus once again confirming the latter's true relationship with the Australian marsupials and demonstrating their common origins.

The situation in the case of the bird fleas is, however, very different. The change over to birds is altogether too recent to provide evidence of host relationship. What these fleas often provide, however, is a clue to the past *geographical* history of the bird. For example the European chough fleas (*Frontopsylla frontalis* and *F. laetus**) which may still be added to the British list are descended from a genus of the Amphipsyllidae, a family of fleas from Central Asia and China. The choughs are considered by many ornithologists to be a strictly Asiatic group which has extended its range into Europe some time during the Pleistocene, so the presence of these fleas supports their theory. The penguins breeding in the Australian and South African areas have fleas clearly of South American origins and this indicates from which area these birds extended their range eastwards. Other examples of this type could be given, but sad to say here again no definite conclusions can be drawn from the British fauna, because not enough is known about the fleas of our own birds. It is amazing how little collecting of bird fleas has been done by British ornithologists, especially if one considers the attention now given to almost every aspect and detail of bird life.

HOST SPECIFICITY AND HOST PREFERENCE

Among bird fleas there are three main types of host preference. The first and most obvious is when a species of flea is adapted to one species of bird only—in other words it displays strict host specificity. In an ancient group of bird parasites like the Mallophaga, where louse

*Since discovered in Aberdeenshire (Allan 1950) in the nest of the house-martin.

and bird have evolved through the ages together, this is the rule rather than the exception. Fleas having, on the other hand, only relatively recently moved on to birds, there has not yet been time for many such close relationships to develop. An example of strict host specificity in the British fauna is provided by *C. rossittensis*, which has never been recorded except on the crow (*Corvus corone*), either in this country or on the continent. The rock-dove flea, the sand-martin flea and the four house-martin fleas can also be considered host-specific although a limited amount of straggling occurs.

The second type of host preference is illustrated by fleas which show a more or less marked predilection for certain families of birds. For example a North American flea, *C. diffinis*, is essentially a parasite of the thrushes, and despite its wide variety of hosts in Britain *C. garei* is undoubtedly partial to ducks and geese. This becomes more apparent when it is surveyed throughout its range.

Finally we have a third type consisting of a few species which apparently show no host preferences and are equally at home on all birds. When sufficient collecting has been done and the results properly analysed it will be found that this indifference is more apparent than real. No one will deny that *C. gallinae*, with its sixty-five different bird hosts in Britain alone, has catholic tastes, but the statement so frequently met with in print that it is "common on all birds" is equally false. The hen flea has not, for example, been recorded off ducks and geese (order Anseriformes) or from plovers and waders (order Charadriiformes).

In the chapter on distribution it has been mentioned that the three commonest bird fleas in Britain can be "zoned" according to the type of nesting site which they favour. Despite the considerable overlap which occurs it is true to say that the highest proportion of *C. gallinae* infestations are found in nests in tree tops or elevated situations (dry aerial nests), the highest proportion of *D. gallinulae* in nests in lowly situations such as brambles, walls and small bushes (damp nests), and the highest proportion of *C. garei* infestations in ground nests and in swampy situations (wet nests).

At times host preference and nesting site preference must cut across one another. A nest may be all that the larvae require but the host prove unattractive to the adult—or vice versa. For example the nesting habits of the pheasant and partridge are to all appearances remarkably similar and in fact these birds not infrequently use each

other's nests, which seem in every way equally suitable to fleas. All the three common species referred to above have been found in the nest of the pheasant but so far the only flea recorded from the partridge is *C. garei*. It would appear that in some way the partridge is unattractive to *C. gallinae* and *D. gallinulae*, a fact which overrides the suitability of the nesting site.

The swan is a bird from which no fleas whatsoever, even stragglers, have been recorded, despite the fact that its nest is both obvious and accessible to collectors, and appears ideal for the requirements of *C. garei*. We can do no more than guess at the reasons for its immunity. Possibly the blood of the swan is unattractive to fleas, or its skin so tough that the flea's mouth parts fail to pierce it, or the nest débris is in some way unsuitable to the requirements of the larvae.

One of the facts which strikes every student of bird fleas is the relatively large variety of species which parasitise martins and swallows. No less than seventeen fleas are specific to these hosts. Out of our own fauna of fourteen bird fleas, five are martin fleas and of the rest, all but four have been recorded from them as stragglers. Moreover, an unusually high proportion of martins' nests are infested, and the flea population within individual nests is relatively very large. It has already been pointed out that the habits of martins are helpful to fleas. Thus they frequently build compact mud nests, or make nests in holes in the ground or in caves, which suit the larvae and originally favoured successful straggling. They also associate in colonies, so that fleas off a dead host have not far to seek another suitable victim. What is even more important, martins tend to return year after year to the same nesting sites. These characteristics in themselves, however, are not sufficient to ensure either a large or a varied fauna. For example the swifts also construct mud nests, associate in colonies and return year after year to the same site, but they have failed to acquire a single flea peculiar to themselves. The only species recorded from their nests are the hen flea and sparrow flea, both of which were probably imported by sparrows which frequently usurp old nests and leave behind a few parasites. The fact is we do not know why one whole group of birds, such as the swifts, is unattractive and another, like the martins, is apparently equally attractive to fleas.

ENEMIES OF FLEAS

At all stages of its life history the flea no doubt has enemies. But these have been imperfectly studied and it is not known how populations of fleas are kept in check and whether their numbers are reduced by parasites and disease.

As an adult the flea's most important enemy is undoubtedly the bird itself. Buxton has shown (p. 80) what large proportions are eaten by their mammalian hosts. Birds are scrupulously clean and probably their thoroughness in preening has forced their fleas to become nest dwellers. In other words, only fleas which are to a certain extent pre-adapted to a life in the nest can succeed as bird fleas. However, the nidicolous existence exposes them to dangers from other animals occupying the same habitat. Staphylinid and Histerid beetles have been observed in nests catching and devouring fleas by the dozen. Ants also, if they come into contact with fleas—which most often happens in old ground nests—devour both the adult and larval stages.

The sand-martin flea is particularly susceptible to a Gregarine (Protozoan), a hyperparasite which is found in the mid-gut of larvae, pupae and adults. Damp nesting sites favour the survival of the spores and the reinfection of the flea, and for this reason between 65 and 100 per cent. of the sand-martin flea population may be infested, but in the case of *C. gallinae* the figure is steady at about 5 per cent. Its effect on the flea is not known.

The plague bacilli can often prove fatal to the fleas which transmit them, by multiplying in their gut and thus mechanically blocking the proventriculus, when the flea starves to death. Certain roundworms, apart from those which use fleas as intermediate hosts, feed on their reproductive organs and can effect complete castration.

A hymenopterous parasite, *Bairamliia fuscipes*, lays its egg in the flea larva and eventually kills it, during the course of its own development. The only records from Britain are from squirrel and hen fleas.

By far the most famous parasites of fleas are the mites which live in the nest and destroy their larvae and pupae. There are numbers of different species which inhabit both bird and mammal nests, and they originally sprang into fame when Loewenhoek, over two hundred years ago, first described them preying upon the larvae of the pigeon flea. This discovery inspired the hackneyed but immortal lines: "Big fleas have little fleas upon their backs to bite 'em." Hirst found that these

mites had a special affinity for the pupal case which they completely destroyed. In the laboratory they can, in this way, eliminate whole flea cultures.

One of the most curious and interesting facts about these mites is that in the hypopus stage (see p. 18) they use the adult flea as a means of transport to new nests. They attach themselves to the outside and even creep just beneath the chitinous plates or sclerites and hang on firmly by their sucking disks which are special adaptations for "hitch-hiking" purposes and are developed only at this stage. In some mysterious manner the mites can evidently distinguish between the sexes of the fleas, for they almost always attach themselves to females—a wise precaution for a parasite preying on the larval stages of the flea. The mites differ considerably in size. The species found on *O. rothschildi* (Plate V b) is one of the largest parasitising British bird fleas. Those illustrated on Plate V a, which look like ghosts beneath the sclerites of the host, are considerably smaller. These mites have not been identified with certainty. Sometimes as many as 150 hypopus larvae have been found attached to a single "transport." Such numbers greatly hinder the movements of the flea and in some cases may even cause its death.

We have already seen that when the bird host dies and grows cold, the fleas leave it and seek their fortunes elsewhere. Similarly, when the flea dies the mites also leave it. They moult, shed their sucking disks and change into octopod nymphs. How is it that the "hypopus" mites are aware their transportation has broken down? Perhaps the sudden cessation of movement is the stimulus to which they respond. One of the older writers observing them at such a moment wrote: "In bestirring themselves from their inactive condition one would imagine that a state of demoralization had seized them, for they were seen to pry free the sucking disks, leave their perch and move away from the dead host."

CLASSIFICATION

It is convenient to classify animals—that is to name them, describe them accurately and then arrange them in groups—just as it is convenient to name and classify the goods for sale in a shop. It is reasonably easy for a customer to locate cheese in Harrods' stores, because food, as

a commodity, is sold in one part of the building, and certain *types* of food, such as meat, fish, and groceries, are conveniently assembled at different counters. The commodities in Harrods' stores are, broadly speaking, classified according to their *function* in the world of men. That is to say goods intended for wearing, eating, drinking, reading or smoking are sold in different departments. This makes shopping easier than if they were, for example, classified according to their colour, when you would find fire engines, tomatoes, "Who's Who," sealing wax and flannel petticoats all in the same department.

Animals are classified scientifically with two main objects in view. Firstly, to render the animals in question easy to deal with from a purely practical point of view—to identify them quickly and accurately, to be able to describe them in print clearly, and to read about them with understanding. Secondly, to demonstrate their biological position among all living things. In other words they are classified according to the degree of fundamental relationship which exists between them.

To the layman it is obvious that a cat and a leopard are more alike than a cat and a canary. On the other hand they might well be deceived by a whale's superficial and outward resemblance to a shark, and be excused for thinking that both these animals are fish. Similarly a man from Mars might decide after a glance at a Dutch cheese, that its rightful place in Harrods' stores was the toy department and not the grocery counter.

Classification should serve as an aid to study, but man's passion for pigeon-holing knowledge frequently results in the creation of a hopeless muddle. "The human understanding, from its peculiar nature," remarked Francis Bacon, "easily supposes a greater degree of order and equality in things than it really finds." Animals cannot be forced into a fixed scheme, and however profound the biological truths reflected in such classification, all workable and practical schemes of this sort are to a certain extent arbitrary and therefore unsatisfactory.

When a classification is being built up all the characteristics of the animals concerned have to be taken into consideration, ranging from morphology and life history to differences in behaviour and habits. In practice, however, there are some characters which vary more than others, some which prove more reliable and more stable, and again others which are more easily seen under the microscope or which lend themselves to relatively brief and simple description. Thus, for example, the bones and teeth are largely used as a basis for dividing up the

mammals into families and genera, whereas the *exoskeleton* or hard outer-covering, is used in the case of fleas.

It is not easy to describe the simplest object in precise language. The layman complains bitterly about the obscure wording of legal documents, emergency regulations and scientific papers. Yet anyone who has tried his hand at describing a piece of linoleum or a gate-legged table in such a way that it cannot be mistaken for any other type of floor covering or table, will appreciate some of the difficulties involved. A trained lawyer is required to draw up a legal document and a trained biologist to classify an insect correctly and adequately.

Although unavoidable, the use of this technical jargon is, at first, rather irritating and confusing to those who are unfamiliar with scientific descriptions. This fact, and also the obscure nature of some of the characters used in separating one species from another, makes systematics and classification seem fantastically dull to the average layman. Sooner or later even the professional zoologist reflects gloomily that all roads lead to the counting tray or to the measurement of combs and beaks. Nevertheless this detailed and rather tedious work is absolutely essential. Commenting upon the fact that the spread of epizootic plague is governed by the flea-species factor Hirst remarked: "The discovery is but further testimony to the essential unity of science in its bearings on the welfare of the human race, for it is the natural outcome of the purely zoological researches of Rothschild and Jordan on the systematics of the Siphonaptera." In fact sound systematics are the foundations upon which all biological theories, great or small, are built. Disgruntled zoologists should reflect that Darwin's first important publication was a treatise on the systematics of barnacles.

Fleas are insects, and share with all other insects certain characteristics of their Class. Within this huge assembly they form a rather isolated Order. They are descended from winged ancestors—a fact which can be inferred from their structure and the study of analogous cases—but the various intermediate types have become extinct and there are no living insects which show the transitional stages or even suggest what they were like.

When the fleas themselves are divided up they fall into two fairly well defined superfamilies, and here again we can do little more than guess at the characters shared by the common ancestors of these two large groups. The superfamilies, families, genera and species, which

each represent more and more restricted categories, are distinguished by such characters as the form of the sclerites and their internal supporting rods, the presence or absence of certain combs or spines, the shape and structure of the genitalia and so on.

As we move down the scale and reach closely related species, minute differences have to be taken into consideration. These differences may seem trivial and even unimportant to the unpractised eye, but they have been selected after a comparison of all known fleas. They are the characters which specialists have found from experience can be relied upon, and which reflect the natural relationship of the order as a whole.

In written scientific descriptions no detailed account of the animal in question, or group of animals, is given—only the essential points are described. For practical purposes such descriptions must be as brief as possible.

The two superfamilies into which the fleas are divided can be characterised as follows :—

I. Superfamily Ceratophylloidea. (Plate XVII). This is a large superfamily with the following morphological characters : A sword-like ridge running down the inside of the outer wall of the mid-coxa. A pointed tooth present at the apex of the outside of the hind tibia. Abdominal terga II—VII with more than one row of bristles. Pygidium with more than sixteen pits on each side.

This superfamily includes the Ceratophyllidae which contain thirteen out of our fourteen bird fleas.

II. Superfamily Pulicoidea. (Plate XI). No swordlike ridge running down the inside of the outer wall of the mid-coxa. No pointed apical tooth present at the apex of the outside of the hind tibia. Abdominal terga II—VII with at most only one row of bristles. Pygidium with fourteen or fewer pits each side (Plate XIX).

This superfamily includes the family Pulicidae which contains the most notorious of all fleas, the tropical rat flea (*Xenopsylla cheopis*), the vector, *par excellence*, of bubonic plague, and the human flea (*Pulex irritans*). The only representatives among the British bird fleas are the shearwater flea (*Ornithopsylla laetitae*) and Hen Sticktight flea (see p. xiii).

Although the characters separating these two families appear rather obscure, they present in practice quite a striking contrast. The Pulicidae

are small, compact, and rather dumpy, whereas the Ceratophyllidae are elongated, loosely built fleas.

All the characters mentioned here, besides of course many others, can be picked out on the labelled photograph.

THE BRITISH BIRD FLEAS*

THE COMMON HOUSE-MARTIN FLEA, *Ceratophyllus hirundinis*; FARREN'S HOUSE-MARTIN FLEA, *C. farreni*; THE SCARCE HOUSE-MARTIN FLEA, *C. rusticus*; THE SCOTTISH HOUSE-MARTIN FLEA, *Orneacus rothschildi* (Plates XIII-XVII and Map 1). All the first three species are found pullulating in the nests of house-martins. The fourth, the Scottish house-martin flea, is very rare and has only been found once—in Scotland. Nine specimens were revealed among 4,000 *C. farreni*, thus showing that it is well worth while examining all the fleas present in a single nest.

The first reference to a British bird flea concerns one of these species. Hill (1752) remarked that "fleas are not confined to man and quadrupeds but are also found in swallows' nests." However, he shared Linnaeus' view that they were all one species. Long after it was known that mammals harbour different sorts of fleas, it was still thought that all bird fleas were one and the same "*Pulex avium*", until Dale's unfortunate decision to name every flea from a new bird host as a different species greatly increased the confusion.

C. hirundinis is described as the commonest and most widespread of the British house-martin fleas, *C. farreni* as a fairly common species, and *C. rusticus* as rare. The two former species have both been recorded in several thousands from single nests, but until quite recently (see below) *C. rusticus* has only been found in small numbers. The ecology of these fleas is extremely interesting but the study of it has so far been entirely neglected. All three species have been found in the same nest, in the same locality, in the same season and apparently all occupy the same ecological niche. They would, therefore, appear to come into direct competition with one another. This is of course a most unlikely

*Since the completion of this manuscript Allan (1950) has found a further species in the nest of the house-martin in Scotland, *Frontopsylla laetus*, a bird flea with an alpine-boreal type of distribution. He also collected a further series of *Orneacus rothschildi* from the same nest.

state of affairs and it remains to be seen what are the limiting factors within the nest for each species.

The total records of these house-martin fleas, collected from all known sources, in Great Britain and Ireland are as follows :—

<i>C. hirundinis</i>	<i>C. farreni</i>	<i>C. rusticus</i>	<i>O. rothschildi</i>
61 records	43 records	33 records	1 record

It seems likely that *C. rusticus* is on the increase in this country. Up to 1923 it had only been recorded six times and was absent from both Tring and Ashton. In 1935, Rothschild examined sixteen nests from these two localities and it was present in them all. The three species were represented as follows :—

<i>C. hirundinis</i>	<i>C. farreni</i>	<i>C. rusticus</i>
722	74	353
(present in 15 out of 16 nests)	(present in 11 out of 16 nests)	(present in 16 out of 16 nests)

It is a well known fact that in recent years a few British butterflies, such as the comma and white admiral, have increased their range and changed their status from "rare" to "common." Similar fluctuations may easily occur among the Aphaniptera.

The vast numbers of these fleas in single nests raise the question as to what factors limit the size of a population. At present it is a complete mystery why a house-martin's nest should regularly harbour hundreds, if not thousands, of fleas and other birds' nests, apparently equally suitable, a mere dozen or so.

The distribution of these fleas outside Britain and their origins are dealt with on pages 85 and 94.

The sternites of the males and receptaculum seminis of the females are figured on Plates XIII-XVI. The vermiform shape of the body of the receptaculum of *C. hirundinis*, *C. farreni* and *C. rusticus* should be compared with the barrel-shaped organ of *O. rothschildi*. The contrast is striking (see pp. 92-95).

It is worth noting that the first specimen of *C. rusticus* described in this country was a straggler off a wood-pigeon. It is one of our smallest bird fleas, generally measuring less than 2 mm. in length.

THE ROCK-DOVE FLEA, *Ceratophyllus columbae* (Plates XIII, XV, XVIIIc). Life in caves brings the various occupants into fairly close proximity and favours the exchange of parasites. It also provides a certain degree of isolation from the outside world. It is, therefore, not surprising that our rock and cave dwelling pigeon (*Columba livia*) should be the one pigeon to harbour a specific flea parasite. In the past there has been much controversy concerning the origins of the domestic bird, although it is now generally agreed that it is the same species as the rock-dove. The presence of *C. columbae* on the wild rock-dove and on our domestic pigeon is another piece of evidence in support of this theory. *C. columbae* has never been recorded in Britain from the stock-dove and only once from the wood-pigeon, and this was in London where it can be regarded as a straggler from a tame pigeon. It also occasionally wanders on to sea birds which nest on rocky cliffs.

C. columbae is a particularly easy species to identify, especially in the male sex, which has a characteristic bundle of bristles right at the end of the eighth sternite. Its absence from the dove cotes of the United States has been noted by Jordan.

THE DUCK FLEA, *C. garei*, and the BOREAL FLEA, *C. borealis* (Plates XII, XV, and Map 2; see also p. xiii). These two fleas, which are almost black to the naked eye, are so alike that only a specialist can be expected to tell them apart. Both are primarily parasites of ground-nesting birds, and *C. garei* is the only British flea which can tolerate the conditions found in ducks' nests. It is recorded from the eider duck, pintail, shoveler, red-breasted merganser and so on, hosts from which no other British bird flea has been taken. Nevertheless, it is at home in a really large range of nests, and in Britain alone, is recorded from 48 different species of birds, including such widely different hosts as the corn-crake, bearded tit, redshank, wryneck, artic skua, long-eared owl and goldfinch.

Its range extends from the Shetlands south to Cornwall and it is also recorded from Ireland (Map 2).

C. borealis has a much more restricted habitat and is found in Britain only in the outlying Western Islands and Orkney (see p. 87). In this country it appears to have a slight preference for the wheatear and has also been collected from the same host on the Island of Ushant during the birds' return passage from Africa. The only flea known from the cuckoo is *C. borealis* also taken from a specimen in Ushant.

The bird may have picked it up from the nest of its fosterparents (Plate XXXVIIIb) or during migration along the same route as wheatears, pipits or wagtails.

Both *C. garei* and *C. borealis* have, fundamentally, a circumpolar or alpine-boreal distribution not unlike that of *C. vagabunda* (p. 87), but *C. borealis* has apparently become confined to inaccessible islands and the European Alps, whereas *C. garei* is established over quite a wide area. It seems possible that these species come into direct competition with each other when they meet in one area and that *C. garei* is eventually successful and replaces *C. borealis*. At the same time one wonders if in turn *C. garei* is slowly being ousted by *C. gallinae* for in the past it may well have occupied all birds' nests, wet and dry. One can foresee the day when it will be forced to occupy a more and more restricted habitat until it has become a very rare flea, entirely confined to ducks breeding in marshy ground.

THE HEN FLEA, *C. gallinae* and THE CROW FLEA, *C. rossittensis* (Plates XIV, XVI, and Map 3). In Britain *C. gallinae* is the commonest and the best known of all the bird fleas. It has been recorded from 65 avian hosts in this country and has been found as a straggler on a number of mammals, such as rats, bats, moles, mice, squirrels and stoats. Ducks and geese, however, seem immune to its attacks. It is the flea *par excellence* of dry aerial nests and occasionally is seen in numbers which rival the house-martin fleas. Apart from starlings and sparrows it greatly favours the nests of owls and the crow family. At least once it has been counted in thousands in a single nest. The general belief is that *C. gallinae* was originally a tit flea and certainly it is exceedingly common in nests of blue tits and great tits. In the domestic fowl it has found a new host which suits it admirably, for hen coops are relatively dry and the hens live in close proximity to one another. Sometimes their sleeping quarters are teeming with this flea and continual scratching by the birds has a deleterious effect on their health and reduces egg laying.

In relatively recent years *C. gallinae* has been introduced into the eastern United States (see p. 93) where it infests poultry as well as wild birds. In the western United States the domestic fowl is parasitised by an indigenous flea from wild birds—*C. niger*. It will be extremely interesting to see if this hardy Christopher Columbus from Europe will continue its spread westwards and finish up by ousting the

native flea from the hen roosts of North America—thus emulating the unattractive behaviour of the human settlers from Europe.

The biology of *C. gallinae* has been studied in greater detail than that of most other bird fleas. The life span of this species from egg to the adult's death is on an average 450 to 500 days. As we have pointed out on p. 69 this varies enormously according to the temperature and other climatic conditions. The weather can affect the life-cycle in many ways. For example, egg laying falls off in a very dry spell and so does the proportion of fertile eggs laid.

A nesting box used by blue tits was kept under observation after the young had flown in June. Three months later the first specimens of *C. gallinae* began to emerge and they continued to do so at intervals until the following April. Thus, as the winter advanced, the fleas remained for progressively longer periods in the larval stages. This type of phenomenon has led some people to suggest that fleas can lay fertile eggs in the absence of a mammalian or bird host and breed for several generations in this manner. There is no evidence however, to support this theory, which is pure surmise. On the contrary all the experiments so far carried out go to prove the reverse. Not only does *C. gallinae* require a blood meal before laying, but egg production is confined to the spring and early summer.

C. gallinae is one of the species which has been observed leaving nests in large swarms and as already stated, it is a great wanderer and found in a variety of strange places far removed from a host or nest. We once collected a specimen from a plate of soup in Plymouth. This was a great surprise as most fleas found in such surroundings are cat fleas, dog fleas and human fleas.

Personally we have no great love for this species which has the annoying habit of turning up in rare birds' nests, such as those of the crested tit, or black redstart—even high up in the Alps—and thus providing a series of disappointments for the collector who is hoping for something new and strange.

The crow flea is so like the hen flea that anyone can be excused for mistaking one for the other. Unlike *C. gallinae*, however, *C. rossittensis* is strictly host-specific and is confined to the crow (*Corvus corone*). It has been recorded only once in Britain, from a nest in Cumberland, although its presence here was long suspected owing to its distribution in Germany and Holland. *C. gallinae* is the commonest flea in crows' nests and as the two species are generally present in the same nest, and

C. rossittensis in much smaller numbers, the latter can easily be overlooked.

The host has split into two well marked geographical races. It is claimed that *C. rossittensis* can also be divided into two subspecies—one off the carrion-crow and one off the hooded crow, but the evidence is meagre and the suggestion must be regarded as tentative. Unfortunately, no fleas have been found in the nest of the hooded crow in Great Britain.

The eighth sternites of the males and the shape of the receptaculum seminis of the females show features by which *C. rossittensis* and *C. gallinae* can be separated.

THE MOORHEN FLEA, *Dasypsyllus gallinulae*, (Plate XIII, and Map 4). This strange flea which originally hailed from the South American continent has an isolated position among British bird fleas. It is the commonest species we have apart from *C. gallinae* and one of the largest. It is also particularly easy to identify, both sexes being quite unlike any other of our bird fleas. The two heavy spines, like the horns of an antelope, on one of the genital flaps of the male can be spotted with a hand lens, and the deep "bite" out of the seventh sternite of the female is equally unmistakable.

D. gallinulae is very frequently found in nests with other bird fleas such as *C. gallinae* and *C. garei*, and a closer study of its ecology would no doubt prove extremely interesting. It is found relatively more often on the body of the host compared with hen flea and duck flea, which are essentially nest dwellers. In Great Britain it has been found parasitising 59 different species of bird hosts. These are varied, ranging from the moorhen, woodcock and grouse, to the robin, goldcrest, willow-tit, and tree-creeper, although generally speaking (see p. 101) it prefers nests in low positions.

D. gallinulae varies considerably in size and a series of both small and large specimens will hatch out of the same nest.

THE SAND-MARTIN FLEA, *C. styx* (Plates XIV, XVI). This flea has the distinction of having been mentioned by Linnaeus, but though recording it in numbers in the nests of sand-martins he mistook it for the human flea.

C. styx is a large species about 4 mm. in length and is the hairiest of the British bird fleas. It appears to be a very faithful companion of the sand-martin, and we know of no colony where its absence has been established with certainty. It is one of the most suitable fleas upon which to make studies of population density, sex ratio, hibernation, migration, breeding cycle, but so far the opportunity has been neglected. On the continent this species provides one of the extremely rare cases among fleas of *polymorphism*. That is to say there are two distinct morphological forms of the female, each of which shows a characteristic seventh sternite. This confused Rothschild who thought the second type of female was a distinct species and gave it another name. The error was subsequently spotted and the true nature of the "new" species revealed. Perhaps this second type of female will be turned up in Britain if it is searched for. Sometimes, however, as in the case of the well-known polymorphic female butterfly, *var. valesina* of the silver-washed fritillary (*Argynnis paphia*), one form is restricted to certain localities.

C. styx swarms in the burrows of the sand-martin and no other flea seems able to compete with it. Only once has another species been found sharing a nest in Britain, and that needless to say, was the ubiquitous *C. gallinae*. On the other hand *C. styx* seems fairly closely adapted to life in sand quarries and is not found as a straggler except on the dipper (*Cinclus cinclus*). It has been taken four times from this bird, in considerable numbers, and from widely separated areas. On the whole, however, it can be considered one of our strictly host specific bird fleas.

It has already been noted (p. 80) that *C. styx* over-winters in the nest. It can hibernate either as a pupa or adult. Large numbers have been observed in burrows immediately before the return of the hosts.

It has been claimed that certain mammal fleas develop finer and longer bristles on their legs if they parasitise rodents living in holes in sandy soil. *C. styx* certainly has finer and more numerous bristles than other British bird fleas, and this may be a direct result of the type of soil in which the birds make their nests. The same can be said of the closely related species off the sand-martin in North America. A closer study of fleas will certainly reveal the effect of other external influences, besides the rather obvious ones of the temperature and humidity in the nest.

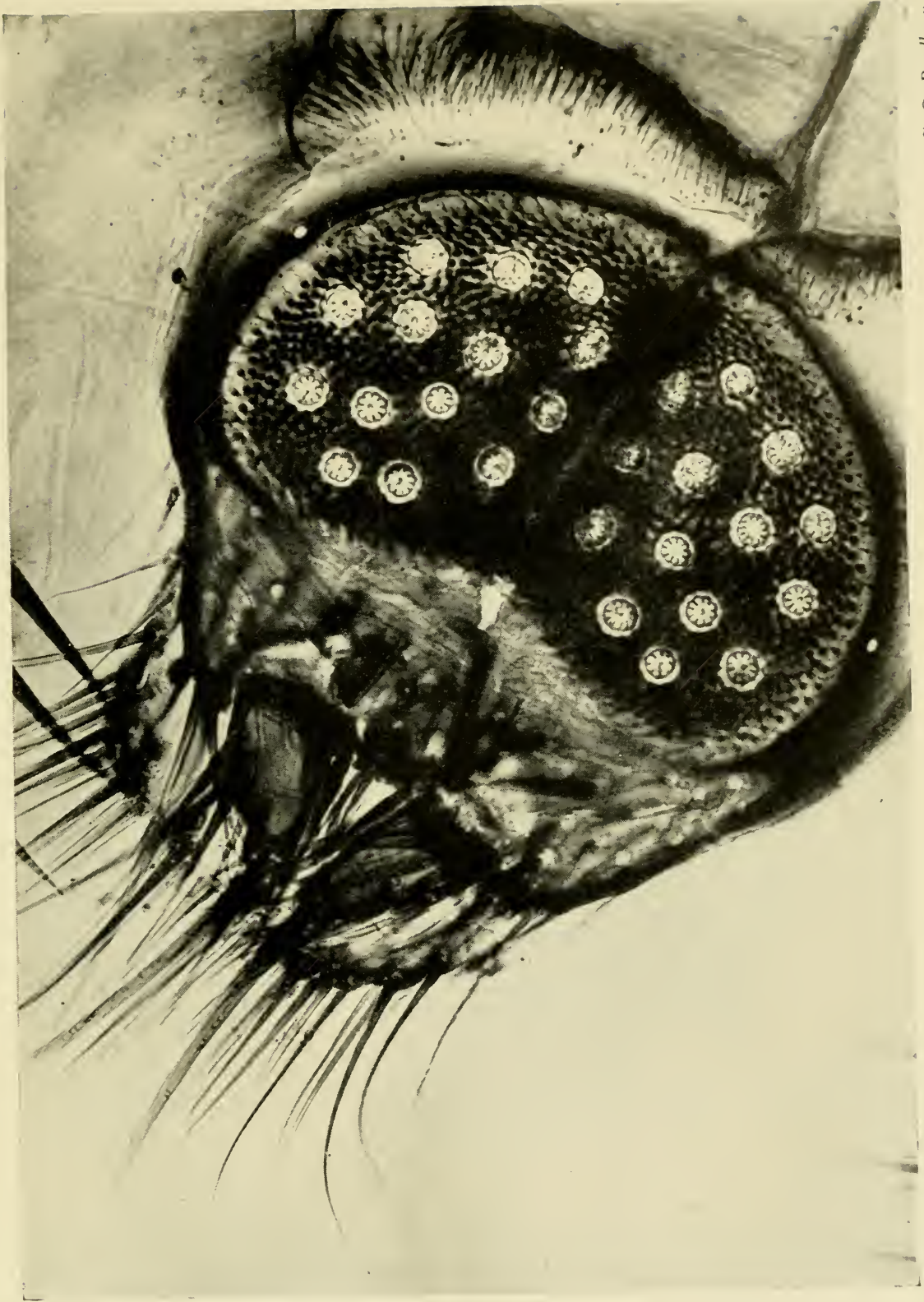




Plate XX

Swan: the feather lice of the white swan are white, and of the black swan are dark—is this protective coloration?

Eric Hosking

THE HOUSE-SPARROW FLEA, *C. fringillae* (Plate XIV, XV). This species is small and pale and gives an impression of delicacy. It is a parasite of the house sparrow, not of finches as its name suggests. Sometimes it is found as a straggler in the nests of other small birds and it has been recorded from the skylark, great tit and pied wagtail. On the other hand its presence in the empty nests of starlings, house-martins, swallows and swifts is no doubt due to the true host's habit of usurping other birds' nests. When the house-sparrow was introduced into the United States *C. fringillae* was either left behind or failed to establish itself in the new surroundings, for up till now it has not been recorded in North America.

The eighth sternite of the male and receptaculum seminis of the female are quite distinct, but this species is frequently mistaken for the hen flea (*C. gallinae*) and published records have, therefore, to be treated with caution.

THE VAGABOND FLEA, *C. vagabunda* (Plate XIV, XV). This is a relatively rare flea found in Britain in the nests of the jackdaw and rock-dwelling sea birds such as the herring-gull, kittiwake and the shag. It is apt to wander on to other cliff-dwelling birds and has been recorded from the peregrine falcon and the rare honey-buzzard in Cornwall and the raven in Ireland. Inland it has been found only three times apart from the five records off the jackdaw which are discussed in the section on distribution. Nests of this bird are easy to collect and it would be of great interest to see how widely spread *C. vagabunda* is on the mainland of Britain. It is well established on jackdaws around Oundle and in such widely distant localities as Herefordshire, Cornwall and Midlothian.

As we have already noted on p. 87 this flea has broken up into subspecies, and the British representative, *Ceratophyllus vagabunda insularis*, is peculiar to these Islands.

THE SHEARWATER FLEA, *Ornithopsylla laetitiae* (Plate XI, XIII, XVI, XXXIII and Map 4). This is the only Pulicid bird flea in Britain and shares with *Orneacus rothschildi* the distinction of being peculiar to our fauna. A glance at Plate XVII will show what a contrast this species presents with any of our other bird fleas. It is relatively compact, short

and dumpy, whereas the Ceratophyllid fleas are long and loosely built. The resemblance between this species and the common rabbit flea (Plate XI) is also quite obvious, as well as the similarity between the receptaculum of *laetitia* and *Hoplopyllus glacialis*, the species off the arctic hare (Plate XIII). In the section on evolution we have discussed the origins of the shearwater flea and seen how in the family Pulicidae the change on to a bird host has accelerated the loss of combs, and a shift of the bristles on the tarsi.

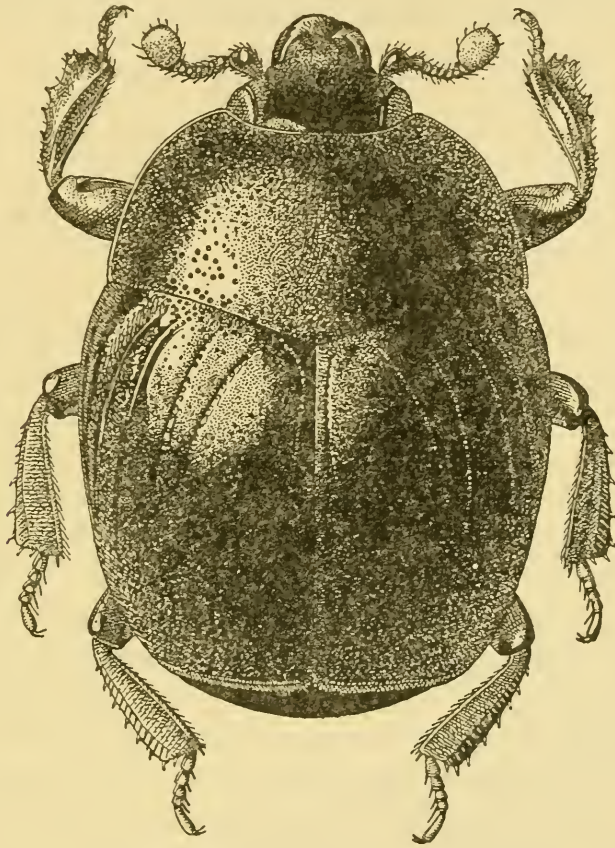
The common rabbit flea congregates on the ears of the host and has become a partially sedentary species. It is attached to the skin of its host by the heavily serrated maxillary lacinia. The shearwater flea has no such modification of the mouth-parts and, as one would expect, is free in the nest and on the host's body.

Ornithopsylla laetitia has so far only been recorded in the burrows of the manx shearwater and the puffin, in the Scilly Isles, Skomer and Skokholm Isles, off the coast of Wales, and Ireland's Eye and the Great Skellig off the coast of Ireland. The hosts occasionally nest on the mainland but so far the flea has not been found anywhere except in these remote islands. The puffin is a popular bird with fleas, six species having been recorded from it, namely: *C. gallinae*, *C. garei*, *C. vagabunda*, *C. borealis*, *O. laetitia* and the common rabbit flea *Spilopsyllus cuniculi*. The shearwater on the other hand has one flea only, *O. laetitia*, and it is probably its true host.

CONCLUSION

Bird fleas are a small group and their chief interest lies in the fact that they have transferred from mammalian to avian hosts in comparatively recent times. Thus, the evolutionary trends associated with the change to life in feathers are relatively easy to observe and a gigantic and instructive field experiment is presented to the naturalist should he care to avail himself of the opportunity of studying it. The cardinal need, in the first place, is further collecting. And again further collecting. The first line on which to concentrate is the fleas from ground-nesting birds, particularly from those species which nest in isolated island habitats, in holes and caves. The student of bird fleas who reads Murphy's *Oceanic Birds of South America* almost expires with

frustration as he notes one unique opportunity after the other thrown away. Scores of nests of rare oceanic birds were dug up out of holes and examined—but no fleas were collected. It is painful to contemplate what a revealing and interesting appendix could have been written to Murphy's first-rate monograph.



Gnathoncus punctulatus (x 37), a beetle
which lives in birds' nests and feeds on fleas

CHAPTER 8

FEATHER LICE (MALLOPHAGA)

(μαλλός=WOOL, φάγος=EATING)

Tell me what company thou keepest, and I'll tell
thee what thou art

CERVANTES

THERE WERE no lice in the Garden of Eden. Such loathsome creatures must have been created after the Fall. "Can we believe that man in his pristine state of glory, and beauty, and dignity, could be the receptacle and prey of these unclean and disgusting creatures?" So mused Henry Denny when compiling his *Monographia Anoplurorum Britanniae*, the first and only book to be written on the Mallophaga of Britain. Today, it is generally believed by entomologists that the feather lice are derived from free-living ancestors which were not unlike the Psocida or book-lice in form and habit. These ancestral Mallophaga probably lived under moss and stones and on the bark of trees, feeding on any organic débris they could find. Book-lice have been taken from the bodies of caged animals, such as white mice, where they were possibly feeding on skin débris, and it is not difficult to imagine that the free-living ancestral Mallophaga might have visited the bodies of resting reptiles. When the reptiles which gave rise to the early birds gradually evolved a feather covering, a hitherto untouched source of food became available. Originally, feathers must have proved a hard and indigestible diet, but one which enabled the insect to occupy a new habitat with an almost unlimited food supply and without competition. Gradually the ancestral Mallophaga became more and more closely adapted to these new conditions so that eventually they could live and breed only in the warmth and shelter provided by the body of their host. The Mallophaga, the feather or chewing lice, are found on all birds and many mammals, but not on man. It is usually believed that they first became

parasitic on birds and later spread to mammals, but here we are concerned only with the species living on birds.

HABITS AND STRUCTURE

To the naked eye the Mallophaga are not unlike small free-living insects. Actually, however, considerable structural modifications have taken place : chief amongst these is the general flattening of the body (dorso-ventrally, not from side to side as in the flea), which enables the insect to slip between the feathers and to apply itself to their flattened surfaces for the purposes of feeding and attachment. The head, especially, has become modified. In a free-living insect, such as the cockroach, or in an animal like a horse, the longer axis of the head lies at right-angles to the rest of the body. In the Mallophaga the head has become flattened from top to bottom so that the longer axis lies in the same plane as that of the body. The head is a hollow box-like structure with thickened walls; these have thinner areas (or sutures, Plate XXI) allowing a limited mobility of the parts of the head for feeding. On the inner surface of the walls are various thickened ridges (Plate XXI) which give strength to the head and form a supporting framework for the mouth-parts. These sutures and ridges are useful characters in classifying the genera of the Mallophaga.

The feather lice, unlike the fleas, show considerable diversity in size and general body form (Plates XXII-XXIII). This diversity has been brought about by the Mallophaga occupying the different types of habitat, such as the head and the wings, found on the body of the bird and becoming specialised and adapted for life in these locations.

In size feather lice range from the minute game-bird-infesting *Goniocotes*, in which the males are just under a millimetre in length—a little less than the proverbial pin's head—to the large hawk-infesting *Laemobothrion* which may be up to ten millimetres (about one-third of an inch) in length.

Feeding. The Mallophaga, originally feeders on various kinds of organic débris, took to eating feathers when they became parasitic on birds. This change of diet did not necessitate any fundamental modifications in the original chewing mouth-parts, which were probably similar to those found in an unspecialised insect like the cockroach.

The strongly-toothed, dark-coloured mandibles (Plate XXI) can be seen either near the centre of the head (Ischnocera*, Plate XXII) or near the anterior margin (Amblycera* Plate XXII). These are used to cut off pieces of feather, usually of constant lengths, which fall into the pouch-like labrum or forelip. Movements of this pouch force the food into the mouth. The maxillae and labium are reduced to simple lobes either without palps (Ischnocera) or with segmented maxillary palps (Amblycera), and probably play only a minor part in the feeding operation.

The feather-feeding forms generally take the down or downy part of the larger feathers. When feeding the louse approaches the barb of the feather head foremost and hangs to it by the second and third pair of legs, the first pair being used to direct a single feather barbule towards the mandibles. The pieces of feather, cut by the mandibles and forced into the mouth by the labrum, pass down the oesophagus to the crop. When full this shows as a black structure lying in the abdomen of the living insect, rounded anteriorly and pointed posteriorly (Plate Ia). If a louse is watched while feeding, strong pulsating movements of the crop can be seen. These movements help in the breaking up of the feather parts, particularly by rubbing them against sets of comb-like structures in the wall of the fore-part of the crop. Small mineral granules are sometimes found in the crop, and it has been suggested that these may act as further grinding agents—an interesting analogy to the grit in the gizzard of the bird. But more than purely mechanical treatment is needed for the digestion of the food. Feathers consist mainly of keratin—a strongly resistant substance—and before this can be acted on by the digestive enzymes of the gut it must be subjected to a strong reducing agent. Such an agent is secreted in the stomach of the louse; the larva of the clothes moth, which also feeds mainly on keratin, secretes a similar substance. The protein-digesting enzyme of the louse is also adapted to enable it to digest the specialised protein of the keratin, when the latter has been broken down by the first secretion.

Some of the feather-lice harbour bacteria, which are confined to special cells lying in groups in various parts of the body. Elaborate methods have been evolved by which the bacteria infect the breeding organs of the female and are passed into the egg, thus ensuring the continued association between bacteria and louse. The exact role

*See p. 139 for explanation of these superfamilies.

played by these bacteria is unknown, but it has been suggested that they are in some way associated with the digestion of the specialised diet of the feather lice. Among the bird Mallophaga, these are found chiefly in the superfamily Ischnocera, which are mainly feather-eaters, and only rarely in the superfamily Amblycera which take blood and other substances in addition to feathers. This fact actually makes the problem more confusing as similar bacteria are found in the sucking lice (Anoplura), the bed-bugs (*Cimex*), the fleas (Aphaniptera), the ticks and certain mites (Acarina) which are all true blood-suckers. It has been shown, for instance, that nymphs of the sucking louse of man (*Pediculus humanus*) cannot survive if deprived of their bacteria.

Some Mallophaga (of the superfamily Amblycera) may live entirely on blood and serum, or add this to a mainly feather diet. One of the chicken lice (*Menacanthus stramineus*), which lives on a mixed feather and blood diet, uses its mandibles to puncture the young feathers in quill and to take the blood from the central pulp supplying the growing feather. Its oesophagus is provided with strong muscles and can exert a sucking action. This species also gets blood by gnawing through the skin of its host.

The members of one genus of Mallophaga (*Piagetiella*) live attached to the inner walls of the throat pouches of pelicans and cormorants, where their diet must consist of blood and serum, and possibly epidermal debris taken from the walls of the pouch. Another species (*Actornithophilus patellatus*) spends part of its life-cycle inside the shaft of the flight feathers of the curlew (Plate Ib), probably feeding on the dried feather core. The nymphal stages of one of the species (*Dennyus truncatus*) found on the swift are said to live on the liquid secretions of the eye of the host. It is doubtful whether any species subsist entirely on epidermal scales and other debris found on the surface of the body of their host, but it is probable that some species, in addition to their normal diet, do undertake a certain amount of general scavenging. In the crop of one louse which he examined Waterston found granules of mica and quartz a butterfly scale, part of a seed coat, a minute fungus, its spore and a fragment of feather. Crops have also been found containing empty Mallophagan egg shells, cast larval skins and parts of mites and other lice—this suggests that the Mallophaga may, at times, indulge in cannibalism.

Locomotion and Sense Organs. Feather lice, as would be expected from the diversity of their body form, show considerable variation in the

speed and manner of their movements. Most species can run backwards and forwards with equal facility; the short round forms (Plate XXI) living on the head and neck do not move great distances, but can slip speedily out of sight into the down at the base of the feather; the narrow elongate forms found on the larger feathers of the body and wings, are fast movers and able to slip sideways across the breadth of the feather and from feather to feather with great rapidity.

The legs are comparatively uniform throughout the bird lice. In the Ischnocera they are adapted for clinging to the feathers by means of the shortened tarsus and paired tarsal claws (Plate XXI). In the Amblycera, which move more generally over the surface of the body and feathers of their host, the legs have a longer tarsus, and are able, through a modified part of this segment, to cling to smooth surfaces; thus they can climb up the sides of a glass tube, whereas the Ischnocera cannot do so.

The Mallophaga are photonegative and have a positive reaction to the warmth and the smell of their hosts, reactions which ensure that the lice keep well within the plumage, and do not stray off their hosts on to other objects which may come within reach. On the death and corruption of the host, when the stimuli of temperature and smell undergo a change, the lice come to the surface and can be seen moving restlessly over the feathers.

Their eyes are probably only able to perceive the difference between light and darkness, and the movement of other objects. Each eye is protected by a sensory hair (Plate XXI) which serves as a tactile sense organ, probably helping to guide the louse in its passage through the feathers.

The antennae (Plate XXI), which can be seen in a constant state of motion in the living louse, are also used as tactile organs in the Ischnocera and in some of the Amblycera, but in this latter group they may be small and completely enclosed in a fold of the head. They also bear sense organs which are possibly connected with the perception of warmth and smell similar to those in the antennae of the sucking louse of man. The male antennae (in the Ischnocera) may be used to clasp the females during copulation, and in some species (Plate XXIIIa) they are larger than those of the female and have hook-like appendages which improve their efficiency as clasping organs.

All parts of the body bear numerous hairs or setae which are supplied with nerve fibres, and serve as further tactile organs.

Life History. The complete life history, from egg to adult, takes place—unlike that of the flea—on the body of the host. Not much is known about this aspect of the biology of the Mallophaga. The female is almost always larger than the male, and in many species the numbers of this sex in any one population are greater than those of the males, and in some, which have been widely collected, males have rarely or never been found. The development of the egg without fertilisation (i.e. parthenogenesis) is known to take place in one of the mammal lice, but the extreme rarity of the males in some species and the normal apparent excess of females over males, could also be caused by the immediate death of the male after mating.

The life history has been studied extensively only in the common pigeon louse (*Columbicola columbae*), and most of the following account refers to this species.

The eggs when first laid are pearly white, and are fixed to the feathers with a cement-like substance secreted by a special gland associated with the female reproductive organs. In *Columbicola* and other species living on the wings they are laid in rows, end to end, along the grooves between the barbs of the flight feathers and under wing coverts (Plate XXIV); in this position they are protected by the edges of the grooves and so escape damage by the bill of the bird during wing preening. The other main egg-laying site is on the feathers of the head and neck, where again the eggs are safe from the preening bill; here they are laid singly or in clusters near the base of the feather. In heavily infested birds the eggs may be found attached to feathers almost anywhere on the body, and some of the Amblycera normally lay their eggs on the feathers of the breast and belly. The curlew quill louse, like the quill mite, lays its eggs in a spiral column on the inner wall of the quill.

Each egg has a cap (or operculum), separated from the rest of the egg by a line of weakness; any pressure applied to the egg will cause a break at this point. The eggs may be objects of some beauty, adorned with various reticulate surface sculpturing and plume-like processes on and around the cap. The normal rate of egg-laying is unknown; a female *Columbicola* kept in captivity at optimum temperature and provided with pigeon feathers, did not average more than one egg every two or three days. The time taken for incubation probably varies in different species. In an incubator at a temperature of 37°C. the eggs of *Columbicola* hatch from three to five days after laying; lowering of the temperature may prolong the period to fourteen days. Nymphs

kept at 33°C. only live a few days. Temperature of the host, therefore affects not only the length of the life-cycle, but also the survival of the young, and may be one of the limiting factors in the establishment of a louse on a new host (see discussion under host specificity, p. 137).

When the nymph, within the egg, is ready to hatch it begins to suck in air through its mouth; this air passes through the alimentary canal and accumulates in the egg-shell behind the nymph. After about five minutes of this sucking action the pressure of the air behind the nymph becomes so intense that the cap or operculum of the egg is forced open. During the next twenty minutes the nymph frees itself from the egg shell by muscular contractions, expansion of the abdomen and further pumping of air. It can at once move freely about on the feathers, but food (which is the same as that of the adult) is not taken until several hours after hatching.

The feather lice, unlike the fleas, have no metamorphosis. The nymph which emerges from the egg resembles the adult in habits and general body form, differing in its smaller size, absence of colour, undeveloped sex organs, and certain other morphological details. The nymph sheds its entire skin three times before reaching the adult state. In *Columbicola* each stage lasts from six to seven days, and after each moult the nymph becomes successively larger, darker and more like the adult. Nothing is known about the length of life of the female or the total number of eggs she lays. But far fewer eggs are required by ectoparasites which spend generation after generation on one individual bird, than by those in which the young are faced with the risky business of finding a new host after hatching.

HOST AND PARASITE

Population Size of Parasite and Effect on Host. The number of lice (or population size) found on any one bird varies considerably from individual to individual, even in the same species. This variation does not seem to be entirely seasonal; a number of birds of the same species can be examined at the same time of year, and some may be lightly infested, some heavily infested and some altogether louseless. Certain species, for example rooks and crows and some of the waders, have a higher proportion of both infested individuals and individual lice, but even amongst these, lice-free birds may be found. A curlew from Ireland, in excellent

condition and plumage, was found to have 1,803 lice, another from Suffolk, 1,047, and a rook from Wiltshire just over 300. These numbers are unusually high, although the curlew is always found to harbour some lice, usually between 50 and 200. In the case of the small passerines, many individuals seem to be louseless, or the numbers found are small, usually between one and ten in number—over twenty lice is uncommon. Young birds tend to be more heavily infested than adults and sick birds more than healthy ones. The world record is held by an East African cormorant (*Phalacrocorax nigrogularis*) which harboured over 7,000. It is doubtful if there is any species of bird in the world which is without at least one kind of feather louse. This pained the early entomologists, one of whom remarked that “even the gorgeous peacock is infested by one of extraordinary dimensions and singular form”; and Benjamin Franklin ruefully laments the choice of the bald eagle as the emblem of America: “as he is generally poor and often very lousy.”

The population of lice may be large without apparently harming the bird, but when it is abnormally heavy, in sick, captive, or young birds, the effect on the host may be serious. The mere movement of the lice is intensely irritating, so that the bird damages itself by excessive scratching. The lice, if too numerous, may denude some of the feather shafts, and cause injury and loss of blood by rupturing the skin during feeding. The punctures made in the feathers when in quill, by the chicken louse, may inhibit their development altogether.

The Mallophaga, up to the present, have never been convicted as effective carriers of any disease, a fact which is reflected in the small amount known about their biology compared to the typhus-carrying sucking louse and the plague-carrying flea. One of the mammal Mallophaga, that of the dog, acts as the intermediate host of a tapeworm; and there is a single record of a bird Mallophaga (*Dennyus*) acting as the intermediate host of a roundworm (*Filaria*), which parasitises the bird host, a swift. Further work may reveal other cases of parasites which spend part of their life-cycle in the host and part in the louse.

Factors Limiting Population Size. The fact that birds tend to be more heavily infested if they are sick suggests that, by their own efforts, they normally help to keep the louse population in check. Preening by the bird (Plate VIII) doubtless eliminates a number of

Mallophaga and their eggs, and tends to restrict egg-laying mainly to the head and neck, or to a modified form on the wing feathers. A specimen of the cuckoo head louse (*Cuculoecus latifrons*) was recently found on the back of a cuckoo in a damaged condition—the thorax and abdomen being attached to one feather, and the severed head to an adjacent one. The louse presumably had strayed from the safety of its normal habitat, and was torn in two during the preening of the back feathers. Further evidence of the importance of preening is shown by the case of a robin which had most of the upper mandible of the bill missing; it was infested with 127 specimens of *Ricinus rubeculae*, the numbers of which rarely exceed 15 on any one bird.

The choice of habitat, the structural modifications of the louse and the position of the egg-laying sites, have probably been largely determined by the preening habits of birds. It is interesting to speculate whether the apparent colour adaptations of some lice to the feather background on which they live are true cases of adaptive colouration. Are they protected from the bird in the same way as the woodcock, whose plumage merges with the dead leaves and bracken amongst which it lives, is protected from carnivorous predators? There are many instances of a resemblance between the colour of the louse and the plumage of its host: white lice on the white gulls and darker lice on the darker but related skuas; white lice on the white swan, dark lice on the black swan; a yellow louse on the golden oriole, a black one on the coot. Such examples could be multiplied almost indefinitely. It has been suggested that the yellow colour of the golden oriole louse is due to the fact that it eats the substance which gives the feather its yellow colour. There is no proof of this, and it is an explanation which cannot be applied to such cases as the white swans and gulls, which in addition to lightly coloured lice, also have other species which are brown and sometimes exceptionally dark in colour. These dark species, it should be noted, are confined to the head and neck where they are out of reach of the beak. It seems probable that certain genera of feather lice, like the last nymphal instars of the human sucking louse, have the ability to respond to the colour of their background. It is not known, however, if the resulting similarity in colour between the louse and the feather on which it lives does in fact serve a protective purpose.

Bathing in water and dust and the subsequent preening (Plate VIII) helps the bird to rid itself of parasites. Lice have been found in the dust taken from dust baths habitually used by chickens. As Pliny

remarked, "These insects . . . are apt to kill the pheasant unless it takes care to bathe itself in dust."

The phenomenon known as "anting" may be another method by which the bird keeps down the numbers of its lice. Russian soldiers were said to clean their lousy garments by putting them on ants' nests, and it has been suggested that the habit of some birds of lying with outstretched wings on an ant's nest allows the ants to run through their plumage and perform a similar service. The subject, however, is both controversial and complicated. There are two types of anting behaviour, one known as "passive anting", the other as "active anting". "Passive anting" by a young carrion-crow is described by Condry: "After a few seconds hesitation he stepped into the middle of the swarming ants . . . When some of the ants found their way via his legs to his feathers, the bird showed apparent pleasure and slowly settled down among the ants with wings outspread and tail fanned. Then he dropped his head down in a swooning posture till his beak touched the ground. He was soon covered with ants . . ."

Many cases of "active anting," which seems to be a more usual phenomenon, have been recorded: Chisholm describes this curious procedure carried out by some immature starlings:

"Each bird snatched up an ant from a gravel path and dabbed it quickly first under one wing and then under the other, after which the insect usually was dropped . . . All the actions of the starlings were very rapid. Two birds in particular nearly fell over backwards while rearing up smartly and applying ants beneath their tails . . . When the birds departed, the path was bespattered with dead and maimed ants, some fifty per cent. of which had their abdomens burst."

There is further evidence which may throw some light on this peculiar habit. Tame or captive birds have been seen rubbing cigar-butts, lemon-juice, vinegar and even beer into their plumage. The American purple grackle (*Quiscalus quiscula*) anoints its plumage with the liquid found inside the walnut, which has a strong acid reaction, and there are other reports of birds applying aromatic oils from fruits and leaves to their bodies. It has therefore been suggested that the birds are smearing insecticides on their plumage. The formic acid within the bodies of the ants is liberated as these are crushed against the feathers, and it is thought that the lice and other ecto-parasites are either killed directly, or through eating the acid-covered feathers.

Some biologists, however, believe that the birds merely get an enjoyable sensual pleasure from the movements of the ants among the feathers, or from the stimulus of formic acid on the skin. It is a well-known fact that tame parrots and owls enjoy having their necks tickled. One tame parrot developed the habit of pushing a piece of apple under its wings or into the back between the shoulders; it was suggested that the acid in the apple cooled or stimulated the skin. Finally those who favour the theory of odour-attraction believe that the bird is scenting itself and that the smell of the formic acid or aromatic oils are a source of pleasure and satisfaction. Although there is as yet no conclusive explanation of the habit of "anting," Chisholm, who has studied and reviewed the subject (1944), considers that the value of the acid as a skin stimulant is the most potent factor. An indirect result which springs from the presence of acids on the feathers is the death of the parasites. It seems possible that the habit may have arisen from birds taking dust baths in the loose earth found on ants' nests, and the additional stimulus and cleansing power of the formic acid was appreciated. Again, many birds when sunning themselves take up the passive anting position (Plate IVb) and the habit may have been initiated by birds sunning themselves in the vicinity of ants' nests. "Howe handsome it is to lye and sleepe, or to lowze themselves in the sunn-shine."

Little definite information is available about any other factors which limit population size. There may be competition between the different species on one host (interspecific competition) or between the individuals of one species (intraspecific competition). Waterston records finding a specimen of *Goniodes* (a large louse from game-birds) with its crop crammed with pieces of *Goniocotes*, a considerably smaller louse. Mites, when numerous, may also keep down the number of Mallophaga, possibly by the destruction of the eggs, for empty egg-shells have been found occupied by mites.

Little is known about the diseases which attack the Mallophaga. Occasionally parasitic fungi have been observed in the form of colourless club-shaped projections on the bodies of the larger lice, and it is probable that they are in some way harmful to the host. Mites and their eggs are also found attached to feather lice. These mites, which belong to a genus peculiar to the Mallophaga and closely related to another genus found on the louse-flies, have been recorded from *Trinoton* (Plate XXII) and *Ancistrona* only, which are particularly large in size. They seem to be relatively harmless. Thus in the case of some of the larger

feather lice at any rate, Addison's remark is justified: "A very ordinary Microscope shows us, that a louse is itself a very lousy Creature."

ORIGIN—EVOLUTION—CLASSIFICATION

If the photographs of Mallophaga in this book are shown to an expert he can say after a superficial glance from which order of birds each specimen was collected. Similarly if you were to show the expert a louse and say: "I took this off a snipe," he might reply: "Yes, but that day you also shot a partridge and put it in your game bag with the snipe." This is possible because groups of related birds—say the game-birds, the waders, the hawks—each have their distinctive types of lice.

Close correlation between bird and parasite can be explained by the theory that birds were parasitised at an early stage of their evolution, before they had diverged greatly from the generalised ancestral type. As the birds evolved and became adapted to different environments and ways of life, there were modifications and changes in their body form, in the physical structure of the feathers, and in the temperature and secretions of the body. The Mallophaga, closely associated as they are with the surface of the body and the feathers, had to become adapted to these changes. Each step, therefore, that took a group of birds further away from the ancestral type and from other evolving groups, was followed by the Mallophaga living on it. The morphological changes in the feather lice, however, were slower and less drastic than in their hosts, and the differences between any of the Mallophaga are now less than those between say a penguin and a peacock. The environment of the Mallophaga is formed mainly by the external characters of the bird—the feathers and skin texture—together with the temperature and secretions of the body. The changes in this environment were probably smaller than those in the external environment of the bird, and the resulting modifications in the structure of the louse are, therefore, less. It is also possible that the Mallophaga after an initial evolutionary spurt became more stable, in the evolutionary sense, than their hosts, and thus remained more constant in form.

This slower rate of evolution in the Mallophaga is the reason why they have changed less than their hosts, and have retained more characters which show their relationship to each other. The curlew and the oyster-catcher, both waders (*Charadrii*), belong to different families

(Scolopacidae and Haematopodidae); but the head lice of these two birds are more similar, being closely related species of one genus—*Saemundssonina*. Again, the three suborders of the Charadriiformes—the waders (Charadrii), the gulls (Lari) and the auks (Alcae) contain birds which differ greatly from each other in appearance and habits, but their head lice are similar and can be placed together in the genus *Saemundssonina*. As we would expect from our theory of evolution, however, the head lice found on the curlew, for instance, are more like those of other waders (Charadrii) than those of either the gulls (Lari) or auks (Alcae).

The evolutionary story of the birds is sometimes pictured in the form of a tree. The trunk represents the ancestral stock, giving rise to branches, which themselves branch and branch again; the subdivisions of one branch being more closely related to each other than to those of any other original branch. The larger subsidiary branches may be taken to represent the orders, such as the game-birds (Galliformes) or the ducks, geese and swans (Anseriformes), with the smaller branches as families and genera down to the twigs which represent the species. If we place a similar evolutionary tree for the Mallophaga against this one we shall find that a branch representing a genus of Mallophaga will not correspond with a branch representing a genus of birds, but may, like some straggling piece of ivy on an elm, cover all the subsidiary branches forming an order of birds. Thus, in a great many cases there is a genus of Mallophaga which is found on one order of birds and no other. For example, the Ciconiiformes (the storks and herons) harbour five genera of lice found on no other birds; the Procellariiformes (petrels) have ten and the Galliformes (game-birds) have at least seven genera of lice which are peculiar to them. Hence it follows that by examining a bird's Mallophaga it is often possible to say to which order the bird belongs.

In addition to these genera restricted to one order of birds there are a number parasitising birds belonging to two or more, often quite distantly related orders. The presence of such genera cannot be explained solely by this particular evolutionary theory and certain other factors must be considered before we can even try to understand the complications of the present day distribution and relationships of the Mallophaga.

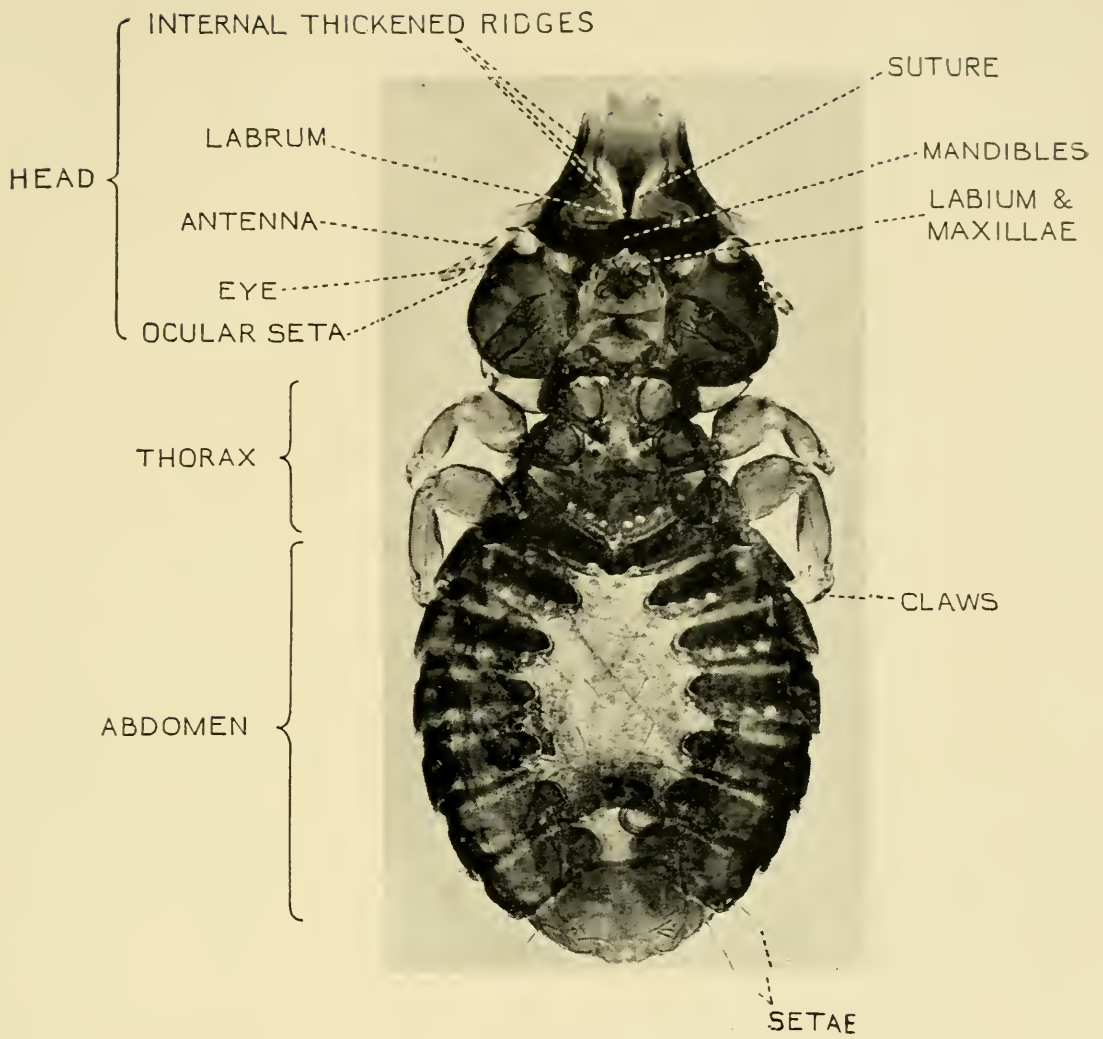


Plate XXI

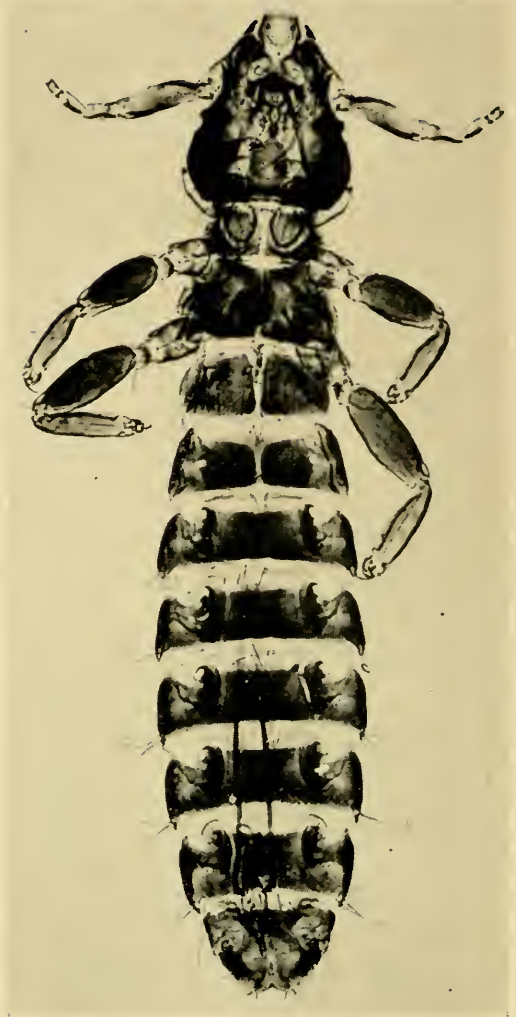
J. G. Bradbury

Head feather louse, *Saemundssonina* sp., from common tern, showing important characters (× 46)



W. H. Pollen

a. Amblycera: *Trinoton* sp., from duck
($\times 19$)



W. H. Pollen

b. Ischnocera: *Pectinopygus* sp. from
cormorant ($\times 34$)

Plate XXII

THE TWO MAIN TYPES OF FEATHER LICE

Ecological Niches. If the louse population of any individual bird is examined it is evident that this comprises a number of quite different types of lice. Each of these is distinguished by habits and general body form and most birds are found to harbour five or six, some even up to twelve of these different genera. This diversity of lice can be explained by the theory of ecological niches.

It is a truism that no place which can support life is without life. Every possible habitat and source of food—that is, every ecological niche—will be utilised by some form of organism. It can be stated broadly that all the higher categories of classification, such as the orders, are based on the original divergence of the ancestral stock to fill available ecological niches. The order Anseriformes (ducks, geese and swans) is descended from a line which became adapted to life in the water, and the Ciconiiformes (storks and herons) from one that became adapted to life in swamps and marshes.

We have seen that the reptile-like ancestors of the birds developed feathers and thus produced a new type of environment—an empty ecological niche. This was occupied by a primitive free-living insect which gave rise to the parasitic bird-lice of to-day.

The invasion of any new territory, where food is unlimited and competition absent, seems to act as a great stimulus to evolution. The primitive, unspecialised, ancestral Mallophaga finding such a territory, must have rapidly filled the ecological niches then available on the body of the host, and also those formed subsequently through the differentiation of the plumage during the evolution of the birds. The occupants of each ecological niche diverged from one another as they became specialised and adapted to the particular environment in question—whether of the head and neck or wings and back. In the same way the marsh dwelling birds with their long legs, long necks and long pointed bills which adapt them for life in that particular ecological niche, differ from the birds of the ponds and lakes, with their short legs, webbed feet and flattened beaks.

Looking at the louse population of most birds it is a simple matter to pick out the lice adapted to two of the ecological niches, namely, those of the head and of the wings and back. The Mallophaga living on the head and neck, where they are out of reach of the bird's beak, have less need for rapid movement and have become adapted to a comparatively sedentary life on the feathers. The abdomen is short and round and not particularly flattened, the legs are short with strong

claws adapted for clinging to the feathers, and the head large to accommodate the heavy strong mandibles and their supporting framework (Plate XXI). Such fat-bodied forms on other parts of the body would be easily picked off by the bird or crushed by its bill. The eggs are laid on the feathers of the head and neck, singly or in bunches, and need no special modifications to protect them as they are out of reach when the bird is preening.

On the wings and back, where the louse is always in danger from the bill, a flattened elongate, long-legged type is found (Plate XXIIIc) which is able to move rapidly, mainly by slipping sideways across the feathers. The eggs, which are laid on the wing feathers, are elongated and usually placed between the barbs, which protect them during preening.

Apart from these two extremes—the large-headed, short-bodied and the flattened elongate forms—there are many others which are intermediate in body form and have different habits. These presumably occupy different habitats on the bird, but our knowledge of the territory of the majority of lice in general is lamentably small. In some birds, such as the common mallard, there is one head louse (*Anatoecus*) and one wing louse (*Anaticola*), but in other birds there may be two or more genera occupying the same habitat. In the game-birds, for instance, there are two genera apparently adapted to life on the wings.

The Mallophaga we have just been discussing belong to the superfamily Ischnocera (Plate XXII). The majority of birds also harbour one or more species of genera belonging to the other superfamily, the Amblycera. The members of this superfamily have, in general, become less closely adapted to particular habitats on the bird's body. They are nearly all fast runners and probably move freely all over the host's body, and are not specialised for life on particular feathers. This absence of specialisation results in less well marked divergence, and the Amblycera are thus divided into far fewer genera than the Ischnocera. Using the term genus in its broad sense the Ischnocera are represented by about forty genera on British birds and the Amblycera by twenty-two. Again, if the nine genera found on the British game-birds are considered, we find that six of these belong to the Ischnocera and only three to the Amblycera. It is usually believed that the Amblycera have retained more of the habits and hence the morphological characters of the primitive ancestral Mallophaga. The most specialised character of the Amblycera

is the fold of the head, which envelops the antennae, and is probably a modification to protect these structures when the louse is moving rapidly through the feathers. A somewhat similar device is found in several other groups of ecto-parasites.

Two unusual ecological niches have already been mentioned—the throat-pouches of pelicans and cormorants occupied by the genus *Piagetiella* and the quills of the wing-feathers of the curlew by a species of *Actornithophilus*. The fact that these two are members of the less specialised Amblycera suggests that the occupation of the two niches is comparatively recent. The limited distribution of the pouch-louse within the order Pelecaniformes and of the quill-louse within the order Charadriiformes also supports the idea of a relatively recent colonisation of these two habitats.

Many of the problems confronting systematists are caused by animals leaving their original ecological niche in favour of another. They subsequently develop characters which adapt them to their new environment : these are superimposed upon, and more or less obliterate the original characters which would form the basis for their scientific classification. The flamingoes probably illustrate a case of this kind. They are placed by most ornithologists with the storks and herons, but by a few with the geese and ducks. There are convincing arguments to support each theory. The evidence provided by the Mallophaga on the systematic position of these long-legged ducks or duck-billed storks will be discussed later. Our knowledge is still insufficient to enable us to recognise all the genera of Mallophaga which have possibly changed their ecological niches, but there seems little doubt that this has happened in the case of one genus on the passerine birds. The head louse (*Philopterus*) of passerine birds is a typical inhabitant of the head niche—with a short round body and large head (as in Plate XXI). The starlings, however, lack a typical passerine head louse, but a species (Plate Ia) is found on the head which resembles it in general body form. A detailed examination of this species shows that it is, in fact, more closely related to another genus of body louse with a small head and a more elongated body, also found on the passerines. It is tempting to speculate that the original passerine head louse on starlings became extinct, for some unknown reason, and that the empty ecological niche was filled by members of another genus which have now assumed the general body form of a typical head louse.

Convergent and Parallel Evolution. The case just described is an example of convergent evolution. That is to say, a louse which is not closely related by recent common ancestry to other head lice has assumed similar characters in response to the same environment. Their resemblance thus indicates a similar history rather than a similar ancestry. Problems caused by convergent evolution may be responsible for many of the difficulties in the classification of the Mallophaga. Sometimes it is relatively easy to unravel these relationships, but if sufficient time has elapsed to enable the new occupant to adapt itself along closely similar lines so that it comes to resemble the original inhabitant of the niche, mistakes can easily be made. It is consequently difficult to decide which characters in the louse indicate relationship or derivation from a common ancestor, and which are developed as a result of living in the same environment. On many birds the lice belonging to different genera will show a number of similar characters. Some of these, without doubt, are developed as a response to the type of feathers forming the plumage of the host. The lice living on birds with iridescent feathers, for instance, sometimes have a thicker exoskeleton with a sculptured or pitted surface.

Another factor which may be responsible for some of the present confusion in the classification of the Mallophaga is so-called parallel evolution. This term is used to describe a case where two primitive stocks of lice, after diverging, have evolved along similar lines. Parallel evolution is, therefore, the independent acquisition by related groups of similar characters during their evolution. In contradistinction, convergent evolution is the acquisition of similar characters by unrelated groups in response to a similar habitat—the whales and the fish being a well known example. It is often difficult for the parasitologist to decide whether two groups of species are strikingly alike because they are close relatives or whether the likeness is due to parallel evolution.

Discontinuous Distribution. Discontinuous distribution is a term used to describe populations of animal species which are divided from one another by large geographical areas in which their own kind is totally absent. It is believed that many animals which once had a continuous range over a wide geographical area, such as Europe, have become extinct in parts of this range, leaving isolated populations here and there. Since isolation is an important factor in species formation (see p. 138) these animals may evolve into new species or even new genera.

On the other hand if the extinction of the intervening populations is a recent phenomenon and, if at the time of their isolation, the species was for some reason stable in the evolutionary sense, there will be a clear case of discontinuous distribution. Although the term is generally used in connection with free-living animals it can equally well be applied to the host distribution of permanent parasites. It can also be applied to the distribution of genera as well as species, for some genera are confined to specific geographical areas, whereas others show a world-wide distribution. The distribution of certain genera of Mallophaga can only be explained by assuming that these are stable genera which were once found on all birds, but have now become extinct on some orders. The genus *Laemobothrion* is found on the storks, the rails and the hawks; *Colpocephalum* is found on eleven out of the twenty-seven orders of birds, ranging from pelicans to passerines. Thus, the species of these genera must have remained relatively stable throughout a vast expanse of geological time. It is generally accepted that most of the present families of birds were in existence by the Upper Eocene, some forty-five to seventy million years ago, and such a widely distributed genus as *Colpocephalum* must have already been living on the ancestors of these families.

The Species and Host Specificity. If we return to our expert with another louse he can tell us not only that it is a parasite of a game-bird, but also that it came from a partridge and not a pheasant. In other words many birds have host-specific lice (see p. 43). Occasionally it is easier to distinguish two lice from each other, than to separate their respective hosts : the common and arctic terns, which are often confused, harbour species of lice which, in the males at least, can be separated with ease. In other cases one species of louse may be found on two or more related birds.

Host specificity in the Mallophaga, at least in some cases, is now firmly established. The lice of parasitic birds such as the cuckoo clearly demonstrate this fact. The cuckoo is reared by foster parents and their lice have ample opportunity for passing to the young bird. This does, in fact, occasionally happen : two specimens of a louse normally infesting a passerine bird were found on a young cuckoo, probably still being fed by the fosterers. If there were no host specificity the lice of the foster parents could have established themselves on the cuckoo and might even have replaced the original cuckoo lice. If this happened the

cuckoos of the British Isles would have no particular species of lice, but they would be parasitised by a variety of passerine-infesting species. This however is not the case. The adult cuckoo in England is infested by three species of lice belonging to the genera *Cuculoecus*, *Cuculicola* and *Cuculiphilus*, which, as their names imply, are true cuckoo-infesting genera found on species of the cuckoo family throughout the world, but not on the Passeres. Thus, although the lice of the passerine foster parents have ideal conditions for transference—continuous contact and no competition—the host specificity already developed makes establishment on the new host impossible. There is no satisfactory explanation of how the cuckoo acquires its normal lice. In most birds the lice can pass from the parent to the young in the nest, but in the case of the cuckoo contact between individuals takes place only during mating, and it must be presumed that the lice are usually transferred at this time. Transport by louse-flies (further discussed below) in the cuckoo's winter quarters may be another method by which lice are passed from adult to young birds.

For dispersal and survival the lice must pass from individual to individual of the same species of bird host. This may take place during mating, brooding of the young, roosting of gregarious species and by the use of common dust baths. On the death of the bird the lice are doomed to extinction unless they can transfer themselves quickly to another individual, for the lice soon become torpid without the warmth of their host. As the bird begins to cool the lice come to the surface of the feathers and will leave them for any warm or rough-textured object. This desire to leave the dead and now unattractive body of their late host probably accounts for the many recorded cases of "phoresy" (see p. 18) among the Mallophaga. Chewing lice have frequently been found attached to louse flies (tail-piece p. 157) and have also been recorded once on a flea, three times on mosquitoes, once on a *Haematobia* (a blood-sucking fly), a dragon-fly, a bumble bee and a butterfly—this last record by Kirby and Spence (1826) seems to be the earliest mention of phoresy in the Mallophaga. In the first four cases, the lice had attached themselves to another parasite off the same host; in the last three, the louse had probably boarded the insect when it had alighted for a few minutes on the corpse. An interesting case of phoresy was observed in the Shetland Isles one summer, where most of the starlings were found to be infested by feather lice and louse flies. One starling examined immediately

after death, had seven lice attached to the inside of the webs of some of the left wing feathers, and eight in a similar position on the right wing, making fifteen in all. The bird was wrapped in a piece of cloth and two hours later immersed in chloroform fumes to kill the ecto-parasites. When it was shaken out over a piece of white paper, eight of the lice fell out and one louse-fly (*Ornithomyia fringillina*); the remaining seven lice were found clinging to the abdomen of the fly. These seven lice must have attached themselves to the fly after the death of the host, using it as a lifeboat for escape in the emergency. If the louse-fly in such circumstances finds another starling, the lice are saved, but as the fly is less host-specific than the Mallophaga, they must often find themselves transferred to a different species of bird, on which they die, probably from starvation—the lifeboat has transported them to a desert island.

Other opportunities for lice to pass to hosts of a different species are not frequent under natural conditions. The lice of brood parasites such as the cuckoo have already been discussed. Another normal association is that between predator and prey, and hawks and owls are sometimes found harbouring a few lice, which could only have come from a recently eaten victim (Plate VI). Such stragglers probably do not survive long. Dust baths may be another method by which lice are transferred, for where chickens and sparrows use the same dust baths, the latter on examination have been found with a few specimens of chicken lice. In captivity and under domestic conditions there are naturally frequent occasions for lice to pass to new hosts.

Lice do not normally leave the living bird and they are only rarely found away from their hosts, except in the nest where they have been seen crawling over the eggs and in the nesting material.

Some of the factors which prevent establishment on a new host, even if the difficulties of transport are overcome, have already been discussed, (p. 124). These include the physical structure of the feathers which may make the movement, clinging, feeding and egg-laying of the louse difficult or impossible, the chemical composition of the blood and feathers which may be lethal, and the temperature differences which may affect the development of the eggs and nymphs of the strange louse. Apart from these factors, the immigrant louse must face the competition of the normal louse population already well established and better adapted to the environment on its own host. Furthermore, the establishment of an immigrant louse species on a new host naturally requires the presence of individuals of both sexes or a fertilised female.

Establishment on strange hosts must have become progressively more difficult as the louse became more specialised and more closely adapted to the feathers and other features of the environment afforded by the particular kind of bird on which it lived. Furthermore, as the birds diverged from each other during their evolution the environment of the lice on different groups of birds diverged concurrently. In this way host specificity becomes more and more extreme, each change in either the louse or the bird making the interchange of lice more unlikely.

The actual barriers which stand between a louse and a new host, including the development of host specificity, have resulted in the extreme isolation of the populations found on any one host species. These are analogous to populations of free-living animals found on oceanic islands. Transference of other species from the mainland or other islands is difficult and infrequent, and should this occur the competition from already well established species, not to mention lack of adaptation to the particular island environment on the part of the new arrivals, makes survival unlikely. It is generally believed that isolation favours the acquisition of new characters. If these characters prevent or discourage interbreeding between the two isolated populations a new species will result, and the two populations will not re-unite if break-down of their isolation subsequently enables them to mingle with one another again. This "speciation by isolation" probably accounts for the large number of species of Mallophaga now existing. The fleas, in which isolation of populations is far less complete, have developed many fewer species. In some genera of Mallophaga parasitising one order of birds, each species of bird harbours a distinct species of louse; in other cases a species of louse may be found on two or more closely-related birds. Some of these may be distinguished from each other only by small differences in size, in the characters of the male genitalia, or in the arrangement of the spines and hairs; females of closely-related species are often indistinguishable.

General Classification. It is now possible to summarise the evolutionary trends which have been responsible for the great number and diversity of forms found in this group of ecto-parasites. As we have seen, the Mallophaga are most probably derived from free-living ancestors which also gave rise to the Psocida or book-lice. The nearest living relatives of the feather lice are the Anoplura or sucking lice of

which *Pediculus humanus*, the human louse, is a well-known example. The sucking lice, which are found only on mammals, feed solely on blood, their mouth-parts being highly modified for piercing and sucking. The Mallophaga and the Anoplura are classified as suborders of the same order—Phthiraptera—thus showing the relationship between the two groups. The primitive ancestral Mallophaga must have split at an early period into two stocks which evolved on different lines, and which gave rise to the two distinct superfamilies, the Amblycera and Ischnocera (Plate XXII). The early Mallophaga, especially the Ischnocera, occupied the different ecological niches found on the bodies of their hosts, and became specialised and adapted for the characters of each niche. This, as we have seen, meant considerable modifications in the external morphology (Plates XXI and XXIII), involving many superficial distinctions, although the characters of the internal anatomy and basic morphology of the Ischnocera are mostly very similar. This last fact suggests that evolution of the basic Ischnocera type was relatively rapid and took place before their occupation of the different ecological niches, to which they subsequently became adapted. Possibly the primitive birds had a more uniform feather covering, somewhat similar to that of the ostriches and rheas, which did not provide the different ecological niches present in the more recent orders. This is partly confirmed by the Mallophaga of these present-day primitive birds which present only one generalised type, none being specially adapted to the neck or wings. The basic similarity of the Ischnocera, in spite of their superficial differences, makes the classification into families difficult, and the present unsatisfactory arrangement will not be discussed here.

ORDER

PHTHIRAPTERA

SUBORDER

MALLOPHAGA (chewing lice)

ANOPLURA (sucking lice)

SUPERFAMILY

AMBLYCERA

ISCHNOCERA

For scientific purposes the birds are classified or divided into groups or orders, and those characters which affect the louse, such as the minute structure of the feathers, are generally uniform throughout the order. Consequently the lice which occupy an identical ecological

niche on hosts belonging to one order are generally very similar in character, and fall naturally into distinct genera. Thus as a rule all the head lice parasitising one order of birds such as the raptors (Falconiformes) belong to one genus (*Craspedorhynchus*) and all the wing lice to another (*Falcolipeurus*).

As the evolution of the birds lost its initial momentum and slowed down, the character differences which affected their Mallophaga must have been greatly reduced. The waders, gulls and auks, which together comprise the order Charadriiformes, show great diversity in habits and general body form, such as legs, beak, and size, but the environment they provide for the parasite—for example the physical and chemical composition of the feathers and blood—is probably constant throughout the order. Even if lice become isolated on one species of bird, or group of species, within this order they are not subjected to any violent change. This results in the development of only small constant distinctions, in other words, specific differences. A number of these species makes up the genus distributed throughout the order. Even when a group of closely related hosts appear to provide the parasites with an exactly similar environment, the lice on each host may be distinct species, differing in non-adaptive characters—often the male genitalia—which have developed as the result of isolation and time.

The isolation of lice *within* an order of birds has occurred much later than the isolation *between* orders—hence the lice of gulls and plovers differ from each other less than the lice of ducks and plovers.

Many birds are parasitised by four or five species each belonging to a different genus, and in addition may harbour two or even three species of one of these genera. These latter species may differ in small ways only, such as the arrangement of hairs on the abdomen, or by some character of the male genitalia, or the presence or absence of enlarged antennae in the male.

This is, of course, a highly over-simplified picture of the process of evolution in the group. In reality it has become modified and the lines obscured by various causes which will be further discussed on pages 142-145, but until we have more information on the distribution, morphology, biology and genetics of the group no definite conclusions can be reached. However, these tentative suggestions may serve some useful purpose in demonstrating the complexity of the many factors which have influenced the evolution of the Mallophaga. "By reason of their subtlety, intricacy, crossing, and interfering with one

another, and the apparent resemblance they have among themselves, scarce any power of the judgment can unravel and distinguish.”

PHYLOGENY OF HOST AND PARASITE

The evolution of the birds, in comparison with many other groups of animals, is believed to have been rapid. The earliest known bird—or perhaps feathered reptile would be a better description—is represented by a fossil (*Archaeopteryx*) from the Jurassic rocks some 120 million years old; but by the Upper Eocene, some 60 million years later and between 40 and 70 million years ago, the fossil record shows that most of the present orders and even families of birds were established. This relatively rapid divergence and the fundamental changes which took place have left few traces of the primitive arrangements of bones and muscles, characters upon which relationships in the vertebrates are mainly based. This, together with the paucity of the fossil record, due to the fragile nature of the bones of birds, has left the student of bird evolution largely groping in the dark. It would be of the utmost value, therefore, if the present distribution and relationships of the Mallophaga could throw some light on the phylogeny (or evolutionary relationships) of their hosts, the birds. The course of evolution in the Mallophaga has resulted in related bird hosts harbouring related Mallophaga. It has been shown, for instance, that the head lice of all the waders are closely related species of one genus. Can we make the reverse deduction and affirm that the hosts must be related if the parasites are related, and perhaps convince the ornithologist that relationships between the parasites can be a fruitful and reliable source of evidence for relationships between the hosts?

The flamingoes (Phoenicopteridae) provide the classical example of the usefulness of such deductions. In modern classifications, as we have seen, these birds are usually placed with storks and herons (Ciconiiformes), more rarely with swans, geese and ducks (Anseriformes). The flamingoes are parasitised by species of three genera of feather lice (*Anatoecus*, *Anaticola*, and *Trinoton*) which are found elsewhere only on the Anseriformes. The species parasitising the Ciconiiformes, on the other hand, belong to different genera and are quite distinct from any found on the flamingoes or the Anseriformes. The most likely explanation of the presence of three duck-infesting genera on the

flamingoes is that these genera were already established on an ancient Anseriformes-stock before it gave rise to the flamingoes on one hand, and to the modern ducks, geese and swans on the other. This would mean that the flamingoes are more closely related to the ducks and geese than to the storks and herons, and, hence, should be included with the former in the Anseriformes and not in their more usual position with the Ciconiiformes. The ostrich (*Struthio camelus*) of South Africa and the rheas (*Rhea americana* and *Pterocnemia pennata*) of South America provide a similar case. In modern classifications it is assumed that these birds are not closely related and hence they are placed in separate orders, the Struthioniformes and the Rheiformes. Both the ostrich and the rhea, however, have closely related species of a genus of Mallophaga (*Struthiolipeurus*) which is found on no other bird. This strongly suggests that the rheas and ostriches must have shared a common ancestor, also parasitised by the genus *Struthiolipeurus*, and that this genus was in existence in its present form before the separation of the continents of S. Africa and S. America.

These two examples are instances where the evidence from the parasites apparently conflicts with the evidence from the anatomy of the birds. Has the evidence been incorrectly interpreted by the ornithologist or the parasitologist? Here we can discuss only how the latter may have been mistaken, and for this it is necessary to consider the possible factors which may have influenced and obscured the original evidence, and thus misled the parasitologist.

Discontinuous distribution. We have already discussed (p. 134) the discontinuous distribution of certain genera of Mallophaga. If we are trying to deduce relationships between different birds from the fact that they are parasitised by the same genus of Mallophaga, it is at once obvious that genera which show a discontinuous distribution may be misleading. Passerines and game-birds in this country are both parasitised by species of the genus *Menacanthus*, but this does not suggest a close relationship between the two orders, for we also find species of this genus on the tinamous (Tinamiformes) of S. America, the plantain-eaters (Musophagidae) of Africa, as well as the woodpeckers of this country, while related genera are found on other orders. This suggests that *Menacanthus* was once widely distributed throughout the whole class of birds, but is now extinct on most orders.

Primitive genera. In the superfamily Ischnocera there are some genera or groups of genera, which have a primitive type of head (Plate XXIIIa) and which have not become adapted to any particular habitat on the bird nor to the feather structure characterising any particular group of birds. Examples of these less specialised genera are found on most of the orders, and naturally appear more closely related to each other than to those genera which have become highly specialised. Such primitive genera cannot, therefore, be used in the consideration of relationships between birds.

Secondary infestations. It is rare, as we have already seen (p. 135), for a louse from one bird species to be transferred to another, and if this does take place, the host specificity of the louse makes establishment on the new host difficult or impossible. Have there been, nevertheless, cases in the past where a louse has become established on a new and different host and there developed into a new and different species? The answer is almost certainly in the affirmative. Secondary infestation may explain the presence of one peculiar louse species found on the British skuas (Stercorariidae). The skuas are related to the gulls and belong to the order Charadriiformes. They are parasitised by species of lice belonging to four genera found throughout the Charadriiformes including the gulls. In addition, three of the species of skuas which visit this country are parasitised by a louse belonging to another entirely unrelated genus, which is otherwise peculiar to the petrels (order Procellariiformes). This strange distribution can be explained by assuming that lice from a petrel managed to transfer to a skua, became established and gradually developed into a new species. Skuas in this country are known to feed on the dead bodies of at least one petrel, the manx shearwater, which suggests a possible way in which the original transfer might have occurred. Because the event has presumably taken place in relatively recent times it is still possible to deduce what has happened. The discovery of one species of petrel louse on the skuas does not tempt us to suggest a relationship between the skuas and the petrels—any more than some future etymologist would suggest a relationship between English and Tamil because the word “curry” occurs in both languages. However, the petrels are further parasitised by a genus which is also found on the gulls and throughout the Charadriiformes. This group is one of the head-lice genera, which tend to become specialised to a particular host, and are unlikely to be relics of a universal distribution.

It may well be that there are certain superficial resemblances between the external characters of gulls and petrels due to adaptation to life at sea, which has favoured a certain limited interchange of lice. The possibility of such secondary infestations—whether ancient or relatively recent in origin—must always be borne in mind when considering the distribution of a genus of feather lice in relation to host affinities.

Convergent and parallel evolution. The classification of birds, which is intended to reflect their true relationship, is based mainly on the characters of the muscles and skeleton—structures which do not directly affect the parasite. If two unrelated groups of birds, perhaps in response to the same environment, developed similar external characters, then the adaptations to these characters forced on their Mallophaga might produce in the latter a superficial resemblance to one another even though they were really not closely related. This type of convergent evolution in the parasites can suggest false relationships between the hosts. For example, *Philopterus*, a head louse genus parasitising the Passeriformes, is mostly very uniform in character. Certain species, however, have developed a line of thickening on the front margin of the head, and have a different arrangement of head sutures and of the struts supporting the mouth-parts. Lice with this type of head have been found on eleven species of Passeriformes belonging to nine different families and also on the family Momotidae (the motmots) usually placed in the order Coraciiformes. Does the similarity of these Mallophaga suggest that the families of birds on which they are found are more closely related to each other than to any other of the families of passerines? There is no evidence of this from ornithological sources, but it may be that the bird species all have some character in common: the head feathers of some, at least, of the hosts are hard and shiny, showing iridescence. The species of the genus *Philopterus* are sedentary and highly adapted to the particular feathers on which they move and feed. Any change in feather structure will tend to affect the front of the head which is used to push through the plumage, and also the mouth-parts and their supporting structures used in grasping and feeding. In the case of these species from the motmots and some of the passerines, therefore, it seems possible that they have responded with similar modifications to a similarity of the feathers, possibly a hardening of the surfaces. The resemblance between these lice is, therefore, due to convergence in response to a similar environment. In such cases it is easy

to draw false conclusions concerning the natural relationship of the hosts.

Parallel evolution as we have seen (p. 134) can give rise to a false impression of close relationship. The occurrence on two groups of birds of similar, but in fact not closely related, genera naturally does not indicate relationships between the hosts.

Lack of knowledge. The prudent parasitologist will do well also to admit his ignorance. Ignorance of distribution, biology, ecology, genetics and morphology accounts for our inability to answer many questions. At present we are unable to distinguish which of the various causes may have been responsible in any particular case. Through lack of morphological knowledge errors may be made in the classification of the lice themselves and thus any deduction concerning the relationships of their hosts will be invalidated.

Evidence from other parasites. It is obvious that any supposed relationship between birds which is deduced from the relationship between their Mallophaga will be greatly strengthened if the case can be supported by evidence from other parasites. The ornithologist who is altogether sceptical of the parasitological evidence will nevertheless find it difficult to explain the presence of closely related species of feather lice, parasitic worms and mites on two birds which he does not consider are related. This is the case with the ostrich and rhea. As we have seen these two birds are now placed in different orders by the ornithologist. Nevertheless, their feather lice belong to the same genus (*Struthiolipeurus*) which is found on no other birds, they are parasitised by closely related subspecies of the same tapeworm (*Houttuynia struthiocameli*), which is not found in other birds, and the same two species of mites (*Paralges pachynemis* and *Pterolichus bicaudatus*) occur on both hosts. The presence of these parasites belonging to widely separated classes cannot be explained away by the theories of discontinuous distribution or of parallel and convergent evolution; nor is it likely that two birds separated by the Atlantic Ocean could have become infested with each other's parasites.

It is necessary for the workers on the various groups of parasites to co-operate and to present to the ornithologist as complete a picture as possible of the parasitic fauna of the birds. It is also necessary to emphasise which part of the evidence is considered reliable and which may be misleading. This is particularly important in the case of parasites with

intermediate hosts, such as the flukes, which may show a false host specificity due to the common habitat and diet of their hosts (ethological specificity, p. 45).

In conclusion it can be said that as a general principle the relationships between the Mallophaga reflect those existing between their hosts. Birds with a doubtful systematic position cannot be placed on the evidence of their Mallophaga if only one genus of feather lice is available from which to draw conclusions, for this may be an ancient straggler or a relic. If, however, these birds harbour three or more genera common to the birds of another order this may be taken as strong presumptive evidence that the hosts in question belong to that order. The flamingos are a case in point. The ornithologist should accept the evidence from this source at least as a clue to relationship, just as he accepts anatomical evidence of bone loss or the arrangement of a muscle. Alone, any one point will not establish the position of a bird of doubtful affinities, but the total sum of such evidence from many sources may be overwhelming. In the future, when the feather lice as a group are as well known as the butterflies, the evidence from this source may be of great significance in the study of the origins, relationships and ancient distribution of various families of birds.

The student of Mallophaga, in this aspect of his work, can be compared to the palaeontologist. He delves into the past, not by quarrying in the rocks for fragments of bones, but by studying the morphology and distribution of these living fossils. As he pieces together the story of their evolution, he likewise unfolds the story of the evolution of the birds.

THE MALLOPHAGA OF THE BRITISH ISLES

The distribution of the Mallophaga is, in general, a host distribution, not a geographical one. The jackdaw, whether living in England, Scotland, Germany or Scandinavia is parasitised by the same species of lice. The Mallophaga of Britain are, therefore, the Mallophaga of British birds. For this reason there is little object in listing the feather lice of any specific geographical area; attention should be concentrated on the study of the louse fauna of a group of related birds, for such groups are the equivalent of the geographical range of free-living insects. This statement, nevertheless, needs qualification. There does



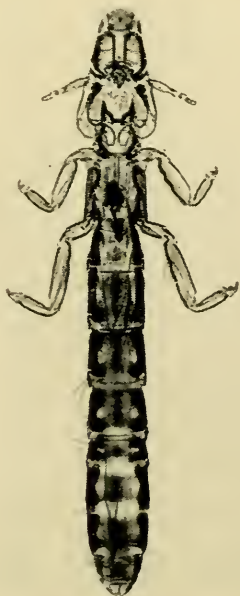
W. H. Pollen

a. *Cuclotogaster* sp. from partridge, showing primitive type of head



W. H. Pollen

b. *Quadriceps* sp. from little gull



W. H. Pollen

c. *Halipeurus* sp. wing louse from Manx shearwater ($\times 27$)



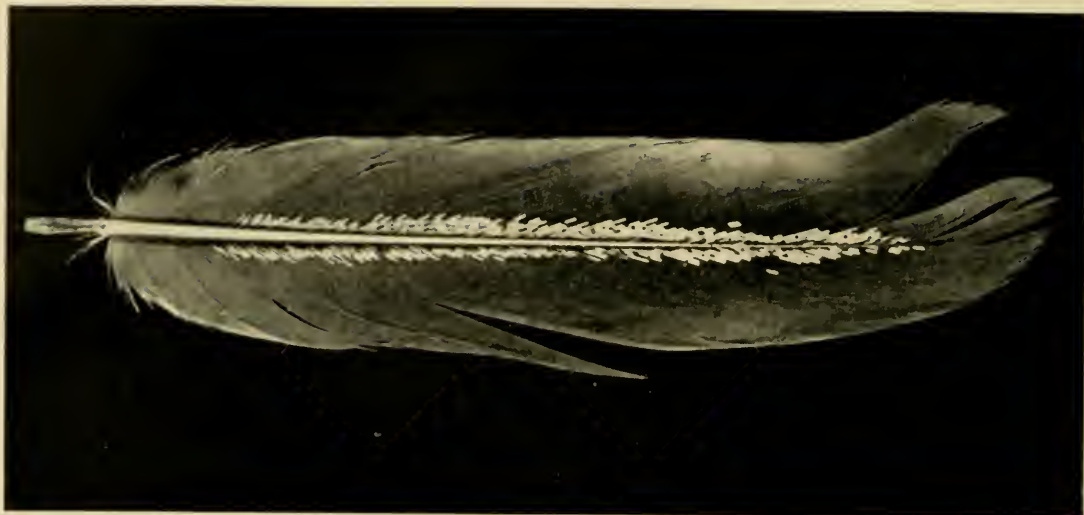
W. H. Pollen

d. *Ricinus* sp., from meadow-pipit ($\times 23$)

Plate XXIII

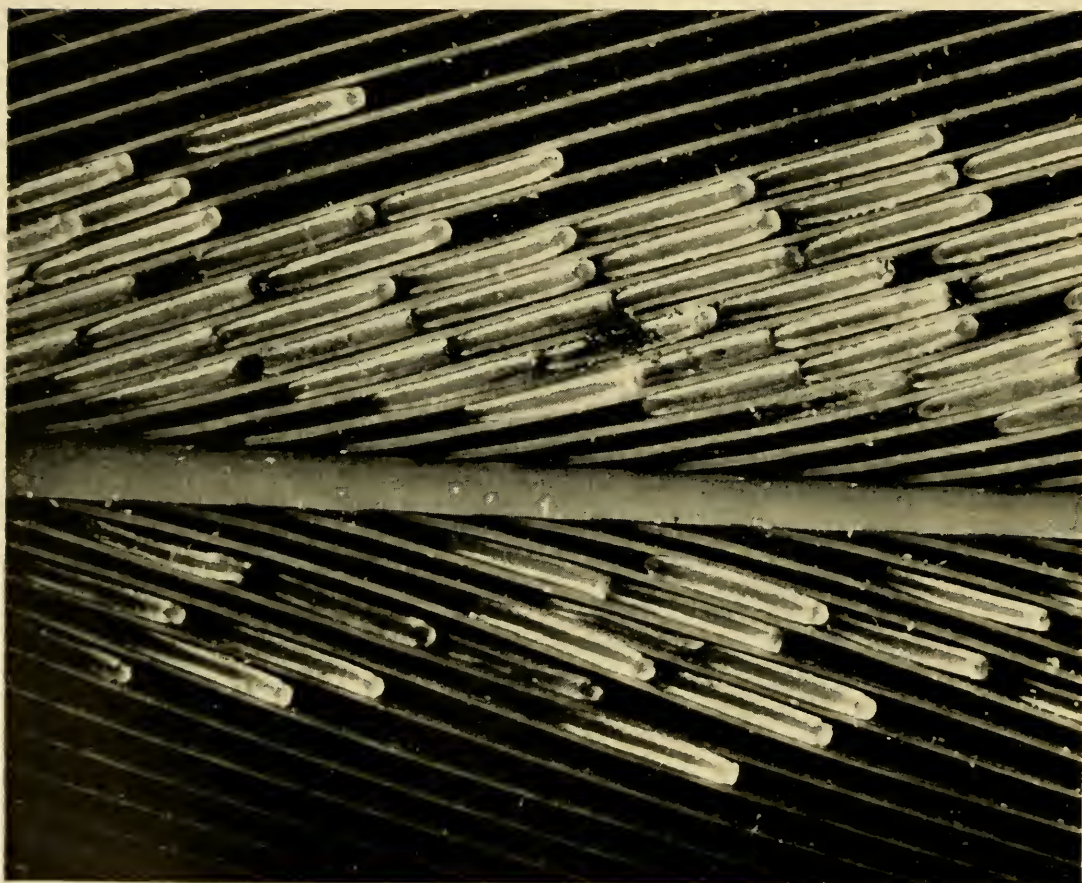
DIFFERENT TYPES OF FEATHER LICE

(a.—c. Superfamily Ischnocera; d. Superfamily Amblycera)



a. Secondary feather showing eggs ($\times 1.4$)

J. G. Bradbury



b. Close-up showing eggs lying between barbs ($\times 16$)

J. G. Bradbury

seem to be in some cases a true geographical distribution superimposed on the host distribution. A higher percentage of infested individuals may be found in parts of a bird's range, and certain species of lice seem to be absent from their host in some localities. The pouch-louse, found in all the pelicans (*Pelecanidae*), has been recorded from the related cormorants (*Phalacrocoracidae*) from the New World and Antarctic species, but never from those of Africa and Europe.

We have already seen that each bird species supports the representatives of a number of genera of feather lice; some birds may also harbour two or more species belonging to one genus. The sanderling has five, the rook may have six and one of the S. American tinamous is parasitised by the bewildering number of twenty-one species belonging to twelve genera and three families. Although many of the species of Mallophaga are found on more than one kind of bird it follows that there must be a large number of them in the world. Of these probably less than half have been named, and many not even collected. The number of species likely to be found on the 400 or so birds on the British list can only be estimated within wide limits, say 500—1,000. Again, a number of these still has no valid scientific name; even two of the lice from the common rook are undescribed and consequently are still nameless. There are few specialists working on the group, for it is of no medical and of little economic importance. Hidden as they are in the plumage of the bird, feather lice do not attract the immediate attention of the naturalist and few people even know that they exist. Moreover, they are difficult to collect, and when collected must first be treated and mounted on glass slides and then examined under the microscope. Species are distinguished from each other mainly by the details of the male genitalia, which for microscopic study must be dissected and mounted separately. When the louse is ready for identification it is first necessary to know whether it has already been described or named. This is not easy. The early authors—the first figures were published in 1668 by the great Italian biologist Redi—did not realise the importance of the small characters necessary for separating species, so that their descriptions and figures can only serve to identify the genus, and that sometimes doubtfully. Nor did the early authors always name the host from which they took the louse, or they recorded it from three hosts, which are now known to harbour three distinct species of lice. Lastly, the systematics of the Mallophaga are cursed by records of straggling feather

lice. A "new" species is described from a hawk, which in reality is a straggler from a wader, shot at the same time and put in the same collecting bag. If the original description is inadequate a species of wader louse appears in the literature, the host of which may never be found, and which naturally baffles the expert. It is like expecting an ornithologist to identify an exotic finch from an inadequate description coupled with the information that it was obtained in England—where its presence was solely due to an aviary door having been left open. Thus, there is a great deal of work to be done in the interpretation of the old names and the accurate re-description of these species, before many of the British Mallophaga can be named or descriptions of new species made.

The general classification of the Mallophaga has already been outlined (p. 139), and we can now discuss, in rather more detail, how this can be applied to the feather lice found on British birds. It must be emphasised that, for the reasons already considered, the present classification is far from satisfactory and will need drastic modification as our knowledge of the group becomes more extensive.

As we have seen, the suborder of the Mallophaga is divided into two superfamilies: the Amblycera and Ischnocera.

Reference has been made in the preceding pages to these two superfamilies, and it will have become apparent that they show considerable differences in habit and form (Plate XXII). The Amblycera, as we have seen, show less diversity in structure and are divided into a smaller number of families and genera. There are three families of Amblycera found on British birds, the Laemobothriidae, Ricinidae and Menoponidae.

The Laemobothriidae are represented in this country by one genus, *Laemobothrion*, found on hawks. This genus contains the largest of the Mallophaga, and at the present time has only been taken from the kestrel although from non-British records it is known to parasitise other hawks on the British list.

The Ricinidae is also represented in this country by only one genus, *Ricinus* (Plate XXIII) restricted to passerine birds of which the robin and the chaffinch are the common hosts. It is the largest of the species found on this group of birds, and the comparatively large shiny white eggs can often be seen in great numbers on the feathers of the neck and throat.

The Menoponidae (Plate XXIIa) contains a number of genera,

examples of which are found on all the British orders of birds. These genera do not differ greatly from each other and for the present are contained in the one family.

The Ischnocera, as we have already seen, are more specialised and adapted to particular environments, and hence show a greater diversity in their structure (Plates XXI and XXIII, a-c). This fact is reflected in their classification by the larger number of families and genera into which they are divided. The species found on British birds are contained in forty-three genera. No attempt will be made to give the characters of the families and genera, which is a detailed and specialised subject outside the scope of this book. The large number and anonymous state of the Mallophaga make it impossible to do more than mention some of the more interesting ones found on British birds.

PASSERIFORMES

Genera of Mallophaga recorded in Britain: *Colpocephalum*, *Myrsidea*, *Menacanthus*, *Ricinus* (*Amblycera*); *Brüelia*, *Sturnidoecus*, *Penenirnus*, *Philopterus* (*Ischnocera*).

In this country the passerine birds may be parasitised by species of any of these eight genera. Five others have been recorded from this order in the New World. The rook harbours five of these genera, which in Britain is the maximum for any one species of passerine, but they are not necessarily all found together on one individual. These lice illustrate the rather curious fact that the size of the birds in an order has no bearing on the number of different genera which may be found upon them. The Passeriformes have thirteen genera, the Struthioniformes (ostriches) only one. The passerine birds also illustrate another unexpected fact, namely that the genera containing the largest lice are not necessarily found on the largest hosts, despite the fact that there is often a correlation between the size of host and louse within a given genus. In *Ricinus* (Plate XXIII), a genus confined to the Passeriformes, the largest females may measure 4.5 mm. (about one-fifth of an inch) in length. Feather lice of a comparable size are found, amongst British birds, only on hawks, ducks, and fulmars, all of which are considerably larger than the robin and the finches which are the most usual hosts of *Ricinus* in this country.

APODIFORMES

Genera of Mallophaga recorded in Britain : *Dennyus*, *Eureum* (Amblycera).

The swifts are the only order of birds known from which no member of the superfamily Ischnocera has been recorded. They harbour species of two related genera of Amblycera, which are unlike those found on any other order of birds and confirm the isolated position of the swifts within the class Aves.

CAPRIMULGIFORMES

Genus of Mallophaga recorded in Britain : *Mulcticola* (Ischnocera).

The British nightjar has only one species of Mallophaga, a wing louse. Other kinds of nightjars found in the New World are, however, also parasitised by a head louse.

CORACIIFORMES

Genera recorded from the order in Britain : *Alcedoecus*, *Alcedoffula* (Ischnocera) from kingfishers; *Meropoecus*, *Brüelia* (Ischnocera) from the bee-eater; *Menacanthus* (Amblycera), *Upupicola* (Ischnocera) from the hoopoe. There are no records from British-taken rollers, but one genus *Capraiella* (Ischnocera) has been found on rollers from the continent of Europe.

This order is represented in Britain by one resident, the kingfisher and three vagrants, the bee-eater, the hoopoe and the roller. The kingfisher is parasitised by two closely related genera of Ischnocera but lacks Amblycera; these two genera are not closely related to those found on any other bird. The kingfisher is a case where the Mallophaga throw no light on the relationships of the host, but the feather lice found on the three vagrants mentioned above suggest that they are related to the Passeriformes.

PICIFORMES

Genera of Mallophaga recorded in Britain : *Menacanthus* (Amblycera); *Brüelia*, *Penenirmus* (Ischnocera).

The species of Mallophaga found on the British woodpeckers belong to genera also found on the passerine birds, which tends to

support Lowe's theory that the woodpecker should not be placed in a separate order. It has been suggested that if the habit of anting by birds helps to rid them of lice, the green woodpecker, as a frequent visitor to ants' nests, should be less heavily parasitised than the other woodpeckers; this has not been found to be the case.

CUCULIFORMES

Genera of Mallophaga recorded in Britain: *Cuculiphilus* (Amblycera); *Cuculicola*, *Cuculoecus* (Ischnocera).

The method of dispersal and other interesting points connected with the lice of the cuckoo, a brood parasite, have already been discussed. Another curious fact is that the Mallophaga of the cuckoo—superficially so like a hawk and also mobbed by other birds—belong to genera which are either the same or apparently closely related to those found on the hawks. At the present time we cannot say what the significance of this fact may be, but when considering the Mallophaga only, the parasitologist is reminded of the words of Pliny: "The cuckoo seems to be but another form of hawk."

STRIGIFORMES

Genera of Mallophaga recorded in Britain: *Colpocephalum*, *Kurodaia* (Amblycera); *Strigiphilus* (Ischnocera).

The members of this order in Great Britain are parasitised by only three genera of lice, one belonging to the Ischnocera, and two to the Amblycera. Owls, like hawks, may also have a temporary population of lice which have straggled from their prey. A short-eared owl from S. Uist was infested with five specimens of lice belonging to three different genera which must have come from a wader it had recently killed.

FALCONIFORMES

Genera of Mallophaga recorded in Britain: *Colpocephalum*, *Kurodaia*, *Laemobothrion* (Amblycera); *Degeeriella*, *Falcolipeurus*, *Craspedorrhynchus* (Ischnocera).

The British hawks are usually parasitised by two species of Ischnocera, one a typical head louse, the other belonging to a more primitive,

unspecialised genus; a third genus (*Falcolipeurus*) has only been taken from the golden eagle. The Amblycera are represented by three genera, and there is a fourth which has not been taken from British birds of prey. Two of these genera illustrate the kind of anomalous distribution which may bring the student of Mallophaga into conflict with the ornithologist, since one of them is also found on the owls, the other, as we have already seen, on the cuckoos.

In modern classifications the Raptores, owls and cuckoos are not considered to be related in any way.

CICONIIFORMES

Genera of Mallophaga recorded in Britain: *Colpocephalum*, *Ciconiphilus*, *Ardeiphilus* (Amblycera); *Ardeicola*, *Neophilopterus* (Ischnocera).

The two members of this order resident in Britain, the heron and the bittern, each have two species of lice. The plumage of the heron seems to offer no attraction for the Mallophaga, for it is a bird which seldom supports a large population and many individuals are altogether louseless. A head louse is absent, although one is present on other members of the order such as the spoonbill. One wing louse is recorded—a species that is flabby and pale in colour, due perhaps to the soft texture and light colour of the heron's plumage—and one member of the Amblycera. On the other hand the white stork, a vagrant to Britain, harbours species belonging to no less than four genera of feather lice.

ANSERIFORMES

Genera recorded in Britain: *Ciconiphilus*, *Holomenopon*, *Trinoton* (Amblycera); *Anatoecus*, *Anaticola*, *Ornithobius* (Ischnocera).

The ducks and geese in Britain are usually parasitised by four genera: one short and round in form and adapted to life on the head and neck, one flattened and elongate and living on the back and wings, while the other two genera belong to the Amblycera. One of these (*Trinoton*, Plate XXII) seems to be the fastest runner of all lice. It probably roams through the plumage and requires speed, not only to escape the bill during preening, but to be able to get well into the plumage in the case of a crash dive by the duck. The swans have, in

addition, species of another rather large genus (*Ornithobius*). It is interesting that this louse, as well as the one found on the wings, is pale in colour, as if to match the white plumage of its hosts. The head species has retained the usual brown colour characteristic of the members of the genus (*Anatoecus*) which parasitises all the Anseriformes.

PELECANIFORMES

Genera of Mallophaga recorded in Britain: *Eidmanniella* (Amblycera); *Pectinopygus* (Ischnocera).

The cormorant, the shag and the gannet each have species of only two genera, one belonging to the superfamily Amblycera and one to the Ischnocera (Plate XXIIb). It is interesting that there is no louse adapted to the head niche, and it may be that the short feathers of the head do not provide sufficient covering for the lice of birds which spend some time under water. The grebes and divers also have no head lice.

PROCELLARIIFORMES

Genera of Mallophaga recorded in Britain: *Austromenopon*, *Ancistrona* (Amblycera); *Halipeurus*, *Perineus*, *Trabeculus*, *Saemundsonia* (Ischnocera).

Mallophaga have been recorded from three of the resident British petrels—the storm-petrel, the manx shearwater (Plate XXIIIc) and the fulmar. The manx shearwater has five species of Mallophaga, one of which belongs to a genus of large species (*Ancistrona*). Species of this Amblyceran genus on related shearwaters (*Puffinus*) have been found with eggs and adults of a parasitic mite attached to their abdomens. The only other record of this mite (*Myialgopsis trinotoni*) is from the genus (*Trinoton*) found on ducks, geese and swans—the species of which are also among the largest of the Mallophaga.

PODICIPITIFORMES AND COLYMBIFORMES

Genera of Mallophaga recorded from the grebes in Britain: *Pseudomenopon* (Amblycera); *Aquanirmus* (Ischnocera). Genus recorded from the divers in Britain: *Craspedonirmus* (Ischnocera).

The British grebes and divers each have one characteristic genus of Ischnocera. These genera do not appear to be related to each other nor

to any other genus—which reflects the belief that the grebes and divers themselves are not closely related to each other, nor to any other living order of birds. This wholly supports the evidence obtained from a study of their tapeworms (see p. 193).

COLUMBIFORMES

Genera of Mallophaga recorded in Britain: *Colpocephalum*, *Hohorstiella* (Amblycera); *Campanulotes*, *Coloceras*, *Columbicola* (Ischnocera).

The British pigeons may harbour species of lice belonging to five genera, and one of these (*Campanulotes*) illustrates the correlation between louse size and the size of the host (further discussed below). Thus the three species of this genus found on the wood-pigeon, the stock-dove and the rock-dove are very similar, but that from the wood-pigeon is noticeably larger than those from the other two. Further, if a large number of specimens from the two latter hosts are measured, those from the rock-dove are found, on the average, to be smaller. The lice may, therefore, reflect some hitherto unrecorded differences in the size of the host.

CHARADRIIFORMES

Genera of Mallophaga recorded in Britain: *Actornithophilus*, *Austromenopon* (Amblycera); *Rhynonirmus*, *Lunaceps*, *Carduiceps*, *Cummingsiella*, *Quadriceps*, *Saemundssonina* (Ischnocera).

The members of this order, which contains the waders, gulls and auks, may be parasitised by species of any of eight genera of lice. The most interesting louse found on the waders is the quill-louse (*Actornithophilus patellatus*, Plate Ib) of the curlew. The information about this species is still incomplete, but from records of curlews examined in this country it is known that 44 per cent. have specimens of the quill-louse on their bodies, and of this 44 per cent., over half have holes in the shafts of the wing feathers. There is a remarkable symmetry in the position of the holes, and it is usual for the same quills to be attacked in both wings. If the seventh to the eleventh primaries are entered in the right wing, the seventh to the eleventh will also be entered in the left. The primaries on each side are also attacked in the same order: if the sixth to the ninth on the right wing have completed holes, with the beginning of a hole on the tenth, this will often be repeated in the

left wing. There is also symmetry in the position of the two holes on the opposite wings. Thus, in one curlew examined, the hole in the seventh primary on each side was 51 millimetres from the base, in the eighth primary 57, in the ninth 54, and in the tenth 57 millimetres. Some of the feathers may have more than one hole. The louse can hardly be credited with the human passion for symmetry, nor is it at all likely that specimens on one side of the bird know what transpires on the other. The answer is most probably that there is a correlation in moulting time between the two wings and that the louse attacks the feather at the earliest moment after its maturity and at the easiest place for boring the hole. The Mallophaga seem to feed on the feather caps left by the withdrawing papilla. The eggs, as in the case of the quill mite, are laid in spiral curves within the shaft; the young develop within the quill and again like the mite leave the quill before the moult is due. A great deal more information on the biology of this louse is needed, including such details as the condition both of the feathers attacked and those not utilised, and the time of year when the unhatched eggs and nymphal stages are found within the shafts. Anyone who has the opportunity of handling a dead curlew should look out for such points and record them. This louse has been taken from the wings of the curlew, both in this country and America, but from no other wader; all birds, especially waders, should be examined for the minute holes on the shafts of the primaries and secondaries which are made by the quill lice.

The head lice of three of the British terns are a good illustration of the frequent correlation found between louse size and host size. The smallest louse is found on the little tern, the largest on the sandwich tern and a louse intermediate in size on the intermediate sized host, the common tern. What accounts for this correlation in size? There may be a close relationship between size of feather parts and size of bird, and this might directly affect the dimensions of the louse. At the present time little is known about the differences in feather structure of related species of birds.

RALLIFORMES

Genera of Mallophaga recorded in Britain *Pseudomenopon*
(Amblycera); *Rallicola*, *Incidifrons*, *Fulicoffula* (Ischnocera).

The British rails may be parasitised by three or four species of lice. The large *Eulaemobothrion* has never been found on any of the British

rails, but has been taken from the coot in Morocco, India and the U.S.A. the moorhen in Uganda and the Sudan. This is an example of geographical as opposed to the more usual host distribution of a parasite.

GALLIFORMES

Genera of Mallophaga recorded in Britain: *Menacanthus*, *Amyrsidea*, *Menopon* (Amblycera); *Cuclotogaster*, *Lipeurus*, *Oxylipeurus*, *Lagopoecus*, *Goniocotes*, *Goniodes* (Ischnocera).

The game-birds of Britain harbour species of nine different genera of Mallophaga. Not all of these are found on any one of the game-birds, five being the greatest number of species recorded from a single host. Pheasants, because they are frequently reared under hens, may be infested with lice of their foster-parents. These birds, introduced into Britain probably by the Romans, harbour exactly the same species of Mallophaga as the wild pheasants of Afghanistan—a case where the parasite is unaffected by the geographical locality in which the host is found. The same may be said about the domestic hen which harbours a similar species of *Goniodes* to the wild jungle fowl. The fleas, on the other hand, which infect game birds in Britain, are species which they have acquired in temperate climates.

CONCLUSION

It will have become evident while reading these pages that our ignorance of the feather lice is abysmal. What we do not know far exceeds what we know. Their biology particularly requires investigation. Lice cannot be kept alive off the host except in an incubator at the right temperature and humidity, and a supply of fresh feathers of the appropriate host must be available. Providing these conditions can be fulfilled the solution of a large number of problems could be attempted. These relate to life history, food preferences, host specificity, and the louse in relation to its environment in general. More information is also needed concerning the morphology, distribution and the particular habitats of the lice on any one bird, distribution of lice on the same host species in different geographical areas, and distribution on the different host species within one order of birds. The student who intends working

on the Mallophaga should take warning that he will be tried almost beyond endurance by the paradoxes and complexities which beset his subject but he will also find, in the dual and inter-related aspect of insect and bird, an infinite fascination.



Phoresy; louse-fly transporting feather lice (x 10)

PART THREE

INTRODUCTION

If I should count them they are more in
number than the sands.

PSALM 139:18

IT WOULD have been most satisfactory if, in Part III, we could have supplied a complete check list of the parasites of British birds. Such compilations make dull reading but from the practical, scientific angle would provide a valuable and badly needed piece of work. The chief bar to drawing up a check list of this type is the vast numbers of scattered records of parasites recorded *abroad* from birds on the British list, coupled with the paucity of genuine records from birds in Britain. A list restricted to the latter parasites would be altogether misleading and practically valueless, even if the species likely to occur in this country were included, whereas the compilation of the former list represents a herculean task few would feel inclined to undertake—certainly not the authors.

The following chapters are, therefore, intended to give the reader a rapid survey of the main groups of bird parasites in Britain and to point the way to further ecological and systematic work, and, in particular, to emphasize the need for further collecting and the accurate identification of specimens.

CHAPTER 9

PROTOZOA

There is nothing funny in the thought that even man, who was made in the image of God, bears about in his vital organs various forms of loathsome creatures, which riot on his fluids and consume the very substance of his tissues.

PHILIP HENRY GOSSE

ANIMALS which perform all the functions of life within the compass of a single cell outnumber all the other animals by a million to one. These single-celled organisms, which are known as Protozoa (Fig. 2), vary considerably in size but the largest are only just visible to the naked eye. The simplest forms like amoeba consist of a blob of protoplasm containing a nucleus. In a fluid medium they sometimes assume a spherical form and under the microscope each is somewhat reminiscent of a fried egg—although the nucleus is colourless, not yellow like the egg yolk. In some of the parasitic forms, such as the Coccidia, the body has a spherical or ovoid shape which lies motionless within the cytoplasm of the host's cells. On the other hand many types which live in lymph or blood and other body fluids vary considerably in appearance and structure. They are endowed with the power of active movement like the free-living Protozoa which swarm in water and damp situations.

It is generally believed that the parasitic forms are derived from free-living ancestors, and as almost every higher animal harbours one or more species of parasitic, commensal or symbiotic Protozoa, the number of dependent forms is large. Although only single-celled organisms, they display many of the adaptations to the parasitic mode of life which are found in multi-cellular animals. Thus, in some forms special organs of attachment are developed. A good example of this type of structure is found in the sucking disc of *Giardia* (Fig. 2, g & h)—flagellate which

attaches itself firmly to the surface of the intestinal cells of vertebrates, including birds such as herons, shrikes and avocets. In certain groups the mouth (cytostome) is frequently missing although this organ is present in related free-living forms. Cyst formation is also characteristic of parasitic Protozoa, such as *Eimeria* from the grouse. Cysts provide the chief means of transference from host to host, since they protect the enclosed parasite against the influence of the external environment and resist the action of the digestive juices of the stomach. These properties enable the protozoon to gain access to the internal organs of the bird when swallowed with food and water. An enhanced power of reproduction involving multiple fission instead of the more usual binary fission is also a typical feature of the parasitic forms. Complicated life-cycles, with alternating vertebrate and invertebrate hosts, are found in many Sporozoa and Flagellata from birds. The development of host specificity and increased virulence are also characteristic of numbers of these organisms—two phenomena which have been considered in previous chapters. The parasitic Protozoa of birds (Fig. 2) belong to the three classes, Sporozoa, Mastigophora and Rhizopoda, of which by far the most important types are those grouped in the Class Sporozoa.

CLASS SPOROZOA

The Sporozoa are exclusively parasite and live and feed in the cells and body fluids of other animals. In the absence of a mouth the food—which is in solution—passes into the body in liquid form and is absorbed by osmosis. The proteid which is in solution is absorbed in liquid form. During much of their life-cycle Sporozoa lack organs of locomotion. They are also characterised by a highly specialised type of reproduction. At some stage of their development they produce cysts (oocysts) within which the infective forms called sporozoites are found. In the *Coccidia* these are carried to new hosts within this protective envelope.

The life-cycle is complicated, with alternating sexual and asexual phases. In the asexual phase, instead of simple division into two separate individuals the nucleus of the growing parasite, known as the trophozoite, divides repeatedly. Each resulting nucleus becomes surrounded by a portion of the cytoplasm, and the body of the parasite, now known as a schizont, breaks up into daughter individuals. The

number of these daughter individuals corresponds to the number of nuclei present. This process is known as schizogony.

An alternation of hosts frequently occurs, and in such cases one stage of the life-cycle may be passed in an invertebrate and another in a vertebrate animal.

ORDER COCCIDIA

In temperate climates Coccidia cause a greater loss to domestic poultry, pigeons and game birds than any other group of Protozoa. They are also common parasites of wild birds. Shipley pointed out that the name is somewhat misleading since the public are apt to think of a Coccidium as a bacterium or *coccus*, whereas it no more resembles this organism than a crocodile resembles a crocus. The best known family is the Eimeridae (Fig. 2,a) which occurs in birds, mammals, reptiles, amphibians, fish and arthropods. The whole of the growth period of these parasites takes place within the cytoplasm of a host cell. The oocysts are discharged in the droppings of infected birds, and may contaminate food and water. If ingested by another bird while eating or drinking, the oocysts pass into the duodenum where their thick resistant wall is dissolved and the sporocysts are liberated. Each of these sporocysts in turn sets free two active motile sporozoites which bore into cells lining the intestine. Here they grow at the expense of the host tissue. Within these epithelial cells, multiplication by schizogony occurs repeatedly. The daughter individuals known as merozoites eventually escape into the lumen of the intestine and from there invade new host-cells. After several of these asexual cycles the resulting merozoites become differentiated into ovoid macrogametes (female cells) and flagellated microgametes (male cells). Each type develops in a separate cell of the host. Copulation and fertilisation take place by a liberated male cell penetrating a female cell; a resistant wall is formed round the fertilised cell or zygote which now becomes an oocyst and bursts out once again into the lumen of the intestine. It is, however, incapable of further development until it is voided with the bird's faeces. Conditions in the outside world are favourable and after some time the single cell within the oocyst divides into two or four spores (sporocysts). The oocysts have then reached the so-called infective stage and if swallowed, are capable of infecting another host.

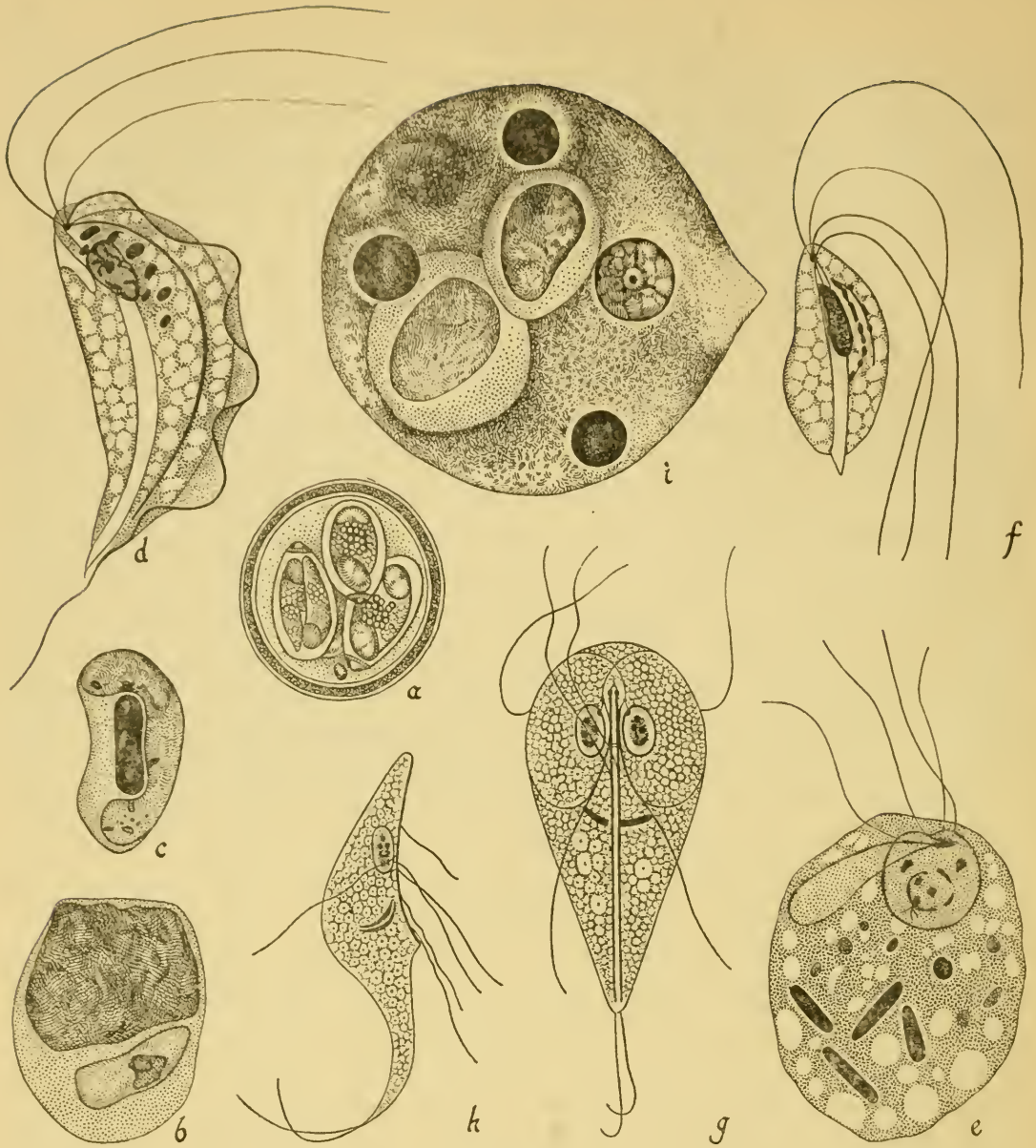
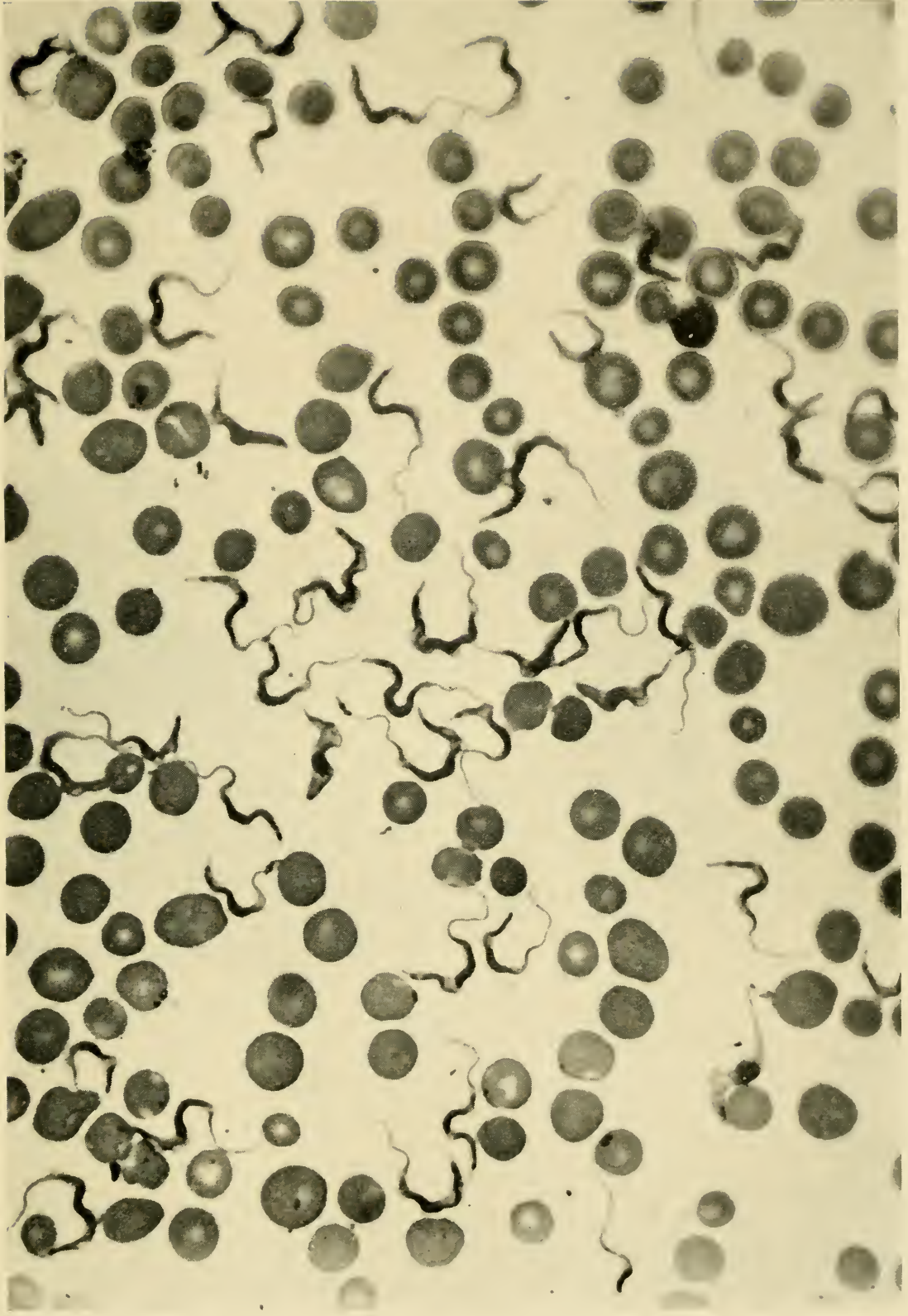


FIG. 2

Different types of parasitic Protozoa (adapted from Wenyon)
a., *Eimeria avium*, class Sporozoa, order Coccidia (x 1300); *b.*, *Leucocytozoon* sp., class Sporozoa, order Haemosporidia (x 2000); *c.*, *Haemoproteus* sp., class Sporozoa, order Haemosporidia (x 2000); *d.*, *Trichomonas eberthi*, class Mastigophora (Flagellata), order Protomonadida (x 4100)*; *e.*, *Chilomastix gallinarum*, class Mastigophora (Flagellata), order Protomonadida (x 4100); *f.*, *Eutrichomastix gallinarum*, class Mastigophora (Flagellata), order Protomonadida (x 4100); *g.*, *Giardia intestinalis*, ventral aspect, class Mastigophora, (Flagellate), order Diplomonadida (x 5100); *h.*, *Giardia intestinalis*, lateral aspect, class Mastigophora (Flagellata), order Diplomonadida (x 5100); *i.*, *Entamoeba* sp., class Rhizopoda, (x 2000)

* (Note: a drawing of *Trypanosoma* will be found at the end of Chapter 9)



Trypanosoma among blood corpuscles ($\times 1625$)



The usual sites of infection of Eimeridae are the cells lining the intestines although occasionally they are found in other organs. Heavy infestations may cause extensive destruction of the epithelium, which, in turn results in inflammation and bleeding and the ultimate death of the host. In small numbers they appear to do little damage and many birds which harbour Coccidia are apparently in perfect health.

The two most familiar genera from birds are *Eimeria* and *Isospora*. The latter is found principally in perching birds and is recorded from various passerines, and also from kingfishers (Coraciiformes), hawks (Falconiformes), woodpeckers (Piciformes), owls (Strigiformes) and cuckoos (Cuculiformes); 127 species are known to be hosts in the United States alone. The incidence of infection is also very high—often an entire population is affected. *Eimeria*, on the other hand, parasitises the more primitive orders such as geese (Anseriformes), cranes, coots and moorhens (Gruiformes), pigeons (Columbiformes), cormorants (Pelecaniformes) and game birds (Galliformes). Both genera are said to infect plovers (Charadriiformes) but this record requires corroboration. Owing to the fact that *Eimeria* is a pest in farmyards while *Isospora* does not attack poultry, the latter escapes attention except from the specialist. The various species are said to be strictly host-specific, that is to say, they are peculiar to one sort of bird only. At the same time seven species of *Eimeria* are recorded from the domestic fowl alone and three from geese. Some authorities regard the whole lot as varieties of one species *E. avium*, which in Britain was first reported from wild birds, in the grouse (Fig. 2,a). The largest number of victims are found among chicks under six weeks of age. Altogether young birds are more susceptible than adults. After an infection has been present for some time in an individual bird, schizogony gradually decreases and only male and female gametes are produced by the parasite. This leads to the formation of oocysts which pass out of the body and thus infection gradually ceases. The cause of this change is not really known, but we can hazard the guess that it is due partly at any rate, to changes in the blood serum of the host, or acquired immunity.

Eimeria does not need an intermediate host in order to complete its development and birds can be infected directly by ingesting oocysts. The spread of the parasite may be assisted by flies, which act as transport hosts. These insects, both in the larval and adult stages, ingest the oocysts along with the faeces of the birds, on which they feed. They

pass unchanged and unharmed through the alimentary canal. In this way, the oocysts are widely dispersed and they are often ingested by a bird which catches and eats the fly.

Several workers have claimed that the oocysts appear in the faeces of infected birds at definite times of the day, between 3 and 8 p.m. for *Isospora* and 3 and 9 p.m. for *Eimeria*. The metabolism of the parasite would therefore appear to be closely linked to the host and the voiding of oocysts at definite times may be regulated by the bird's responses to light and dark.

The genera *Eimeria* and *Isospora* present an interesting problem in evolution of host and parasite. Some time in the remote history of birds the ancestors of these Protozoa parted company. It is interesting to follow their development in the various orders of birds and to see if other parasites show a similar divergence among the groups in question.

ORDER HAEMOSPORIDIA

"Of all the human diseases," wrote Chandler in 1946, "there is none which is of more importance in the world to-day than malaria. It has been estimated to be the direct cause of over one-half the entire mortality of the human race." Man, however, is only susceptible to one genus of the family Plasmodiidae, while birds fall victim to all three. It is difficult in the present state of our knowledge to estimate the damage inflicted on populations of wild birds by these parasites. Judging from observations made on canaries and other species kept in captivity, and domestic poultry such as ducks and turkeys, the harmful effects must be considerable, even if the mortality rate is not high.

One of the most extraordinary facts in the whole field of bird parasitology is the lack of research into true malaria (*Plasmodium*) in British wild birds. This seems even more peculiar when it is realised that the transmission of the malaria parasite was first demonstrated by Ross using wild birds in India. The actual species concerned were a crow (*Corvus splendens*), two pigeons, four larks (*Calandrella dukhunen-sis*) and six sparrows (*Passer domesticus indicus*). Moreover, one of the most effective modern therapeutic drugs, paludrine, was discovered in this country; canaries and chickens were used for the experiments concerned. The fact remains that except for a record made over thirty years ago by Coles, we should not know for certain if true malaria existed in British wild birds. It is safe to assume that it is not uncommon, for avian plasmodia undoubtedly occur in every part of the world where

both birds and mosquitoes are found. After considering all the available data, Hewitt calculated that the mean rate of infection for all birds is about 5 per cent. In Germany and Italy the figures are between 4.4 and 4.8. per cent., but in California they rise to 18 and 19 per cent. Passerines are more susceptible than other birds but a wide range of hosts—over 200 species—is recorded. These include about 40 on the British list such as the great tit, white wagtail, swallow, nightjar and various finches, buntings, thrushes, warblers, larks, shrikes and so forth. About twelve species of bird *Plasmodium* are now recognised although many have been described several times over in error, so that the literature is cluttered up with invalid names. Probably not more than four or five can be expected to occur in Britain. The insect vectors are mosquitoes, of which by far the most important is the house-gnat (*Culex pipiens*), the commonest of all British mosquitoes. Certain other species found in this country such as *Aedes geniculatus* and *Theobaldia annulata* are also known to be carriers of the disease.

THE LIFE-CYCLE OF *Plasmodium relictum*

Various species of *Plasmodium* parasitise mammals, birds and reptiles but the sexual stage of the life history is always passed in insects. The cycle of the malaria parasite is extremely complicated and the organism passes through a constant series of changes of form. *P. relictum* (formerly known as *P. praecox*) was the species with which Ross carried out his famous experiments. It is common in birds found in tropical and subtropical countries, but to a lesser degree it also occurs in temperate climates and has been recorded from North America, and in Europe from France, Germany, Austria, Switzerland, Italy and Russia. Some authorities (see Appendix : Hewitt, Wenyon) assume that the unnamed *Plasmodium* which Coles recorded from three song-thrushes and a blackbird in the Bournemouth district of England refers to this species.

The life-cycle (Fig. 3) in the vertebrate host commences when the sporozoites in the saliva of the mosquito are introduced into the bird during the process of blood-sucking. The sporozoites at this stage are minute active worm-like *vermicules* and, on entering the blood stream, they are taken up by leucocytes or endothelial cells of different organs, in which they assume a spherical form and multiply by schizogony. After several generations of so-called exoerythrocytic schizogony, the merozoites enter the circulatory system and invade the red blood corpuscles in which their subsequent development takes place. Once

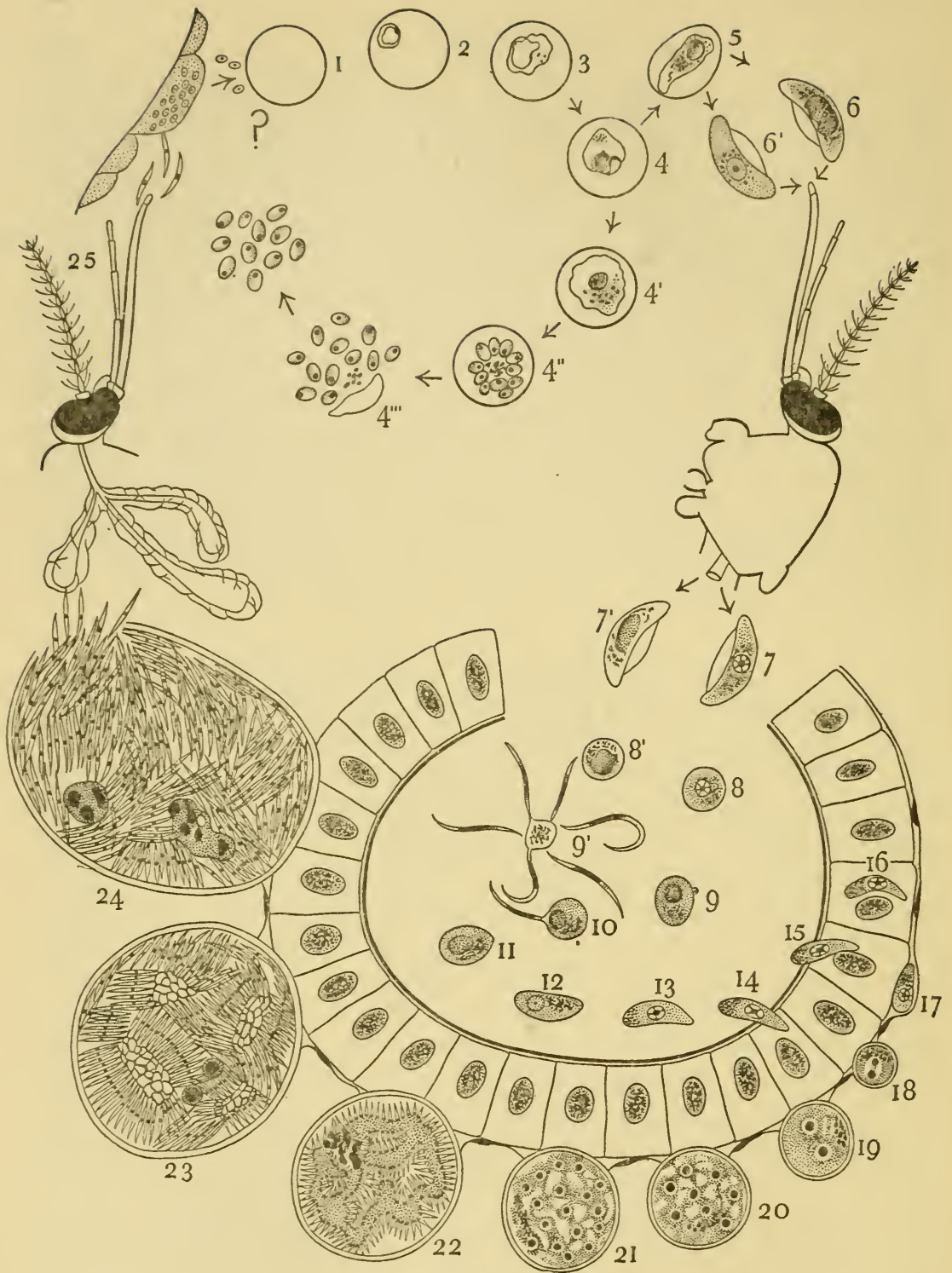


FIG. 3

Life-cycle of *Plasmodium falciparum* in man and mosquito (adapted from Wenyon and Brumpt). The cycle of *P. relictum* is similar.

within a red blood cell the merozoite becomes rounded off as a small mass of protoplasm with a single nucleus, and begins to grow at the expense of the blood corpuscle. The parasite absorbs haemoglobin and this is transformed into a pigment consisting of haematin which appears in the cytoplasm of the parasite as characteristic black or brown granules. These granules are also found in infections of the allied genus *Haemoproteus* but not *Leucocytozoon*. After a few days of growth the parasite multiplies by schizogony, giving rise to merozoites, the number of which varies in different species. These burst out of the blood corpuscle, which is entirely destroyed, and escape into the plasma of the bird. Here each merozoite attaches itself to a healthy blood corpuscle and actively forces its way in. Growth follows and schizogony is repeated all over again. The periodical attacks of fever, so characteristic of malaria, occur when the corpuscles are ruptured by the escaping parasites and poisonous substances are liberated in the blood stream.

After several generations of merozoites have been produced a striking change occurs. The merozoites develop into gametocytes instead of schizonts which remain within the red blood corpuscles until they are ingested by a mosquito feeding upon the blood of the bird. Even at this stage it is possible to distinguish between the male and female gametocytes. In the former the protoplasm stains faintly and the nucleus is large and diffuse, while in the latter the cytoplasm stains deeply and the nucleus is small.

On entering the stomach of the mosquito (Fig. 3) the gametocytes, apparently affected by the change of temperature, burst out of the restraining membrane of the blood corpuscles. Long thin processes are then formed from the surface of the male cell (microgametocyte) which lash about continuously. These are the microgametes, which break loose at intervals and swim about among the corpuscles in the stomach of the mosquito. Meanwhile the liberated female cell (macrogametocyte) remains as a more or less motionless sphere with the nucleus displaced somewhat towards the surface of the cell. When a microgamete comes near, it quickly penetrates the macrogamete and its nucleus unites with that of the female cell. The spherical zygote resulting from fertilisation rests for a while and then begins to elongate until it assumes a wormlike form. It then makes its way through the contents of the stomach by a gliding and bending motion until it reaches the epithelial lining of the gut. Here it penetrates between the cells and finally comes to rest under the elastic membrane which covers the outer surface of the

stomach. Afterwards the zygote becomes surrounded by a membrane partly secreted by the tissue of the host and partly by the parasite itself. The *Plasmodium*, which at this stage is known as an oocyst, continues to grow and the nucleus multiplies by schizogony thus giving rise to numerous minute daughter nuclei. Then the cytoplasm begins to break up and form finger-like processes into each of which a nucleus passes. In this way numerous spindle-shaped sporozoites are formed which eventually break away from their point of attachment and remain as a tangled mass within each oocyst. Sometimes as many as 30 or 40 such oocysts, each containing up to 10,000 sporozoites, are found beading the surface of a gnat's stomach—all in different stages of development. When ripe the oocyst bursts, liberating the mass of sporozoites in the body cavity of the mosquito. These pointed, spindle-shaped cells move about by waves of peristaltic contraction and by a gliding motion, by means of which they insinuate themselves into every organ of the mosquito's body. Large numbers reach the salivary glands and pass up the duct with the saliva. During the insect's next blood meal they are injected into the blood stream of the bird and the asexual cycle begins once again.

In recent years some extremely interesting work has been carried out by James and Tate in England, and by Huff in the U.S.A., using the fowl malaria parasite (*Plasmodium gallinaceum*). They have demonstrated that the initial asexual cycle in the bird is passed in the white blood corpuscles and in the endothelial cells of the spleen, heart and brain. This exoerythrocytic development is followed by invasion of the red blood corpuscles in which the parasite continues to multiply by schizogony. These discoveries paved the way to similar discoveries made by Shortt relating to the human malarial parasite and have proved very valuable for studying problems of relapse and treatment of malaria in man.

The time required for the completion of the sexual cycle in the mosquito varies with the temperature. Under certain conditions it may take only five days for a female mosquito to become infective, but in other cases sporozoites only appear in the saliva after two months have elapsed.

Some species of bird *Plasmodium*, of which *P. relictum* is a good example, are easily transmitted to different kinds of birds, but others show more or less well-marked host specificity. *P. gallinaceum*, which is a parasite of the fowl, will not develop naturally in any other bird,

although geese have been infected by inoculating them with the blood of an infected chicken. The cliff-swallow (*Petrochelidon albifrons*) from America is a bird with a strictly host-specific *Plasmodium*, which, up to date, has not been recorded from any other bird.

These various species of bird *Plasmodium*, and in fact most of the parasitic forms, can only be studied and identified after submitting them to elaborate staining processes. Without the sharp contrasts produced by artificial dyes the minute structural differences would remain invisible to the human eye. A drop of blood from an infected bird is spread thinly on a glass slide and then dried. Subsequently this film is treated with certain dyes to which the various parts of the blood cells and the parasite react in a particular manner.

The different species of bird *Plasmodium* are separated on such characters as the shape of the gametocyte, the number of merozoites in one cell, the shape of the pigment granules and other similar types of peculiarities. It is a matter of considerable difficulty and the accurate identification of *Plasmodium* is unquestionably a matter for a highly trained specialist.

The allied genera of bird malaria parasites. We have already mentioned that the unfortunate class Aves is afflicted by two allied genera of Protozoa, to which man is luckily immune. One of these, *Leucocytozoon* (Fig. 2,b), was found by Coles to be the commonest parasite in the blood of British birds. It is recorded from a number of hosts including the thrush, blackbird, jay, starling, blue-tit, moorhen, pigeon, grouse, tawny owl and brambling. Swallows are especially susceptible and possibly acquire their heaviest infections if they gather in flocks in reed beds prior to autumn migration—for, as nestlings, they are free of infection. About 68 species of *Leucocytozoon* have been named, all of which are confined to birds. In the United States it is sometimes the cause of fatal epidemics among domestic ducks and turkeys. The known insect-vectors are species of black-fly (*Simuliidae*).

The genus *Haemoproteus* (Fig. 2,c), which also parasitises reptiles, has been found in the blood of various wild birds in Britain including the chaffinch, thrush, blackbird, starling, wood-pigeon and grouse. About 45 species have been described and named from various countries, but many of these are probably only new names for "old" species. *Haemoproteus* is widely distributed and very common—a fact which is readily appreciated when it is realised that in the United States this parasite is found in 50 to 60 per cent. of certain thrushes and in 80 per cent. of

mourning-doves (*Zenaidura carolinensis*). Over 500 different species of birds have been recorded as hosts. The only known insect carriers, in which the sexual cycle occurs, are louse-flies (Hippoboscidae).

In *Haemoproteus* the adult gametocyte encircles the nucleus of the red blood corpuscles like a halter. This characteristic stage induced an early worker to bestow the name *Halteridium* upon the parasite—a name by which the group is still often known. In the case of this genus and *Leucocytozoon* the only forms of the parasite which are found in the red blood cells are the gametocytes. For this reason these two genera, unlike the malarial parasites, cannot be transmitted in the laboratory from bird to bird by injection of blood. Transmission occurs only as a result of a bite by an infected insect carrier. The stages of the asexual cycle (schizogony) are passed in the endothelial tissues. Some authorities have consequently divided off the two genera *Leucocytozoon* and *Haemoproteus* from *Plasmodium* and placed them in a separate family, Haemoproteidae.

OTHER SPOROZOA

Another group of Sporozoa, *Toxoplasma*, which infects the white blood corpuscles and various tissues, has been recorded from many wild birds, including the English sparrow in the United States. It has been found in two captive squirrels in this country but has not been studied in birds. Haemogregarines and Piroplasms, which are also parasites in the blood of avian hosts, may eventually be found in British wild birds. Both groups have been recorded from wild mammals in this country.

CLASS MASTIGOPHORA (FLAGELLATA)

The Protozoa which are included in this class are known as flagellates, for, typically, they possess one or more flagella. Each flagellum consists of a fine whip-like outgrowth which is capable of lashing or rippling movements, by means of which the organism is enabled to progress through the liquid medium in which it lives. Sometimes flagella are used as organs of attachment rather than locomotion.

The majority of Mastigophora have a single nucleus. They are chiefly free-swimming and many of them live in the body fluids of

other animals. Reproduction is usually by binary fission, the animal dividing into two by splitting along the longitudinal axis.

In the case of parasitic forms the life-cycle may involve development in an intermediate host.

ORDER PROTOMONADIDA

As far as birds are concerned the most important flagellate parasites are concentrated in this order. Of these the best known belong to the family Trypanosomidae (Plate XXV), which are parasitic in vertebrates, invertebrates and certain plants with a milky "juice" in their stem and leaves. The only genus recorded from British birds is *Trypanosoma* (see tail-piece of Chapter 9). Under the microscope these parasites superficially resemble little fish—with a long, undulating crest in place of a dorsal fin. The flagellum runs along the outer margin of this membrane and projects beyond it as a free lash. On a slide some species can be observed wriggling sluggishly among the blood corpuscles while others dart about like lively minnows. Trypanosomes have no mouth (cystostome) and their food is absorbed in liquid form through the cell membrane. The life history of the species from birds has not been fully worked out. Like the majority of trypanosomes, they occur chiefly in the blood, but in some cases they have also been found in the bone marrow and other tissues of the vertebrate host. Generally the birds appear to be unharmed by their presence but in the laboratory when unusual hosts are used death may follow an artificially produced infection

The genus *Trypanosoma* is very common in birds and has been recorded from over 200 species. It is customary to name each one of these as if it represented a host-specific trypanosome. Thus, for example, the one found in the chaffinch is named *T. fringillinarum*. In all probability the same species occurs in a number of different hosts as the organisms in question are very variable (polymorphic). In Britain *Trypanosoma* has been found in the rook, jackdaw, yellow-hammer, chaffinch, linnet, blackbird, jay, thrush, house-martin and swallow. In Germany it has been recorded from many other birds on the British list, and is often present in the blood of nestlings only a few days old.

Most trypanosomes are transmitted by invertebrate hosts. For instance, a trypanosome of sheep is carried by the sheep ked (a louse-fly), one from the rat by fleas, one from the tortoise by leeches, another from the camel by horse flies and the most famous of all trypanosomes,

those which produce sleeping sickness in man, and nagana in cattle, are transmitted by tsetse flies. Only one of the horse trypanosomes, *T. equiperdum*, is known to have a direct life-cycle and passes from horse to horse during the sexual act. In the invertebrate host these parasites develop in the alimentary canal, finally giving rise to the infective forms. In some trypanosomes the latter are produced in the mouth parts or salivary glands, and are then inoculated into the vertebrate during the blood meal. In others, well illustrated in the rat flea infected with *T. lewisi*, the infective forms develop in the hind gut, and infection occurs when the host accidentally ingests the flea or its droppings. It is believed that trypanosomes have evolved from a more primitive type of flagellate which is normally parasitic in the gut of insects. During the part of the cycle within the invertebrate host the trypanosomes pass through various stages in which they appear to revert to ancestral forms.

The carriers of bird trypanosomes are not known for certain. Some development appears to take place in mosquitoes and it has been claimed that *T. loxiae* and *T. noctuae* (from the crossbill and little owl) multiplied and produced crithidia-like forms after ingestion by the house-gnat. It has been claimed that the red mite (*Dermanyssus gallinae*) can transmit one species of bird trypanosome. The fact that nestlings are so frequently infected in nature suggests that the carrier is an arthropod breeding in their nests.

Very often the blood of wild birds is infected with various sorts of parasites. One thrush examined by Coles was found to harbour simultaneously all three genera of bird malaria parasites (*Plasmodium*, *Haemoproteus* and *Leucocytozoon*) a *Trypanosoma* and a filariid worm. This is confusing, and even trained scientists have fallen headlong into the trap and have described, with great enthusiasm, completely different organisms as stages in the life-cycle of the same species.

Another well known parasite from the same order is *Histomonas meleagridis*. This is a flagellate with an amoeboid phase, harmless if present in the intestine of chickens; but in turkeys it invades the liver and intestinal wall, causing a mortal illness commonly known as "black-head." It does not form a cyst but is transmitted directly when a bird accidentally ingests contaminated faeces or the eggs of the caecal worm (*Heterakis*) which act as transport hosts.

There are also numbers of Trichomonadidae (Fig. 2,d) found in birds. These are spindle- or pear-shaped flagellates with a stiff rod-like

axostyle supporting the body, several free anterior flagella and an undulating membrane bordered by a marginal flagellum. They divide by simple fission and no sexual phenomena have been observed. They do not form cysts but remain alive long enough outside the body to effect successful transference to new hosts. In the intestine of various birds, species like *Trichomonas gallinarum* ingest débris, bacteria and other solid particles and are apparently harmless, although on rare occasions they invade the liver with disastrous consequences. A species, *T. gallinae*, from the mouth, throat and oesophagus of birds such as gulls, falcons, pigeons and poultry, appears to consume leucocytes and attacks the mucous membrane, and *T. columbae*, from the crops of pigeons, is closely related to a species found in the vagina of *Homo sapiens*. Another related species, *T. foetus*, infecting the uterus and penis of cattle, is an important cause of abortion in cows.

Other flagellates found in the intestine of birds include forms such as *Chilomastix gallinarum* (Fig. 2,e) from the caecum of the fowl and *Cochlosoma anatinis* from the intestine of mallard, shoveller, pintail, scaup and other duck.

ORDER DIPLOMONADIDA

The flagellates from this order are strikingly different from all the others. Owing to a duplication of certain organs they are bilaterally symmetrical. This gives the impression that the animal is in the process of longitudinal fission.

Giardia (Fig. 2), which is the best known genus, superficially resembles a pear split in half, with eight flagella arranged in pairs arising from different parts of the body. It clings to the epithelial cells lining the small intestine by means of a sucking disc. Apparently it stimulates a copious secretion of mucus upon which it subsequently feeds. Intermittently it forms cysts which pass out in the faeces and are thus transported to other hosts. *Giardia* is found in vertebrate animals throughout the world and has been recorded from a variety of bird hosts including the common buzzard, shrike, avocet and several species of herons. The allied genus *Hexamita* has also been recorded from birds.

CLASS RHIZOPODA

This class comprises some of the simplest Protozoa known as amoebae. The body has no definite shape or orientation, but assumes a

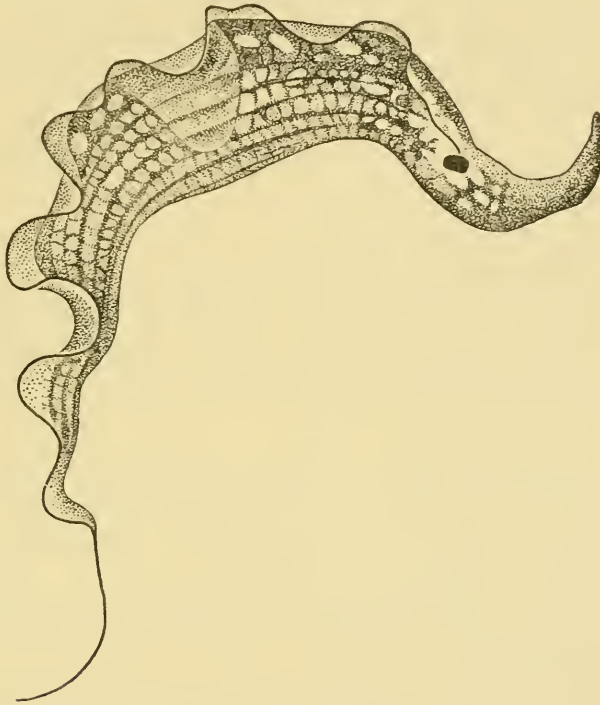
globular form when at rest. Amoebae move and eat their food by means of pseudopodia. Part of the cytoplasm is pushed outwards until it protrudes like a finger. Then the rest of the body flows into it and thus the organism can move slowly from one place to another. By means of these pseudopodia they also encircle particles of food such as bacteria, cysts of other Protozoa or blood corpuscles and subsequently ingest them. Owing to the fact that these naked blobs of protoplasm are the first living animal the average naturalist examines under the microscope, they are, to most of us, objects of great affection and nostalgic pleasure.

Although most amoebae are free-living in soil and water, the majority of vertebrate animals harbour either commensal or parasitic forms in their large intestine. In man there is one highly pathological species which lives on red blood corpuscles and is the cause of so-called amoebic dysentery. The only family which includes important bird parasites is the Amoebidae (Fig. 2,i). The best known British species from wild birds is *Entamoeba lagopodis* from the intestine of the grouse. Multiplication occurs by binary fission. The organism elongates and then splits in two. Cysts with four nuclei are formed and these pass out of the grouse with the faeces. They contaminate drinking water and food and are thus ingested by new hosts. The amoebae themselves cannot survive outside the body.

Various other species have been described, from fowl, domestic ducks and geese, and certain wild birds, with cysts showing one, four or eight nuclei.

The foregoing account of the Protozoa from birds scarcely does the group justice. A great deal has to be compressed into a small space, the terminology is necessarily technical and the subject matter so complicated that little more than a straightforward factual account can be given. Undeniably the chapter makes dull reading. To dispel this impression Protozoa have only to be looked at alive under the microscope. Most people instantly fall under their spell. The great majority of these organisms are colourless and in studying them one enters a fascinating world of relative transparencies. Every species displays some subtle difference in opaqueness, density, refraction or translucence. Protozoa move in countless different ways. Some dash across the field of vision like express trains, some corkscrew around in never-ending spirals, some flicker intermittently like summer lightning, others swim by the rhythmical beating of countless transparent cilia, or lash their way

about in jerky spasms; many move by sinuous and beautiful undulations. Others again push out portions of their own bodies and let their protoplasm stream into the protuberance—thus slowly flowing from place to place. In order to get some idea of this beautiful, obscure and animated crowd it is only necessary to smear a little of the mucus from the crop, intestine, cloaca or other body fluid of a bird on to a wet slide and focus the microscope.



Trypanosoma gallinarum from the fowl
(after Wenyon) (x 2000)

CHAPTER 10

WORMS (VERMES)

In all these the nobler organs seem of such little use, that if they be taken away the animal does not appear to feel the want of them.

BUFFON'S NATURAL HISTORY

WORM has become a term of abuse. In the modern world it conjures up a picture of a henpecked husband or the fellow who lives to fight another day, or something pale and elongated, wriggling in distress when a stone or a piece of decaying meat is turned upside down in the sunshine.

From the naturalist's point of view the term is applied somewhat loosely to four phyla of animals: Platyhelminthes or flatworms, among which are found the tapeworms and flukes; the Nematelminthes or roundworms, which include the nematodes; the Acanthocephala or spiny-headed worms, and Annelida or segmented worms, which include earthworms and leeches.

The tapeworms, flukes and spiny-headed worms are exclusively parasitic, although some of their larvae enjoy a few hours of careless freedom in the water and their eggs are washed about the world in the ebb and flow of urine and faeces.

During the course of their evolution most of the parasitic worms have been forced to become efficient egg machines, but this has not by itself solved the problem of their survival. Despite the vast number of ova they produce, both tapeworms and flukes have had to resort to other methods by which their progeny can be further multiplied. Thus, by a process of asexual reproduction (fragmentation of the germ cell) inside the first host, one egg of a bird trematode can give rise to several million free-swimming larvae, each capable of developing into a complete adult. Some tapeworms bud off multiple individuals in the

larval stage as well as adding new segments in the "neck" region—which is also a form of asexual multiplication.

During their complicated history as parasites all the digenetic flukes, tapeworms and the spiny-headed worms have become involved with various intermediate hosts. In some cases it is difficult to say where the process first began. Possibly the bird, which is now the final host, was a later addition to the original life-cycle and tagged on at the end. It is obvious that by persistently eating an animal infected with flukes a bird must again and again expose itself to infection. Despite this fact, it is sometimes difficult to imagine how the change from invertebrate to vertebrate host can have occurred, but an important clue has been provided by experiments carried out by Baer. He has shown that if the tapeworm *Ligula intestinalis* (see p. 195) is "cultured" in an artificial medium, and the temperature raised, the larval form will lay eggs precociously (progenesis). In view of these experiments it is relatively easy to visualise how, when the worm was introduced into a vertebrate, the sudden change of environment could stimulate egg-production and enhance the species' chances of survival. Under such circumstances the vertebrate host could enter the life-cycle permanently and supplant the original "final" host. There is another advantage which vertebrates enjoy over many invertebrates: on the whole their life is longer, and each individual thus provides the internal parasite with protection and food over a more extensive period. Vertebrates often wander far afield; consequently the parasites which keep up continuous egg-production are enabled to scatter their eggs over a much larger area and during a longer period, if they are lodged, say, in the intestines of a bird instead of the body-cavity of a fly. If man fed regularly upon insects he would probably have acquired many worm parasites which are at present found chiefly in insectivorous birds, but also in bats and other animals, with similar tastes. Hands have relieved him of the grim necessity of eating his own ecto-parasites—otherwise he might easily have become infested with the rat and dog tapeworms which use fleas as intermediate hosts.

In discussions on parasitism it is customary to compare an ill-adapted parasite, which kills the host, with the farmer who killed the goose which laid the golden eggs. In the case of flukes and tapeworms it is equally important from the point of view of their race that the host should survive in order that they can continue to lay their "golden" eggs, for the bird—by scattering them far and wide in urine, faeces and

exudates—counteracts or at any rate minimises the effects of the parasite's isolated and stationary existence.

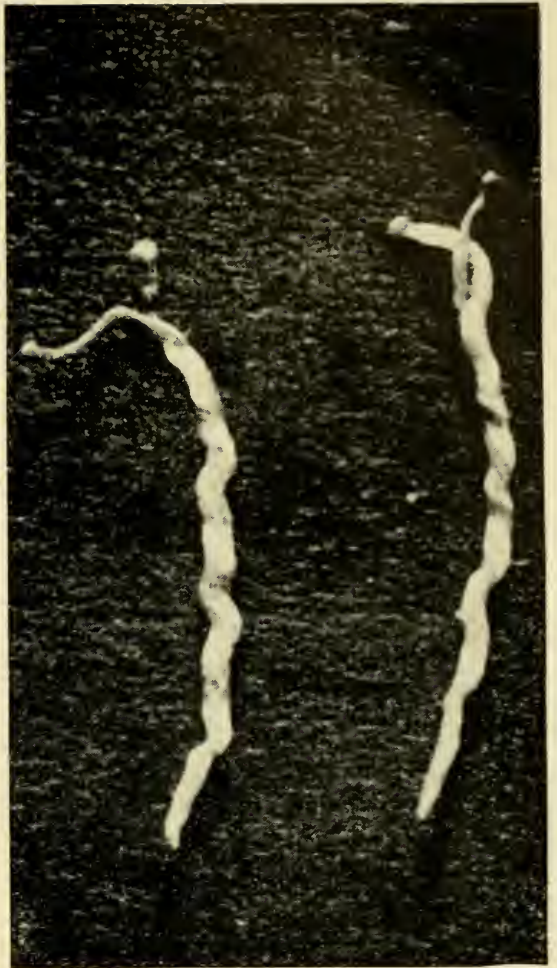
In many cases it seems probable that intermediate hosts have been secondarily interpolated in the life-cycles merely because they provide the most accessible route to the final vertebrate host. It is a striking fact that almost all complicated life histories involve endo-parasites. Ecto-parasites, whether they are flukes on the gills of fish, or feather lice on the quills of birds, generally have a direct and simple life-cycle. It is likely that endo-parasitism, whether the habit arises suddenly or gradually (see p. 48), always tends to involve intermediate hosts. It is often the easiest way, maybe in some cases the only way, of getting in or out of the host's body successfully. A filariid worm not only has to deal with the difficulty of finding a final host which is relatively isolated in space, but has to contend with the greater isolation imposed by confinement within the tissues and bloodstream of the host. The insect vector is one of the few possible solutions. By whatever curious paths the present situation evolved, it is now sufficiently complicated and extraordinary to satisfy the imagination of Salvador Dali himself. In order to complete their life-cycles many flatworms must pass through three different hosts, which may even include one living in the water, another on land and a third flying in the air. Moreover, many of the flukes which, in some stages, may be no bigger than a grain of sand, can only survive in extremely circumscribed areas of the host's body, such as the tentacles of a snail, or the eye of a fish, or the bile duct of a bird. When the flatworms gave up their freedom they certainly began an odyssey compared with which the voyages of Ulysses seem singularly uneventful and commonplace.

Nematodes are the most important group of worms parasitising land birds generally, and exceed in variety and numbers all the others put together. They are found in a large assortment of vertebrates and arthropods, ranging from camels to bumble-bees, and are in no way confined to birds. In this book no attempt is made either to list the species of parasitic worms found in British wild birds or to give an account of their morphology and classification. Thousands of species are involved and all that space permits is to focus attention on a few interesting points concerning each of the major groups.



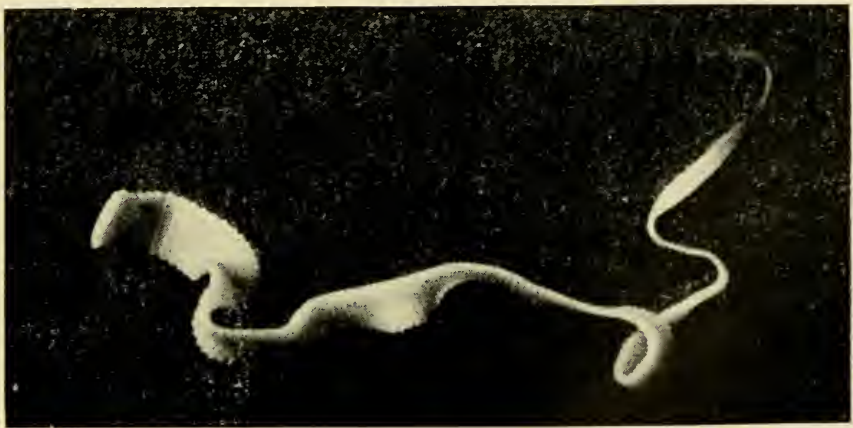
J. G. Bradbury

a. Fluke, *Cryptocotyle lingua*, from intestine of herring-gull ($\times 49$)



S. C. Porter

b. Roundworm, *Syngamus trachea*, male and female in copula ($\times 2.5$)



S. C. Porter

c. Tapeworm, *Dilepis undula*, from intestine of song-thrush ($\times 2.9$)



D. P. Wilson

a. Common periwinkle, *Littorina littorea* (× 0·37)



D. P. Wilson

b. Common goby, *Gobius minutus* (× 1·65)

INTERMEDIATE HOSTS OF THE HERRING-GULL FLUKE, *Cryptocotyle lingua*
Plate XXVIII

ROUNDWORMS (NEMATODA)

The roundworms, as we have already noted, are placed in a separate phylum Nemathelminthes. Although in the popular sense they are quite obviously "worms" a man has more in common with a snake than a roundworm has with a flatworm. Large numbers of nematodes are free-living and are to be found teeming in the soil and water. Their morphology is generalised and rather unspecialised—a fact which has puzzled a great many biologists. Some have concluded that all free-living nematodes are derived from parasitic forms, while others see in the relative simplicity of their anatomy a pre-adaptation to the parasitic mode of life. A great deal of confusion exists, however, in the minds of various writers on the definition of adaptation and modification, as the two following quotations, taken from the works of two leading authorities and both published in 1946, will show. One writes: "The majority of the parasitic forms are relatively giants and are often much modified by their parasitic life." The other writes: "The nematodes, on account of their simplified anatomy, appear to have escaped the effects of parasitism."

Roundworms are cylindrical, generally tapering to a point at both ends. They have a well-developed intestine, a body cavity and—with few exceptions—the sexes are separate. The females are generally larger than the males and the latter have differently formed tails, often with a saucy curl at the tip. Occasionally, there is a marked sexual dimorphism. The females of the blood red spirurid *Tetrameres* found in the proventriculus of many wild birds are almost globular, whereas the males retain the typical cylindrical shape. One male nematode (*Trichosomoides*) which is parasitic in the urinary bladder of rats lives a life of ease inside the vagina or uterus of its own female. The cuticle, although transparent, is tough and apparently impermeable—in many cases reminiscent of the cuticle of arthropods, although it is not chitinous. This cuticle is sometimes expanded into fin-shaped flaps, which are useful for purposes of classification.

The life-cycle of the nematode is simple compared with that of the fluke or tapeworm. Although, between the egg and the adult worm, there are four moults and the successive larval stages may differ in minor structural details, there is no alteration of distinctive larval generations or asexual multiplications either by budding or polyembryony. Their egg production is, however, higher than many of the

flukes and tapeworms and it has been estimated that a large individual nematode from man can lay over 27,000,000 eggs. Sometimes development is direct, but unlike the free-living nematodes, the parasitic forms often require intermediate hosts in order to complete their life-cycle. There is another extraordinary phenomenon well known among nematodes, of which the *Ascaris* from man, affords the best known example. When an egg of this worm is swallowed by the host it hatches in the small intestine, the site where eventually *Ascaris* spends its adult life. However, it appears incapable of developing to maturity without first undertaking a ten-day peregrination inside the host's body. After penetrating the mucous membrane of the intestine it is caught in the bloodstream and swept into the liver, thence to the heart and lungs. Possibly in this location it finds additional oxygen which is necessary for its development—but this is a matter of pure conjecture. The young *Ascaris* then burrows out of the lungs into the trachea and eventually regains the intestine via the throat and oesophagus, where it continues development. Similar apparently meaningless migrations inside the host's body are undertaken by many nematodes. Some authors put forward the view that this is an extension of a "burrowing" habit exhibited by most of these worms at some period of their development. They may burrow into the mucosa lining the intestine and then return to the lumen or merely bury their heads in it, or burrow directly through into the body cavity, or burrow into the tissues of an intermediate host. Other authors believe that the extensive migrations can be explained on the assumption that these nematodes originally became vertebrate parasites by burrowing through the skin, or that at some period of their history the species in question developed in an intermediate host. Now the cycle has been curtailed but the larva still takes a trip which has become redundant since the intermediate host has dropped out. One thing appears certain—these migrations through the host are no joy rides. Like the charge of the gallant Light Brigade—hundreds set out on their apparently pointless mission but only a few come back.

Chickens are excellent hosts for roundworms and over 50 species have been recorded from the fowl. A rapid glance at any manual dealing with the diseases of poultry gives a good idea of what we can expect in wild birds with the same sort of feeding habits.

Perhaps the best known of all bird nematodes is *Syngamus trachea* (order Rhabditida, sub-order Strongylina), a brilliant scarlet worm

about the length of a pin which lives fixed in the trachea of the host and is the cause of the disease known as the gapes. Chickens can become infected in two ways. Either they ingest embryonated eggs which have passed out with the bird's droppings and have developed while lying on moist ground; or they can eat earthworms into which the recently hatched larva has penetrated and subsequently encysted. Various authors claim that birds are easier to infect in the laboratory if they are fed with earthworms containing cysts, rather than the embryonated eggs. House flies, green-bottle flies, springtails and centipedes also act as transport hosts. When infected they become sluggish and are easily caught. Certainly in nature birds can become infected by both the direct and indirect method. After the gapeworm has been swallowed by the avian host it escapes from the intestine and migrates—possibly via the blood stream—to the lungs. Some time is spent in this site before the worm moves on and takes up its final position in the windpipe. *Syngamus* copulates while still immature and the male and female remain joined together for life, thus forming a characteristic Y-shaped figure (Plate XXVIIb). Only a portion of ingested embryonated eggs reaches maturity. From 10,000 larvae fed to a turkey only 235 pairs were recovered from the windpipe and lungs—but this was sufficient to kill the host. The gapeworm is a cosmopolitan species of which there may be a number of different wild strains. The most highly infected hosts in Britain are rooks and starlings but there have also been records from the robin, little owl, magpie, jay, carrion-crow, jackdaw, kestrel, house-sparrow, purple sandpiper and several others. Young birds are much more susceptible than adults and often a very high proportion of nestlings harbour these worms, whereas only a small percentage of the parent birds in the same population are infected. In the case of partridges the females are more susceptible than males. An allied species, *Syngamus merulae*, is found in thrushes and blackbirds in Britain.

Another well known parasite of the chicken and wild birds, which is also placed in the same order, is *Trichostrongylus pergracilis*. This is a small species less than a centimetre in length which may be found in thousands in the caeca of infected birds. In Britain it has only been recorded from the grouse and occasionally the partridge. The life-cycle is direct. The eggs pass out with the droppings and hatch in about two days. Two moults take place and at the end of a fortnight the larvae become infective. When the dew is on the grass or after rain they

wriggle up the stems of heather or some other suitable plant and wait. A grouse, partaking of an early breakfast, inadvertently swallows the larvae which on reaching the caeca undergo two further moults and become adult worms.

One of the most interesting worms found in the caeca of chickens and also in wild birds such as the coot is *Strongyloides avium*. In this whole family there is a most peculiar life-cycle which may possibly throw a little light on the evolution of parasitic nematodes.

The eggs hatch after being voided with the faeces and young worms develop in the soil into both adult male and female free-living individuals. These worms copulate and lay eggs which in turn give rise to larvae which feed, moult and develop into another generation of free-living worms. This process may be repeated several times but sooner or later a different type of larva is produced, which, if ingested by the right host, develops into an outsize parasitic female which reaches maturity inside the bird and lays parthenogenetic eggs. No parasitic male has ever been found.

The worms of this family seem to form a link between the free-living and parasitic forms of nematodes. It is uncertain what causes the production of the parasitic types of larvae, but experiments on allied species suggest that abundance of food and certain other environmental factors influence the course of development. Some strains of the same worms seem more susceptible to a luxurious environment than others and abandon the free-living life and produce parasitic forms more readily. Caullery has suggested that all the special types of reproduction so characteristic of parasites, such as parthenogenesis, polyembryony, strobilisation, budding and so forth, occurred originally because of the particular type of environment in which the eggs happened to develop—conditions not necessarily linked with parasitism, but characters which subsequently made adaptation to such a precarious life possible.

Many of the Strongylata are bright red in colour—due to their habit of sucking blood from their hosts. They bite the intestinal wall or seize it in their mouths, simultaneously pouring out a secretion which prevents coagulation of the blood. They may also perhaps obtain a supply of oxygen, which is lacking in the intestinal tract, by keeping up a constant flow of blood through their bodies. Some species have the power of digesting the tissues of the host without first swallowing them. The secretions of their oesophageal glands are poured out and they then imbibe the pulpy, semi-liquid mass produced in this manner.

The superfamily Ascaroidea is also well represented both in chickens and wild birds. The best known of all the worms of poultry is the caecal worm *Heterakis gallinae*, notorious as the carrier of Blackhead disease (*Histomonas meleagridis*). This worm has a direct life-cycle and the eggs, after a period of incubation on the ground, will hatch in the intestine of susceptible birds if they are swallowed in food or water. Within twenty-four hours the larva has reached the caeca and penetrated the mucosa, where it remains for two to five days. It then returns to the lumen of the caeca where it spends the rest of its adult life. Various related species are recorded from British wild birds such as the sheld-duck, tawny owl, curlew, various geese and game birds. Earth-worms frequently ingest the eggs and may act as transport hosts.

Heterakis is a relatively small worm, only a few millimetres in length. Worms of the genus *Ascaridia* are, however, much longer, sometimes four to five inches long. *A. galli* is one of the commonest worms in poultry and there are many related species in wild birds, especially in game birds such as the capercaillie (*Tetrao urogallus*) but also in some passerines. Young birds are much more frequently attacked than older ones and it has been shown that after goblet cells are developed in the epithelial lining of the duodenum the birds seem to become relatively resistant to infection. Diet also has a considerable influence on the rate of infection and when deprived of vitamins or animal protein the birds easily become parasitised by these worms.

The food of the Ascaroidea, unlike the Strongylata, consists principally of the intestinal contents rather than the blood or the mucous membrane of the host. Several experiments have been planned to prove this. Infected chickens have been fed on beef and charcoal and both ingredients were subsequently recorded from the intestines of the nematodes. On another occasion a certain number of chickens infected with *A. galli* were fed by injections and only given water by mouth. In these birds the worms failed to grow, while in the control chickens, which were fed in the usual manner by mouth, the parasites grew normally.

There are, of course, numbers of related roundworms (Ascaroidea) which are not found in poultry. The genus *Contracaecum* is characteristic of fish-eating mammals, birds and predatory fish. *C. spiculigerum* is a cosmopolitan species found in the proventriculus of cormorants and other sea birds such as auks, guillemots and skuas. Fish serve as first and second intermediate host. Another closely related genus, *Porrocaecum*,

which is also recorded from seals and fish, parasitises a wide variety of birds in Britain. *P. depressum* uses moles and shrews as second intermediate host and birds of prey, such as the peregrine falcon and tawny owl, as the final host.

Chickens harbour a nematode in their eye, another in their crop, stomach, gizzard and intestine, which belong to the order Spirurida—an order which contains only parasitic forms. All these worms require an intermediate host in order to complete their life-cycle. *Oxyspirura mansoni*, which has been chiefly recorded from game birds and domestic poultry, lays its eggs in the eye of the bird and they are subsequently washed down the tear ducts and swallowed, eventually passing out of the bird's body with its droppings. Cockroaches—and possibly other insects—which are notoriously “dirty” feeders, ingest the eggs. About two months later mature larvae are present in the insect. Sometimes they are encysted in the fatty tissues and along the alimentary canal and at other times free in the legs or body cavity. When the cockroach is eaten by a susceptible bird the larvae are freed in the crop. From there they migrate up the oesophagus and through the tear duct leading from the nose to the bird's eye. Larvae may reach the eye only twenty minutes after the infected cockroach has been swallowed. A related species, *O. sygmoidea*, is found in crows and rooks.

The blood red proventriculus worms (*Tetrameres*) live in the glands of the stomach. The females are globular and fit snugly inside the glands, but the males, which are almost microscopical in size, have the typical nematode shape. They often remain attached to the surface of the stomach wall and only penetrate inside the glands for the purpose of copulation. One species, *Tetrameres fissipinus*, is found in various wild birds in Britain, chiefly in goosander, pochard, coot, grebes and other aquatic feeders. In this case a number of different intermediate hosts are used. Those favoured are the water fleas (*Daphnia pulex*), and fresh water shrimps (*Gammarus pulex*), but earthworms, grasshoppers and various other insects are used by the species parasitising poultry.

Another common parasite found in the proventriculus of wild birds, especially raptorial, is *Acuaria laticeps*. It is reported from the kestrel, peregrine falcon, short-eared owl and barn-owl in Britain. Other species of the same genus are found in swallows and martins, another from wood-peckers, herons, and crows (including nutcrackers), and shrikes. The various species are often characteristic of one family of birds. The wood-louse (*Armadillium vulgare*) is the intermediate host for

A. spiralis, but various invertebrates such as *Gammarus pulex* may be used as host. In the case of the well known gizzard worm, *Acuaria hamulosa*, which is generally located near the opening between the stomach and intestine, chickens become infested by eating various insects, like weevils and grasshoppers.

The blood of many wild birds is found to be teeming with larval Spiruroids known as microfilariae. In Britain these larvae have been recorded from blackbirds and thrushes and the rate of infection was said by Coles to be very high. In the United States 60 per cent. of a population of wild crows was found to be infected with microfilariae. The adult worms live in the connective tissues or body cavities of the host. The female gives birth to free-living embryos, the microfilariae, which swarm in the blood where they await ingestion by a blood-sucking insect, which, in the case of the species infecting man, is a mosquito. Inside the intermediate host they undergo further development and, after a certain period, assemble in the proboscis of the mosquito. During the insect's next blood meal they break loose from the mouth-parts and creep out on to the skin of the host. They quickly penetrate through the mosquito "bite" or any other abrasion and by an unknown route return to the original site of infection. In certain of the species infecting man there is a diurnal periodicity in the appearance of the microfilariae in the peripheral blood stream. During the day scarcely any are present, but at night between 10 p.m. and 4 a.m. they teem near the surface of the body. Nobody has so far discovered what mysterious influence drives them outwards, but as certain species of mosquito only bite at night, it has been suggested that this is an adjustment of the life-cycle which brings the larvae into contact with these insects. There, while their host sleeps, they wait like expectant lovers.

Some ingenious person has, with the aid of a microscope, watched microfilariae in the transparent web of a frog's foot. It was seen that they work up the capillaries against the blood stream and are apparently actively attracted to the saliva of the insect vector, which it pumps into the wound at the moment of biting. In the case of *Onchocerca*—a mammalian Spiruroid carried by blackfly—the microfilariae swarm immediately below the epidermis.

The life-cycles of the numerous species from birds are not known, but as those from man, frogs and lizards are carried by species of gnats (*Culex*) it is highly probable that they follow a similar course in avian

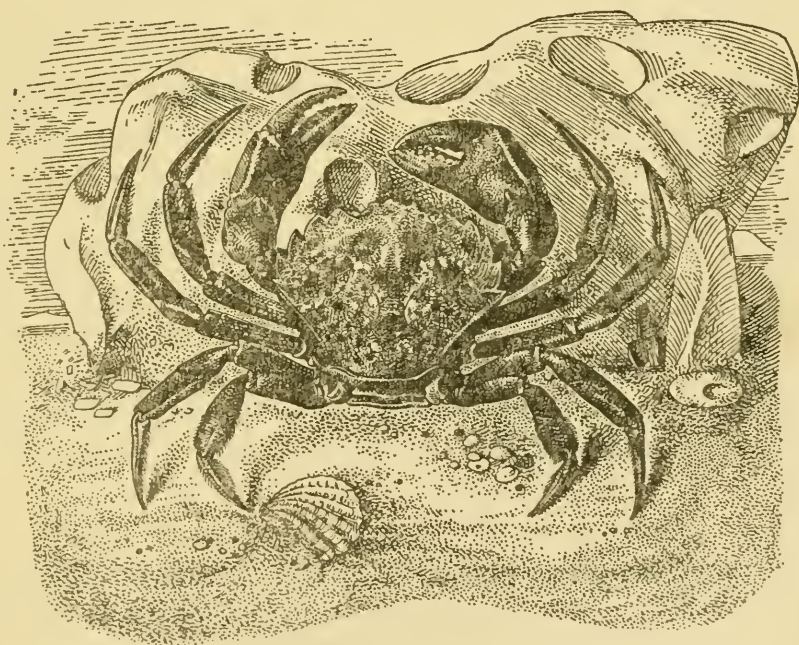
hosts. It is also not known whether the microfilariae in birds swarm periodically as they do in man.

The members of the order Enoplida are often called whipworms because, in some species, the posterior end of the body is thickened and looks superficially like the handle of a whip, while the narrow slender anterior portion is reminiscent of the thong. They are found in a wide range of hosts and in some queer situations. The best known whipworm is *Trichinella spiralis*, which is the cause of a serious, sometimes fatal disease in man, and which is contracted by eating underdone, infected or so-called "measly" pork. When the life cycle of this worm was discovered in 1828 it was thought that a great light had been shed on the ancient Hebrew law which bans the consumption of pig. This superficial and facile explanation is made without any foundation, although some scientific books declare it is "without doubt" true.

Trichurata are particularly common in the crops and intestines of birds. The most familiar genus is *Capillaria*, and needless to say, the unfortunate chicken has its full share of this particular trouble. These worms live more or less embedded in the intestinal mucosa. One of the best known species is *C. columbae*, a hair-like worm less than half an inch in length, which also infects pigeons and peacocks. The life-cycle is direct. The eggs require several days to become infective but only hatch after being swallowed by the host. They enter the mucosa of the duodenum and complete development there before returning to the lumen of the intestine. In certain species, such as *C. annulata*, infecting the crops of chickens and other birds, the embryos have to mature inside earthworms which serve as true intermediate hosts. There are also various species of *Capillaria* which undertake long migrations through the host's body before taking up their final position. A common species in British wild birds, ranging from buzzards to robins, is *C. contorta*. The genus is one of the largest and infects mammals as well as avian hosts.

Chickens with heavy infections of *Capillaria* show an inclination for solitude, become extremely thin, and eventually die. Although many species of worm appear to have little or no effect on their bird host, this is, in all probability, because we cannot ask them about their symptoms. Heartburn, dizziness, insomnia, optical illusions, general nervousness, flatulence, abdominal discomfort, reduced perspiration, palpitations of the heart, dirt-eating and loss of vitality due to nematode infections are listed in a book on human parasitology. This type of

symptom is scarcely likely to be recorded for birds harbouring similar parasites. Mechanical injuries, such as perforation of the intestinal wall, severe bleeding, irritation and inflammation of various tissues, blocking of ducts, thickening or maceration of various internal surfaces, the formation of ulcers or even cancerous growths are the types of injury which attract attention. In nature, however, birds, unlike the barnyard fowl, are not generally subjected to conditions which favour infection with large numbers of nematodes simultaneously. It must also be remembered that infections only last for a limited time, generally less than a year. In due course the worms die and except in a few cases they do not multiply inside the host. Therefore, if only one or two specimens are present at one time, the bird probably recovers from the injuries they inflict and symptoms due to their toxic secretions cease when the parasites are eliminated. Nevertheless, when a bird-watcher puts up his glasses to watch starlings or rooks feeding in the fields he should pause and feel grateful that, unlike the birds, he can cook his breakfast.



Shore crab, *Carcinus maenas*,
the intermediate host of several worms infecting birds (x .5)

SPINY-HEADED WORMS (ACANTHOCEPHALA)

The spiny-headed worms which are of rather uncertain affinities—sometimes placed with the roundworms, sometimes with the flatworms—are also well known internal parasites of birds. They are round, smooth, unsegmented worms, with a large retractable proboscis, armed with closely set, ferocious looking hooked spines, which they force into the lining of the host's intestine and which acts as a powerful organ of attachment. Unlike other flatworms, they have a body cavity and the sexes are separate, but they share with the tapeworms the total absence of an alimentary canal at all stages of development. The females produce large numbers of eggs which lie free inside the body. Situated at the posterior end of the worm is a complicated organ which sorts out the eggs like a superior type of potato riddle—the embryonated ova are passed to the outside and those which are undeveloped are returned again and again to the inside of the worm's body until they have fully matured.

Unfortunately very little has been discovered about their physiology but they are known to carry more fatty substances in their tissues than any other group of helminths. It is hoped that in future parasitologists will give more attention to the physiology of endoparasites in general, for in the process they are bound to make fundamental discoveries concerning not only the parasites themselves but the biochemistry of the alimentary canal and other organs of the host.

Compared with the other parasitic helminths the spiny-headed worms form a small group totalling less than 250 species in all. The popular writer sighs with relief when he considers the nine acanthocephalids (all from the family Polymorphidae) recorded up to date from birds in Britain. A further thirty odd species (four families) from North and Central Europe have been found in birds on the British list. In all probability these will turn up in this country during the course of collecting.

The spiny-headed worms are chiefly parasites of aquatic vertebrates. The vast majority employ crustacea as the first intermediate host, and are found as adults in the intestines of fish, amphibians, seals, whales and water birds. A fair number, however, have become adapted to terrestrial animals and they then use insects as intermediate hosts. Among the nine species from British birds six are from aquatic or semi-aquatic hosts, one from birds of prey, and two from passerines. A typical

example is *Polymorphus boschadis* recorded in this country from the sheld-duck, mute swan, gadwall, scaup, garganey and domestic duck. The eggs pass into the water with the faeces and are swallowed by the fresh-water shrimp (*Gammarus pulex*). After hatching, the embryo or acanthor penetrates into the body cavity or body tissues of the intermediate host and there undergoes further development. After a period of growth it finally becomes surrounded by a delicate cyst and reaches the so-called infective stage, and is then known as an acanthella. If the shrimp is now swallowed by a duck or other suitable host the worm is liberated from its cyst and develops to maturity in the intestine of the bird.

The spiny-headed worms have developed a useful habit, namely the power to re-encyst if ingested by an unsuitable host. If a crustacean infected with the larva of a bird parasite is eaten, say by a small fish instead of the "right" host, the worm is liberated in the intestine but hurriedly penetrates into the tissues of the "wrong" host and becomes re-encapsuled. Numerous transport hosts can be utilised and in this way the worm's life is prolonged and its chances of reaching the "right" host are increased. Possibly a new host may be found in the process, in which development can take place. Sometimes a species like *Centrorhynchus aluconis* which infests such birds as the tawny owl, little owl and the buzzard passes from arthropod to frog, but may then go on to small reptiles or small insectivorous mammals before reaching the final host. In the case of the world-wide genus *Corynosoma* the first host is an arthropod and the second a fish—but a series of the latter may be interpolated before the final host is reached. Some species, such as *C. tunitae*, may be confined to sea birds—the gannet, shag and cormorant—but others appear equally at home in marine mammals and birds. For instance, *C. strumosum* has been recorded from the grey seal (*Halichoerus gryphus*) from Carmarthenshire and in the great northern diver from the Outer Hebrides. Further research will probably show that these are closely related, though not the same species.

The two acanthocephalids recorded from passerines in Britain are *Centrorhynchus teres* from the jackdaw (a species mainly characteristic of the Corvidae) and *Prosthorhynchus transversus* from the starling, song-thrush, blackbird and great spotted woodpecker. On the continent the latter is found in a variety of hosts including the robin and nightingale. There is also one record of *Plagiorhynchus crassicollis*, which is characteristic

of waders, such as the ringed plover, Kentish plover, sanderling, dunlin and oystercatcher. It has also been recorded from the cuckoo. At first sight it appears curious that the cuckoo should share a parasite with this group of birds. On the other hand wagtails, which often act as their foster parents, are infected with certain trematodes which otherwise are chiefly found in waders. One can surmise that crustacea form a certain proportion of the wagtail's diet and the cuckoo may have been fed the larvae as a nestling by its foster parents. Another species found in waders in Britain is *Arhythmorhynchus longicollis* from the purple sandpiper. It is also fairly common in gulls. Finally there is the characteristic duck parasite *Filicollis anatis* recorded from the mallard and scaup in Britain. It has a similar life history to *P. boschadis*, using hog slaters (*Asellus aquaticus*) as intermediate host. There are only two species in this genus, one from Europe where it is also occasionally found in moorhens and coots, and another from South America where it parasitises gulls. In this genus the proboscis is bulbous and when implanted in the intestinal wall of the host forms a powerful ball anchor as the tissue of the host contracts round the narrow "neck" portion below the bulb.

For such a small group acanthocephalids infect a really large variety of birds. In 1933, Meyer listed over 300 host species, ranging from penguins to eagles, and kingfishers to wood-warblers. The most heavily afflicted family is the ducks (Anatidae), but waders, birds of prey and thrushes are among the groups which are heavily attacked. The rock-thrush which has a wide distribution in Asia, India, North Africa and the Palaearctic region and has been recorded about eight times in Britain, acts as an intermediate host for *Echinorhynchus pachyacanthus*, which reaches maturity in predatory mammals such as the lynx (*Felis lynx*) and jackal (*Canis aureus*).

The most impressive feature of an acanthocephalid is undoubtedly the retractile proboscis (see Fig. 4 (3)) with which it anchors itself to the host—for "it was all grown over with thorns." These proboscis hooks are valuable characters for use in classifying the whole group. In three of the four main orders, the spines are arranged radially in long rows on the proboscis, but in the fourth order the arrangement is in the form of a spiral. In two of these orders the trunk spines are absent, but they are present in the others. They are also used as aids for the diagnosis of lower categories such as the families, genera and species. There are thin spines and stout spines, broad, long, stumpy,

hooked, blunt, pointed, bent, curved and tapering spines. They vary not only in shape, size, number and arrangement, but also in many subtle ways such as the proportion of their different parts. A specialist in the Acanthocephala must therefore resign himself to an endless vista of measurements and the drawing of hundreds of little spines. We have estimated that in one publication devoted to this group the author has figured 12,000 spines.

TAPEWORMS (CESTODA)

Tapeworms, as Shipley pointed out, are like recurring decimals. At one end there is a "head" or scolex, which is armed with hooks and adhesive suckers and behind it stretches a long, pallid ribbon of segments which grow out from the "neck" region, each repeating the one immediately behind it. Every segment (proglottid) carries a complete set of organs, and it is, therefore, perhaps more accurate to think of a tapeworm as a long chain of individuals joined together. However, the nerve fibres and muscles extend through the whole length of the body, so if the animal enjoyed any emotions they would be presumably of a communal type.

Although the anterior or "neck" end is continuously producing segments the tapeworm's length is limited, for at the posterior end the oldest segments are dropping off—having gradually lost their initial structure and degenerated into nothing more than bags of eggs which pass out with the faeces of the host. During the course of its life one of the large species of tapeworm has been known to produce seven kilometres of segments.

Each proglottid carries a complete set of both male and female sex organs, sometimes two of each. These are so arranged that each segment can fertilise itself but it is not unusual to find the different segments of a much coiled tapeworm having simultaneous sexual intercourse at a number of points along its length. Everything, in fact, has been sacrificed to communal egg laying, which, admittedly, is highly successful but rather monotonous. One tapeworm has been calculated to produce 36,000 eggs a day and up to two milliard during its entire life.

Tapeworms have no alimentary canal and their food is absorbed through the outer surface of the body. It has been suggested that during

their early larval development the ectodermal covering is cast off and that the endoderm which would normally form the alimentary canal has taken over the duty of a body covering. It has further been suggested that the entire adult tapeworm is an endodermal sac, the lumen of which has been obliterated by the encroachments of the mesodermal tissue. In this case it would be more correct to say that a tapeworm is an alimentary canal without a body, rather than a worm without a digestive tract.

The gut of vertebrates, which is the environment of all tapeworms, presents certain unique features. To begin with it undergoes continual peristaltic movement—that is to say rhythmical waves of contraction pass along it. The tapeworm is continuously in danger of being swept away—like a swimmer in a river with a powerful current forcing him out to sea. The gut also contains protein, fat and carbohydrate splitting enzymes and there is a wide range of pH. (1.7 in the stomach and 9.0 in the intestine). Moreover, the oxygen pressure is low and there are regular physiological changes due to the feeding habits of the host. Tapeworms have had to develop a series of adaptations to cope with this particular situation. The cuticle of the cyclophyllidian cestodes appears to possess a protective action which renders them immune to digestion. Apparently no anti-enzyme is secreted. They have also developed tolerance for a range of pH. varying between 4 and 11. It has long been thought that cestodes were truly anaerobic and could not make use of oxygen under any circumstances. Recently it has been shown that, like roundworms and flukes, they will utilise it if it is provided for them. In the gut, however, the most usual method is anaerobic respiration.

In order to avoid digestion in the host's stomach the larval forms of tapeworms have also become highly specialised in certain directions. For example, if a cysticercus larva is swallowed by the final host the scolex is invaginated into a sort of sleeve which shields it from the action of the gastric juices. The scolex only evaginates when it reaches the duodenum and is stimulated by the presence of bile. The "sleeve" which has received both the acid gastric juices of the stomach, and the alkaline juices of the pancreas, is digested, but the scolex which has been untouched by the former remains undigested and develops into a strobila.

The health of the host and changes in its metabolism affect the worms which parasitise it. In the laboratory it has been found that if

the vitamin B complex is withheld from the diet of the host the tapeworm produces no eggs but increases in size. On the other hand, lack of vitamin B₂ (vitamin G of some authors) in the diet of female rats (but, curiously enough, not in males) causes their tapeworms to remain undersized and stunted. Absence of carbohydrates in the diet and possibly castration of the host, also inhibits their growth. In the laboratory it is frequently found that the host does not "do well" in captivity and then the worms likewise appear in poor condition. All this goes to emphasise a rather obvious fact that the relationship which exists between worms and their hosts is both complicated and profoundly intimate.

In one way, at any rate, cestodes are unique in the animal kingdom. Their protein content is less than the sum of their glycogen and fat.

The tapeworms are certainly a very ancient group and they have probably been committed to parasitism far longer than any of the other flatworms, but their origins are lost in obscurity. There are no free-living species, and apart from the egg, all the larval stages are endoparasitic—"they know not the light."

Birds must have undergone a great deal of their evolutionary history accompanied by tapeworms as well as Mallophaga. They are, therefore, a favourite subject with those systematists who try to demonstrate the true relationship of the parasites and their hosts, by studying them together. Krabbe first pointed out that each order of birds has its own particular cestode fauna and that consequently these worms can throw some light on the relationships of the birds. Over 900 cyclophyllid tapeworms (ten families and 135 genera) are recorded from avian hosts, and of the 45 known orders of birds 41 harbour "Taenias." Baer has elaborated Krabbe's theory and obtained some interesting results from his studies. Grebes and divers for instance harbour quite distinct tapeworms and the fact strongly suggests that the two groups of birds should not be placed together—as they often have been—in a natural scheme of classification. Two genera, *Schistotaenia* and *Tatria*, are confined entirely to grebes and, moreover, occur in this order all over the world. The genera *Gyrocelia* and *Progynotaenia* are found in waders only. Swallows and swifts each have distinct genera of tapeworms and although they share *Anomotaenia* the species are different. This latter genus is very large and spread through many orders, but certain species are often characteristic of closely related species of birds which are separated by wide geographical barriers. Thus, *Anomotaenia constricta* is

found in Britain in the carrion-crow and the rook, and in the U.S.A., in the eastern crow and the fish-crow (*Corvus brachyrhynchos* and *C. ossifragus*). From the same genus *A. nymphaea* occurs in the common curlew in Britain and in the Esquimo curlew (*Numenius borealis*) in the U.S.A., and *A. arionis* in sandpipers (*Tringa ochropus*, *T. stagnatilis* and *Actitis hypoleucos*) in Britain and in the yellowshanks (*T. flavipes* and *T. melanoleuca*) in North America.

In another large genus *Hymenolepis*, which occurs in mammals as well as birds, the same phenomenon can be observed, for species like *H. himantopodis* occurs in Britain in the black-winged stilt (*Himantopus himantopus*) and in the U.S.A. in the black-necked stilt (*H. mexicanus*). Two other species of cestodes, *Acoelus vaginatus* and *Diplophallus polymorphus* are also shared by these two waders on both side of the Atlantic.

The most impressive examples of this type are not, however, found among the British fauna. A separate order has been erected for the monstrously aberrant genus, *Nematoparataenia*, which contains only two species. One is found in the Australian black swan (*Chenopsis atrata*) and the other in the mute swan (*Cygnus olor*) in Sweden. The highly specialised genus *Amabilia* contains one species which is found in both African and South American flamingoes. We have already noted on p. 145 that the African ostriches and South American rheas share the same species of tapeworm, *Houttuynia struthiocameli*. It does not, in these cases, seem unreasonable to suppose that when these hosts diverged from a single stock they already harboured the tapeworms which are still common to them both to-day. In the interval they themselves have developed or evolved along different lines.

The Class is generally divided into two sub-classes, one of which is reserved for the primitive Cestodaria from fish. The other, the Cestoda, contains three orders, of which two infest birds. The first, the Pseudophyllidea, develop as a so-called proceroid larva in the body cavity of Crustacea, such as copepods, and in the plerocercoid stage in the muscles and coelom of fish. The sexual stage is found in aquatic and fish-eating mammals, birds and reptiles. In the genus *Diphyllobothrium* the final hosts include man, the cat, arctic fox, various seals, gulls, and terns.

The great mass of bird cestodes are found in the second order, the Cyclophyllidea (Plate XXVIIc). These tapeworms are characterised by the possession of four cup-shaped suckers on the scolex (see

Fig. 4 (2)), often with a rostellum (or centre piece) armed with hooks. Unlike the worms of the preceding order, only one intermediate host is used apparently, by the cyclophyllids. The cysticeroid larva generally develops in an invertebrate—an insect, mite, mollusc, worm or crustacean. The adult is found in three of the main classes of vertebrates, but principally in birds.

A glance at the cestode fauna of the domestic duck makes a convenient starting-point for studying many of the tapeworms of avian hosts. One of the best known of the duck parasites of the order Pseudophyllidea is *Ligula intestinalis* which has also been recorded in Britain from terns, gulls, grebes, the shag, razorbill and crow. The first intermediate hosts are the copepods *Cyclops strenuus* and *Diaptomus gracilis*. The second intermediate hosts are fresh water fish which feed upon copepods, principally bream, roach, dace, gudgeon (Cyprinidae) but also brook trout, powan (Salmonidae), pike (Esocidae), perch (Percidae) and lampern (Petromyzontidae).

The related genus *Schistocephalus* has similar habits. The first intermediate hosts are various copepods (*Cyclops viridus* and *C. serrulatus*), the second intermediate host is a fish, the miller's thumb (*Cottus gobio*), the three-spined stickleback (*Gasterosteus aculeatus*) and the salmon (*Salmo salar*), and the final hosts in addition to ducks, are divers, grebes, guillemots, terns, gulls, auks and other aquatic birds.

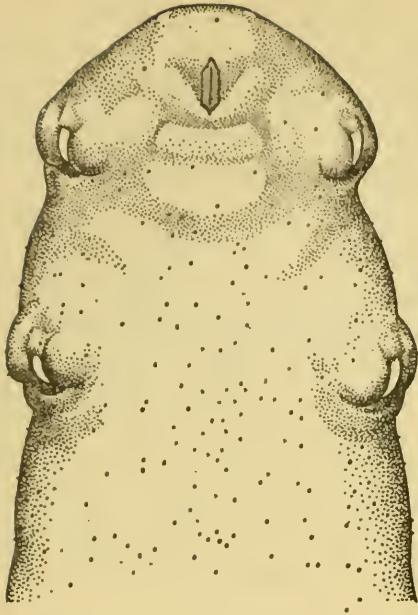
Perhaps the most familiar of all the cyclophyllid tapeworms are contained in the family Hymenolepidae. No less than fifteen species of the enormous genus *Hymenolepis* have been recorded from the domestic duck. The intermediate hosts of *H. anatina*—which parasitises geese and swan besides duck—are Ostracods (*Cypria ophthalmica* and allied species). Other *Hymenolepis* develop in calanoid and cyclopoid copepods, fresh-water shrimps (*Gammarus*) and water fleas (*Daphnia*). Insects serve several species found in poultry and probably a similar type of intermediate host is used by *Hymenolepis* parasitising tits, tree-creepers, nightingales and other small birds.

The common species *Fimbriaria fasciolaris* from the same family infects a wide range of duck including mallard, teal, widgeon, garganey, goldeneye, long-tailed duck, pochard, eider duck, scoters and mergansers. The intermediate host is the copepod *Diaptomus vulgaris*. Another allied genus is *Aploparaksis*, of which *A. furcigera* and one or two other species occur in the domestic duck. Many wading birds are also infected, and *A. flum* is common in the woodcock, jack snipe and

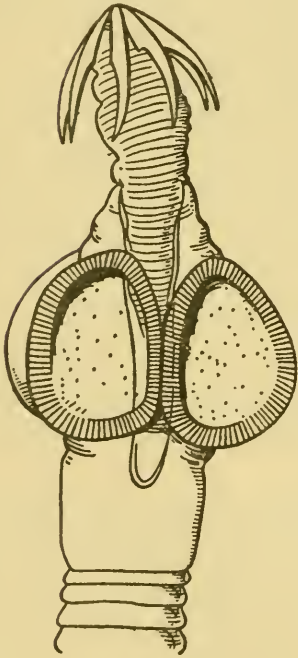
FIG. 4

Organs of attachment in three different groups of internal parasites

(1) Proboscis of tongue-worm, *Reighardiu sterna* (x 5.5) from air sacs of a tern, (after Heymons); (2) Suckers and hooks of a duck tapeworm, *Hymenolepis macracanthos* (x 133), (after Fuhrmann); (3) Proboscis of spiny-headed worm, *Corynosoma turbidum* (x 106) from a cormorant (after Van Cleave)



(1)



(2)



(3)

common snipe in Britain. Other species of the genus are found in gulls and *A. dujardini* is a parasite of starlings and thrushes.

A species of the genus *Tetrabothrius* is found in the eider duck, but not in the domestic duck. This genus, which is a north European, North American and Arctic group, is chiefly characteristic of sea birds, such as the gulls and terns, but is also found in whales. In Britain *T. cylindraceus* has been recorded from the manx shearwater, herring-gull and fulmar, and *T. macrocephalus* from the red-throated diver, black-throated diver and great crested grebe. One specimen of *T. erostris* was collected from the glaucous gull.

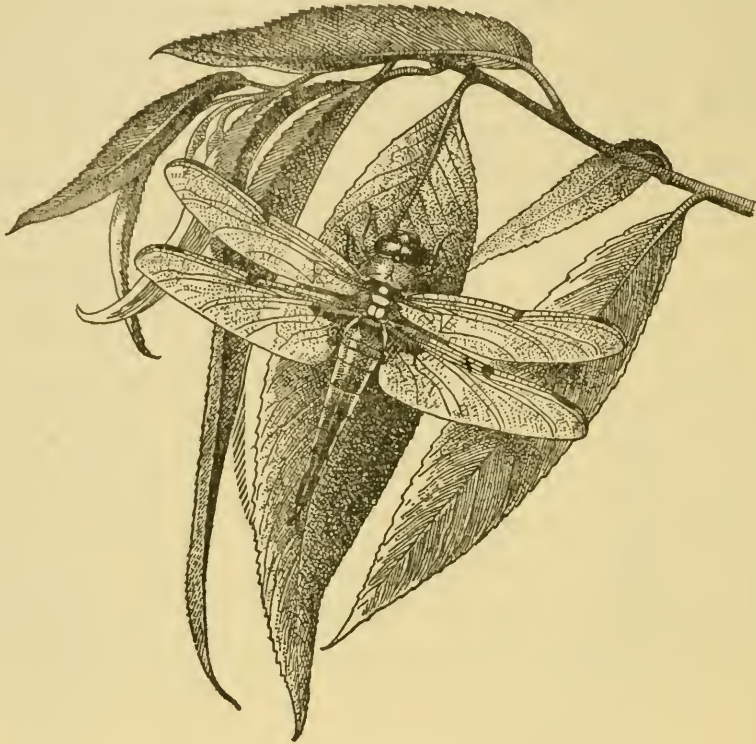
An important family is the Davaineidae, which includes the large genus *Raillietina*. These tapeworms are chiefly characteristic of the orders Galliformes (gamebirds) and Columbiformes (pigeons) although several species, such as *R. anatina*, have been recorded from the duck, but not yet from Britain. The known intermediate hosts include ants, flies, beetles and snails. The same remarks apply to the allied genus *Cotugnia*.

Recently a great deal of attention has been centred on cestodes of the family Anoplocephalidae, which are common parasites of mammalian herbivores. One of the great mysteries of helminthology was solved when Stunkard proved that the intermediate hosts of *Moniezia* are oribatid mites, many of which live near the roots of the grass and are accidentally ingested by the host while it is grazing. It will probably be found that *Aporina delafondi*, which is a widely distributed parasite of pigeons and turtle-doves in the Old World, has a similar life-cycle.

Large numbers of hyper-parasites have been recorded from worms. A book of over 450 pages has recently been published, compiled by Dollfus, dealing exclusively with the parasites of helminths. Protozoa, bacteria, fungi and other worms are the principal enemies. Generally these organisms are mentioned in passing by the authors who are more interested in the worms themselves. Birds must also rank as enemies, for they search systematically for ripe proglottids containing eggs in the faeces of animals and eat them with enthusiasm. We have already mentioned that, at times, the sheath-bill (*Chionis alba*) subsists largely upon the parasitic worms it finds in the faeces of colonial nesting birds, particularly the gentoo penguins. As tapeworms require an intermediate host for development the sheath-bills do not themselves become infected, although they are continually ingesting millions of ripe eggs.

FLUKES (TREMATODA)

Bird flukes (class Trematoda, sub-class Digenea) are colourless, leaf-shaped worms, generally only a few millimetres in length, which live inside the various organs of the host's body. They feed on blood and



Dragonfly, *Libellula quadrimaculata*,
an intermediate host of the oviduct fluke (x .66)

lymph and other fluids and exudates and also possibly on cells of the mucous membrane lining their particular habitat. They attach themselves by means of a sucker surrounding the mouth and also by a second sucker when this is present, situated on the ventral surface of the body. The reproductive system of flukes is fantastically complicated. Except in one family, male and female organs are present in the same individual and self-fertilisation is the rule. When a worm is preserved and stained with various dyes, the different parts of the reproductive system can be clearly seen forming intricate and gorgeous patterns. No objective person can deny that the egg-shell producing glands of a trematode worm are aesthetically satisfying. The excretory system is

also very complicated, consisting of ramifying tubules with cilia arranged at the terminal branches, which keep up a ceaseless flickering, thus lashing the excretory products towards the bladder. These flame cells are objects of great fascination—like candles twinkling on a Christmas tree. On the other hand, the trematode's nervous system is extremely simple and it has no blood circulatory system at all. Nor does it possess a body cavity—so that the various organs lie embedded in the fluke like currants in a cake.

Excellent habitats for the study of bird flukes are mud-flats and saltings. These generally consist of flat stretches of mud and water, the no-man's land of the countryside, treeless, colourless and desolate expanses, which belong neither to sea nor earth. To those curious people who are attracted by lonely communion with nature, the bitter-sweet quality of these tidal deserts affords the acme of pleasure. There they can really get their fill of pale sunshine mixed with the nostalgic cry of curlews, and oyster-catchers twinkling against a skyline where sky and sea merge into a melancholy glassy waste.

Saltings are a paradise for wild birds such as waders, ducks, geese and gulls and for this reason they are also a paradise for flukes. The conditions found in the pools on saltings are about as favourable as they can be for these particular parasites; but the hazards of the trematode life-cycle are so great that survival must always be problematical. The future life for a larval flatworm is only the reward of one in a million.

A familiar bird in these surroundings is the redshank; and this is the host of *Cryptocotyle jejuna* which, in the adult stage, is located in the bird's intestine. The flukes' eggs pass out with the droppings and in this way become scattered over the mud and in the brackish water pools. Another animal which abounds in this habitat is a small mollusc, one of the spire shells (*Hydrobia ulvae*). It is sometimes found in concentrations of 32,000 to the square yard. The eggs of this particular redshank fluke hatch if they are eaten by the snail in question. Whether they are accidentally ingested with other food or whether *Hydrobia* has a fatal weakness for trematode eggs is not known. Once inside the mollusc's alimentary canal the egg liberates the ciliated larva known as a miracidium. This quickly bores its way into the tissues of the snail. In many species of trematode the miracidium hatches in the water and actively seeks the snail host. These microscopical larvae are provided with eye-spots as well as a boring spine and swim vigorously by means of their covering of cilia. They are generally strongly host-specific

and will only attempt entry into the "right" host. Some molluscs, for instance the scallops (*Pecten*), never harbour larval flukes, and appear to be entirely immune to their attacks. Once inside the tissues of the snail-host the miracidium degenerates into a hollow sac and a complicated type of asexual multiplication follows, the exact nature of which is still not understood. One theory supposes that the germ cells, which are carried within the body of the miracidium, segment and subsequently fragment; and these fragments give rise to the different types and different generations of larvae which develop in the snail (germinal lineage with polyembryony). There are numerous other theories, none of which is satisfactory. The larval form following the miracidium is an immobile simple sac-like structure known as a mother sporocyst. The next generation in the case of many species; including the redshank fluke, are larvae of a more complicated type which are called rediae. These are hollow worm-like forms, which possess a pharynx, primitive gut, specialised secretory cells, excretory system, and an ambulatory process. They are capable of a limited amount of movement, and feed actively upon the tissues of the host. Within their body cavity daughter rediae are developed, resembling the mother rediae, which emerge through a birth pore and add to the population, feeding and growing in the reproductive and digestive organs of the snail. Several of such generations are produced and then, for some reason not properly understood, the germ cells dispersed in the bodies of the various rediae, give rise to a different type of larva known as a cercaria. When these cercariae reach a certain stage of development they emerge from the rediae and continue development in the tissues of the snail. Eventually they work their way along certain well defined routes, such as the circulatory system, and escape into the water.

The classical type of cercaria is similar in shape to the adult fluke but provided with a tail. It does not remotely resemble the redia in which it developed. Certain fundamental anatomical features—the excretory system, suckers and gut—characteristic of the adult worm can generally be observed in the cercaria. Many adaptations connected with the free-swimming phase and the entry into the second intermediate host, such as the tail, fins, eye-spots, penetration glands, boring spines and cystogenous glands, are generally present.

In the case of the redshank fluke, thousands of cercariae emerge from one spire shell—all the progeny of a single egg. They are just visible to the naked eye, and, hanging motionless in the water, they

resemble minims on a line of music. The body is a semi-transparent colourless oval and the tail long and thin, and held aloft. The microscope reveals that this tail is provided with undulating frilly fin-folds. The cercariae of the redshank fluke can live in the water about eight hours. They swim strongly for a few seconds and then stop suddenly and sink slowly downwards in the characteristic "minim" attitude. Then, with equal suddenness, they begin to swim again. These cercariae, which have eye-spots, are extremely sensitive to change in light and shadow—a quality which no doubt assists them in reacting to the presence of second intermediate hosts, which in this case are fish—the gobies. If a cercaria accidentally comes into close contact with one of these fish it immediately attaches itself by means of the anterior spines, casts off its tail, pours out the contents of the penetration glands which soften the skin of the fish and quickly bores its way inside. It soon comes to rest a little way beneath the scales and there forms a transparent cyst. Within the cyst it undergoes further development in the direction of the adult fluke, and larval specialisations, such as the eye-spots and boring spine, are lost. In some species of goby the presence of the metacercaria stimulates the host to produce pigment granules in the skin. The hideous black spots covering the specimen on Plate VIIb each mark the site of one cyst of *Cryptocotyle*.

As we have seen the numbers of these larvae emerging from a *Hydrobia* which has eaten one trematode egg may run into several thousands. Occasionally a fish swims into a large swarm and the simultaneous penetration of great numbers of cercariae kills it. But even in small pools which favour high infection rates—for then eggs, larvae and hosts are all present in a small area and are more likely to make contact with one another—it is usual to find that individual fish harbour only a few cysts. When one of these fish is eaten by a redshank—and contrary to general belief redshank are very fond of small fish—the digestive juices dissolve away the cyst wall and the young fluke is liberated and continues its development in the intestine of the bird. Thus the life-cycle is completed.

In this life-cycle there are at least seven distinct phases : egg, miracidium, mother sporocyst, redia, free-swimming cercaria, encapsulated metacercaria and sexually mature adult. This is characteristic of most bird flukes although in some species variations occur. The miracidium can have a free-swimming stage while in others it has none. Again the redial generations may be missing and instead a succession

of sporocysts give rise to other sporocysts and cercariae. Sometimes the mother sporocyst is lacking and a mother redia develops directly within the miracidium. At times the cercaria encysts in the first intermediate host, in the open, on vegetation or on inanimate objects. In this way only one intermediate host is involved, but in other cases an extra, third intermediate host, may be added. Despite these variations the cycle is fundamentally the same and one can trace the egg, miracidium, redia/sporocyst, cercaria and metacercaria stages before the sexually mature adult is developed. This is one of the most mysterious aspects of the digenetic Trematoda. As a group they are highly host-specific with regard to the *first* intermediate host, which is almost always a snail, a fact which has led to the widespread belief that they were originally parasites of molluscs before the evolution of vertebrates. Why have all these flukes followed this same path, and why has none remained parasitic on molluscs in the sexual phase? This appears to be one of the most puzzling phenomena in the whole field of helminthology.

Cryptocotyle jejuna belongs to a large group of trematodes (Opisthorchioidea) which are all characterised by the same type of cercaria. With one or two important exceptions they use fish—fresh water, salt water or brackish water species—as the second intermediate host, and the final host is thus, of necessity, a fish-eating animal. A related species (*C. lingua*) parasitises the herring gull in Britain and many fish-eating sea birds (Plate XXVIIa). The periwinkle serves as the first host (Plate XXVIII) and various inshore fish like gobies (*Gobius*), wrasse (*Labrus* spp.), rockling (*Onos* spp.), blennies (*Blennius* spp.), and butterfish (*Pholis*) as the second intermediate host (Fig 5).

On the saltings it is a familiar sight to see large flocks of geese feeding in the distance. With field-glasses one can sometimes identify brent geese pulling at the eel grass stranded in the shallows—a plant which constitutes one of their staple items of diet. A careful examination of the long ribbon-like leaves reveals that they are often beaded with small, dark, hemispherical pearl-like cysts. This is the metacercarial stage of the trematode *Catatropis verrucosum* which as an adult worm is found in the caecum of various geese and ducks, such as the barnacle-goose, pink-foot, sheld-duck, merganser and so forth. The first intermediate host is *Hydrobia ulvae*. When the cercaria escapes from the mollusc it immediately settles on the shell of the snail or some inanimate object nearby and pours out a secretion from specialised

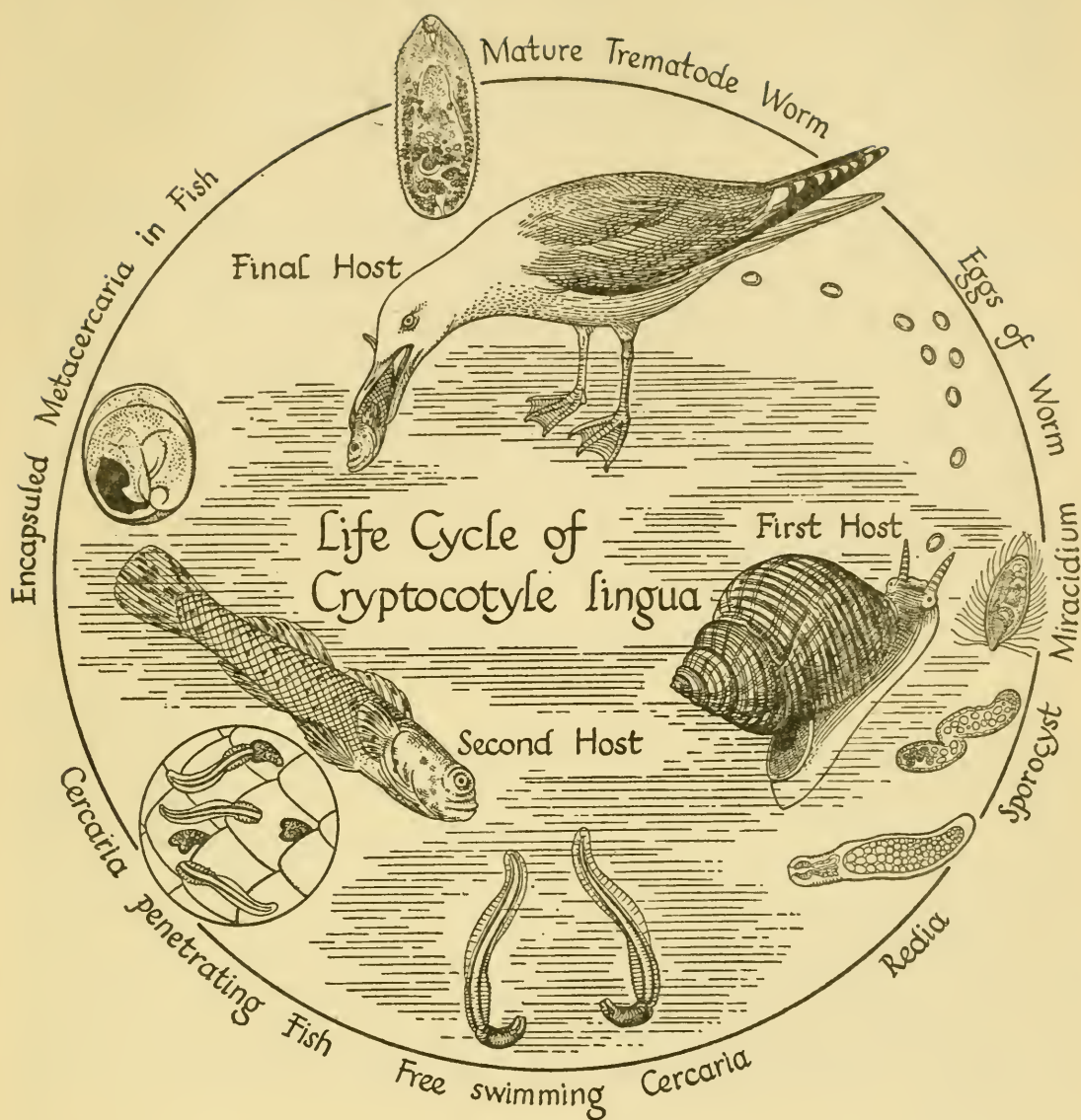


FIG. 5

Life-cycle of the herring-gull fluke, *Cryptocotyle lingua*. This trematode in its final stage is recorded from various gulls; different species of inshore fish serve as second intermediate host, but the first intermediate is invariably the periwinkle, *Littorina littorea*.

cystogenous glands. This fluid rapidly hardens into an impermeable cyst wall. As *Hydrobia* is found in large numbers feeding upon *Zostera*, the larvae when they emerge frequently encyst on the plant itself. The geese and ducks become infected by ingesting them along with the *Zostera* or by accidentally swallowing the minute snails which are encrusted with *Catantropis* cysts.

A few gulls are always to be seen dipping into pools, fishing in the little gullies on the saltings, or sitting in small flocks along the edge of the water waiting for the turn of the tide (Plate XL). No group of birds seems more heavily infested with worms and at least twenty species of trematodes have been recorded from the black-headed gull alone. One of the great groups of flukes, the Plagiorchioidea, is well represented in the gulls. The larvae of these flukes develop in so-called sporocysts—which are morphologically somewhat different from rediae—and although there are many exceptions to the rule, the majority employ arthropods as the second intermediate host. They have trowel-shaped cercariae armed with a minute javelin-like stylet with which they pierce the softer portions of the host's integument.

In the intestine of the black-headed gull and various other crustacea-eaters such as dunlin, godwits, turnstones, sandpipers, plovers, oystercatchers and curlews we find various flukes of the family Microphallidae, which are characteristic of the saltings and the shore. Several different species use *Hydrobia* and *Littorina* as the first intermediate host and the shore crab (*Carcinus maenas*) and *Gammarus* and other amphipods such as sand-hoppers as the second host. In the case of *Maritrema oocysta* (formerly known as *M. humile*) the cercariae cut short the complicated life-cycle, for they never emerge from *Hydrobia*, but cast off their tails and their stylet and encyst within the snail. Thus the redshank, which serves as the final host, becomes infected by eating the mollusc.

Another group of plagiorchid trematodes which infests an incredible variety of bird hosts are the oviduct flukes (*Prosthogonimus*). These worms have attracted a great deal of attention, for their presence in the domestic fowl greatly reduces egg-laying. Sometimes they get caught up in the egg during its development and any trematode the reader may find cooked up with his breakfast is almost sure to be this species. Up to date the known life-cycles all follow a similar pattern. The cercariae emerge from a freshwater snail and swim about in the water. Accidentally they are drawn into the rectal respiratory chamber of a dragon-fly

nymph. With the aid of their stylet they penetrate the integument and later migrate into the muscles of the insect, eventually encysting in the haemocoel. These metacercariae within their cyst are carried over to the adult dragon-fly (see p. 198), when the insect undergoes metamorphosis. Birds become infected by eating either the nymph or perfect insect. On the saltings geese, gulls and duck are frequently infected with *P. ovatus*, but this widespread fluke has been recorded from such varied hosts as skuas, sparrows, guillemots, corn-crakes, hawks and plovers. The only British record is from the crow, although it must occur in many of our common species.

There is yet another large group of flukes, the Echinostomatoidea, which is exceedingly common among the birds on the mud flats and seashore. They are characterised by a collar of spines, which is generally clearly visible in both cercaria and adult. The classical life-cycle for echinostomes which infect birds, involves two molluscs—the first a gastropod such as the winkle, whelk, top-shell, purple or spire-shell. The second is often a bivalve (lamellibranch) like the cockle, mussel or the clam. However, there are many variations and bird flukes of this group can sometimes use the same species of snail as both first and second intermediate host.

Many of the birds which frequent the mud flats and saltings are winter visitors. In the spring and summer they seek other haunts and during the breeding season they frequently become infected with flukes which are confined to fresh water invertebrates as intermediate hosts, and therefore, are not to be found in the larval stages on the mud flats. Different species from many of the large groups of bird trematodes, such as the Echinostomes, Notocotylids and Heterophyids, are adapted to fresh water as well as marine and brackish water, but others, such as the true fork-tailed cercariae, which are found as adults in mammals and birds are restricted entirely to fresh water. Of these the blood flukes (schistosomes) are the most notorious, for they have been a scourge to man in semi-tropical and tropical countries at least since the days of the Egyptian Pharaohs. In Britain there are no blood flukes which parasitise human beings. Birds are less fortunate. The duck mallard, teal, tufted duck and garganey—which form such attractive little parties along the main channels on the saltings—frequently fall victim to these worms on the stretches of fresh water they visit at other times. The snail host of the bird blood flukes (*Bilharziella*, *Gigantobilharzia*, *Trichobilharzia*) are pond snails such as *Limnaea* and *Planorbis*.

The fork-tailed cercariae escape into the water and after swimming about either attach themselves to the surface film, pieces of floating vegetation or each other, by means of their suckers and a slimy secretion. Duck, gulls and grebes, which swim in the water, sometimes come into contact with these cercariae, which by-pass the feathers, quickly penetrate the skin and migrate into the abdominal veins of the bird.

In the family Schistosomatidae the second intermediate host is dispensed with; there is no encystment or metacercarial stage and the cercariae penetrate directly into the final host. Another unusual characteristic of the blood flukes is the fact that the sexes are separate. Parthenogenesis has been recorded in one or two species. In some genera the male is provided with a double flap of skin which forms a ventral groove in which the female is carried about. In a permanent embrace they move slowly against the flow of the blood stream, laying their spined eggs as they go.

Not infrequently bird blood flukes attempt penetration of human beings with whom they make contact in the water. Although they do not undergo development in man, in the process of penetration they produce a disagreeable urticaria, known as swimmer's itch.

The other large group of fresh water trematodes with which birds on the saltings are frequently infected is the Strigeoidea. These are also related to the blood flukes, but instead of simplifying the life-cycle by omitting the second intermediate host, there is a tendency to complicate matters by interpolating extra hosts. In the case of *Cotylurus cornutus*, which inhabits the intestine of birds, the freshwater pond snails of the genus *Limnaea* serve as the first host. The fork-tailed cercariae which emerge into the water then penetrate other snails or leeches where they develop into a special type of metacercaria known as a tetracotyle. Swans, which somehow look vaguely out of place on saltings, and are more at home on artificial lakes and ponds, are often infected. So are duck, like scaup or mallard. Another strigeid, *Apatemon gracilis*, is passed on to smew, mergansers, goldeneye, scoters and wigeon in leeches. Gulls, such as the herring-gull, kittiwake, common gull, great black-backed and black-headed gull, are frequently infected with *Diplostomum spathaceum*, which is also located in the bird's intestine. The first intermediate host is, once again, a pond snail of the genus *Limnaea*. The second intermediate host is a freshwater fish, of which the rainbow trout is the most generally favoured. When the fork-tailed cercariae

have penetrated the skin they work their way through the flesh until they reach the blood circulating system. Here they migrate along the vessels until they reach the lens of the eye, where their peregrination ends. They do not encyst but remain as so-called "Diplostomulum" larvae which are free in the tissues of the host and there undergo further development. The pressure of these larvae often causes blindness in the infected fish and this probably furthers their chances of reaching the final host.

A number of small passerine birds such as wagtails and pipits are regularly seen on the saltings and although their flukes are principally found encysted in insects, some of their characteristic trematodes are essentially part of the brackish water fauna.

These few examples of the flukes found in a small number of representative birds in a restricted habitat scarcely touch the fringe of the subject, for trematodes are found in almost every species of birds and in almost every organ of the bird's body—ranging from the eyeball and frontal sinus to the air sacs, the kidneys, the stomach and the skin. In their life-cycle they utilise a vast network of animals—molluscs, leeches, worms, crustacea, insects, amphibians, fish and even small mammals.

At first sight it appears that adult trematodes are not a suitable group for studying the parallel evolution of host and parasite. It is, of course, obvious that the links between certain hosts which harbour similar worms, are their similar feeding habits, not hidden relationships. The cat, bass, osprey and man are all parasitised by the superfamily Opisthorchioidea—because they all eat fish. Frogs, bats and swallows, because of their predilection for insects, are the victims of the Plagiorchioidea. Nevertheless, once flukes become established within a certain group of animals they begin to evolve parallel with their hosts and in many cases it has been found that particular families of birds are parasitised by certain sub-families and genera of worms. It is certain that this particular line of research among trematodes will prove most fruitful and that more profound studies will reveal far greater host specificity, segregation and parallel evolution with the host, than is suspected at present.

The solving of life-cycles, however, is probably the most interesting and rewarding research in Helminthology to-day. The fluke living under the eyelids of carrion-crows is a peculiarly interesting species—but how does it get there? That is considerably more interesting. In order to solve this question one has to inquire into the habits of the

crow and also, most probably, into the biology and ecology of almost all the other animals with which the crow comes into contact. For instance, one of the bivalves it eats on the saltings might be the intermediate host : or the snails near the river : or one of the parasites which infest its own body : or some larval insect it picks out of a puddle or one of the mice it pounces on in the fields. Moreover, the linking of adult worms with their larval forms often reveals their correct systematic position and their relationship with other groups. Oddly enough, research into bird trematode life-cycles is, in this country, as untouched as the arctic snows. Anyone who cares to examine a few of the commoner brackish water molluscs can turn up a "new" undescribed cercaria with an unknown life history every day of the year. Yet, at the time of writing there is not one single worker in this field in Britain.

LEECHES (HIRUDINEA)

Leeches belong to a much higher category of animals than the other parasitic worms which attack birds. The Annelida are thought by some zoologists to be in the direct line of descent of the vertebrates, for they are metamericly segmented, possess a closed blood system and paired primitive kidneys (nephridia) along each side of the body.

The majority of leeches are predatory and even the parasitic species are only temporary parasites, adhering to mammals, birds, fish and frogs long enough to gorge themselves on blood—rather after the fashion of ticks and mosquitoes. The smallest of them, however, can pierce epithelial surfaces and they have been found in a variety of strange situations—on the gums of crocodiles, the lips of horses, attached to man's tonsils, in the pouches of pelicans, the anus of ducks and the trunks of elephants. The last fact impressed Pliny, who remarked : " The beast is by their tickling and sucking in his snout almost mad; which doth manifestly show the wonderful power of insects; for what is there greater than an elephant? and what is there more despicable than a horse leech? Yet the greatness and wit of the elephant must give way and yield to this Worm."

The only important leech parasite of British birds is the duck leech (*Proteclepsis tessellata*, family Glossiphonidae), which has been recorded in this country in ponds, and from the wigeon, teal and long-tailed duck (see tail-piece Chapter X). It is quite often found adhering to the

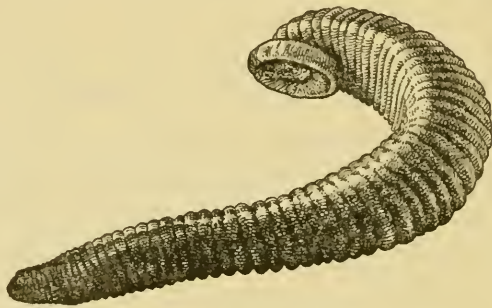
plumage of migrating birds and in this fashion must be carried far afield. Leeches generally attack the mucous membrane of the head, especially the nostrils, and domestic duck are not infrequently choked by an accumulation in their trachea which thus blocks the air passages. Leeches are also occasionally found in the digestive tract which they gain via the vent. The odoriferous greasy secretion of the uropygidial glands of water-birds is said to attract them strongly.

The duck leech, which is extremely active and restless, is quite small, only about 16 mm. long and barely 2 mm. in width. It is a beautiful olive green and pale grey in colour, finely sprinkled with black star-like pigment spots. There is a sucker at each end of the body, although in the preserved specimen figured on p. 210 only the large posterior disc shows up clearly. The mouth is provided with a protractile sucking tube which inflicts a small circular wound. Some leeches which have jaws armed with pointed teeth leave a wound like a three-pointed star. The digestive system is highly developed. The stomach has an acid reaction and is provided with voluminous caeca in which blood can be stored almost unchanged for many months. This enables the leech to undergo long periods of fast. The intestine has an alkaline reaction and in some species is also provided with lateral expansions. Glands which secrete a powerful anti-coagulant are situated in the head. It is this secretion which inhibits the clotting of blood in the wound made by leeches and which can thus be the cause of fatal haemorrhages in the host.

The duck leech is hermaphrodite and after copulation and fertilisation both parties separate, lay eggs and rear young. They are admirable parents, for not only do they brood their eggs but they also carry their 200-300 young about with them attached to their ventral surfaces. The aquatic hirudinids as a group have many enemies and are preyed upon by birds and mammals, frogs and newts and predatory insects such as dragon-fly larvae and water beetles. On the other hand they are carriers of various diseases of vertebrate animals ranging from a fatal frog trypanosome to the virus of fowl-pox. They are also intermediate hosts of several duck trematodes—a fact which demonstrates how persistently they are eaten by these birds.

The medicinal leech (*Hirudo medicinalis*) is a much larger species and, apart from other differences, has bright red blood, whereas that of the duck leech is colourless. Despite the observations of Pliny the presence of leeches is often quite unsuspected by their victims. Their bite is

painless and it is for this reason that they can obtain copious feeds without attracting the host's attention. The medical profession, for hundreds of years, used them for blood-letting and in this manner claimed to cure innumerable diseases. Thomas Mouffet remarked that "it were too tedious to reckon up all the melancholique and mad people that have been cured by applying leeches to the Hemorrods in their fundaments." Nevertheless, he was much impressed by the cure of the noble Richard Cavendish. "Now to the great wonder of the court he walks alone without help and being sound and void of all pain, he lives an old man." It is of course impossible to know for certain if a duck is tickled or worried by leeches attached to its vent, but it is unlikely that their presence is in any way beneficial.



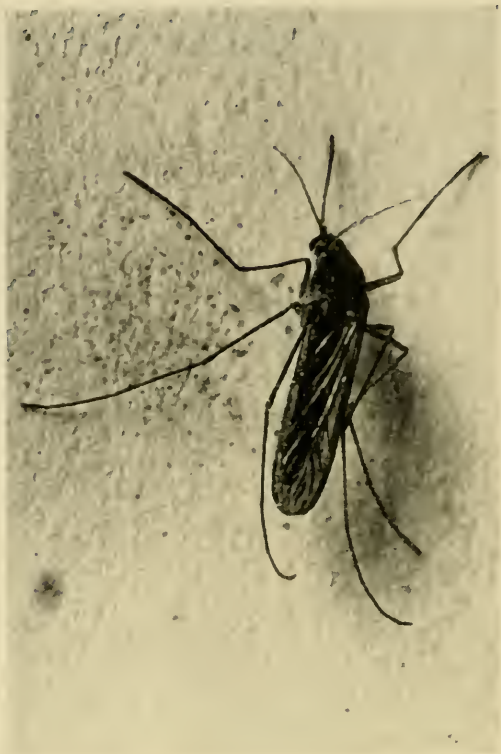
Duck leech, *Protoleipsis tessellata*,
from trachea of a teal (x 5.5)



Plate XXIX

Biting midge, *Culicoides obsoletus* (female, $\times 57$)

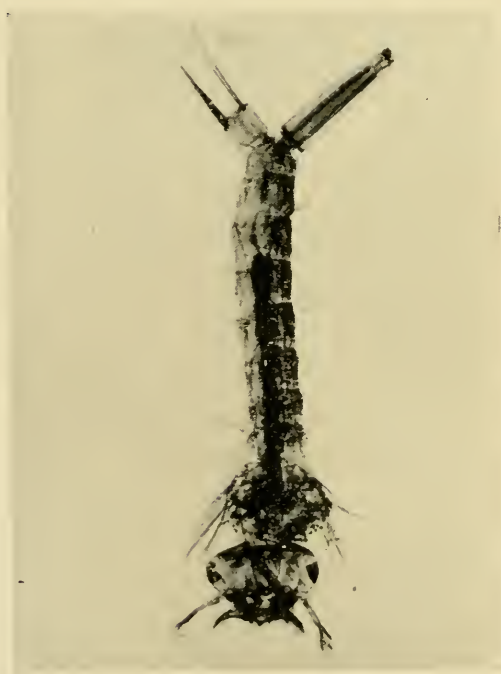
Arthur L. E. Barron



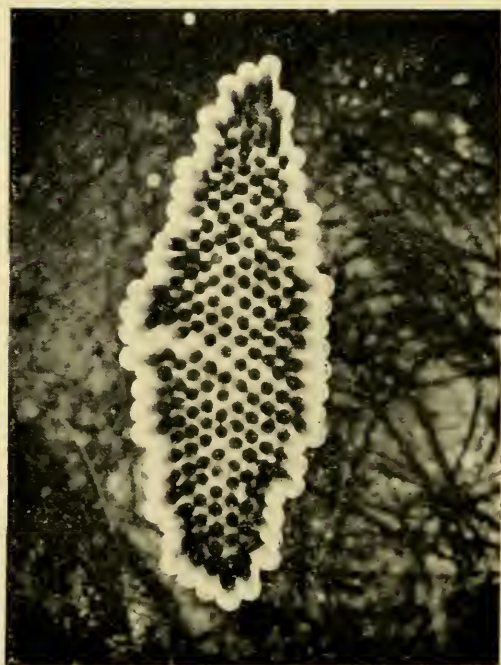
S. C. Porter
 a. House-gnat, *Culex pipiens*, adult female
 at rest ($\times 5.8$)



S. C. Porter
 b. *Aedes* sp., adult female at rest ($\times 5.8$)



J. G. Bradbury
 c. *Culex pipiens*, larva ($\times 9.5$)



J. G. Bradbury
 d. *Culex pipiens*, egg raft ($\times 14$)

CHAPTER I I

FLIES (DIPTERA)

All of them are begotten of filth and nastiness, to which they most willingly cleave, and resort especially to such places which are so unclean and filthy; unquiet are they, importunate, hateful, troublesome, tumultuous, bold, saucy.

THOMAS MOUFFET

LOUSE-FLIES, MOSQUITOES, MIDGES, BLACK-FLIES, HOUSE-FLIES, BLUE-BOTTLES AND NEST-FLIES

IF WE could talk to birds as we talk to each other we would probably find that flies loom very large in their lives and provide one of the major topics of conversation. By day they form a favourite article of diet for many birds, but during the night the tables are turned with a vengeance. Incidentally it is an act of great cruelty to leave a canary uncovered in a cage after dark, for it is then assailed by all the female house-gnats, which, during the day, sit about silently on the walls and ceiling of the room.

Flies are carriers of many diseases of both man and birds, and from this angle are certainly the most important group of insects. They are distinguished by the possession of only one pair of membranous wings (which are lost in some parasitic forms), the second pair being represented by an insignificant pair of knobbed appendages (halteres) which the ancient writers mistook for "eyes hanging by their sides." These can be clearly seen on Plate XXIX. A fly's head is joined to its thorax by a slender flexible neck. The various component parts of the thorax are fused, and this again is joined to the body by a distinct waist. The mouth parts of the various types of flies are profoundly modified according to the food they eat (Plate XII, a and c) but most of the parasitic forms are blood-suckers. The metamorphosis of all flies is complete, that is to say they pass through an egg, larval and pupal stage before

hatching into the perfect insect. The louse-flies and the tsetse fly (*Glossina morsitans*), an African species, which is known to attack birds as well as mammals, are viviparous. An impressive character of most Diptera—as well as many other insects—is the instinctive protection they afford their offspring by selecting suitable spots for laying their eggs or larvae. For instance the sheep bot-fly (*Oestrus ovis*) deposits her young larvae on the wing, striking at the eyes and nostrils of sheep or goats. Sometimes she makes a mistake and darts at the eyes of shepherds whose breath smells of sheep or goat's milk. Some black-flies (Simuliidae) crawl beneath running water in order to lay eggs on submerged vegetation. An even more extraordinary case is that of a South American warble-fly (*Dermatobia hominis*) which sometimes attacks turkeys, causing nodule-like warbles in the superficial layers of the body in which the larvae develop. This fly captures a female mosquito and attaches her eggs firmly to its abdomen. When the mosquito, loaded with ripe eggs, alights on some warm blooded animal to feed, the larvae—apparently activated by the heat—quickly emerge and penetrate beneath the host's skin.

LOUSE-FLIES (HIPPOBOSCIDAE)

The most highly specialised parasitic flies attacking birds are the louse-flies (Plate IX). As adults they live permanently on the body of the host, feed on its blood and pupate in its nest. Compared with a robin a louse-fly is very large. It is over a quarter of an inch in length and a small bird with one or two of these insects creeping about in its feathers can be compared to a man with a couple of large shore crabs scuttling about in his underclothes.

Hippoboscids (which also attack mammals such as sheep, horses and deer) display the classical specialisation for an ecto-parasitic life. Their antennae are sunk in a groove and the mouth parts form a piercing apparatus and a long, sheathed sucking proboscis. Their wings are often reduced or absent. They are flattened dorso-ventrally with remarkably tough leathery cuticles; their legs are large and muscular and armed with formidable toothed claws. The whole integument is covered with ugly backwardly projecting spines. They have also developed an extremely efficient method of moving among feathers—darting and scuttling about at a remarkable speed—and are extremely difficult to catch on a living bird. This manner of progression is, in a

subtle way, very characteristic and was well described in the *Theatrum Insectorum*: "They never fly forward but sidelong, as it were, hopping and skipping as they go." For reasons which defy analysis, louse-flies are particularly repellent insects, and most people experience a shudder of disgust at the sight of them, and are filled with a quite unreasonable feeling of horror if they happen to dart up their sleeves or into their hair while handling the host. A bite from a louse-fly, which is neither dangerous nor painful, is an occupational risk and keepers on grouse moors and members of the Edward Grey Institute of Field Ornithology are among the few people who are bitten fairly often. Louse-flies are too large to infest the host in great numbers, for a big infestation would kill the bird.

The usual hazards of a parasite's life make special precautions for the offspring necessary. Instead of laying large numbers of eggs hippoboscids go to the other extreme. Only one young is produced at a time but it is hatched and nourished within the body of the parent fly. It is subsequently deposited in the nest as a fully grown larva which immediately pupates. In this stage it passes the winter and hatches out the following spring. The adult fly is also rather long lived and may survive several months.

It has already been mentioned that some louse-flies have fully developed wings and some have mere vestiges which are useless for flight; in others again the wings are cast off when the fly reaches the host. The sheep ked (*Melophagus ovinus*) has no wings at all (Plate IXc). It was pointed out in the chapter on evolution that it is a great advantage for a parasite which lives on the body of the host not to have wings. In the case of birds such as the swallows and swifts which return year after year to an old nest, the difficulty of finding a host is greatly reduced. It is therefore not surprising to find that the wings of the swift louse-fly (*Crataerina pallida*) and the swallow louse-fly (*Stenepteryx hirundinis*) are greatly reduced and non-functional (see Chapter 6). In the case of the common louse-fly (*Ornithomyia avicularia*) which is found on a wide variety of birds, ranging from robins to arctic skuas, the difficulty of finding a host still sets a premium on wings, and they are fully developed in this species.

In Britain there are five species of louse-fly known from avian hosts. Apart from the three already mentioned, the finch louse-fly (*Ornithomyia fringillina*) is a common species (previously also known under the name of *O. lagopodis*) and is recorded from many hosts, and the

heron louse-fly (*Lynchia albipennis*) was once taken off a purple heron. In this country louse-flies are rarely if ever found on the bodies of birds during the winter months but up to 50 per cent. of a population may become infested in summer. The young are far more susceptible to attack than adult birds.

It is interesting to find that the geographical distribution of some species does not depend entirely on the distribution of the host. The common louse-fly in Britain has a distinctly southern distribution; farther north it is replaced by the grouse louse-fly. The two species, however, are difficult to distinguish and are often confused; further information is required before defining the exact areas they occupy. Like the fleas, the bird louse-flies spend a part of their life-cycle in the nest, so they are not entirely protected from changes in climate. This factor is probably the key to their respective distributions.

Outside Britain a malaria-like parasite of birds (*Haemoproteus*) is spread by the pigeon louse-fly (*Pseudolynchia canariensis*). Since many wild birds are infected with this disease in Britain it is highly probable that our species of hippoboscids are also carriers of the disease.

MOSQUITOES AND GNATS (CULICIDAE)

Mosquitoes and gnats are small slender flies with long legs and an elongated proboscis adapted for piercing and sucking (Plate XIIc). If they are examined carefully the characteristic fringe of scales—often rainbow-hued—on the veins and margin of the wings can be seen. “The structure and make of the gnat,” wrote one of the early naturalists, “there is no man but may justly admire. For in that so small insect and as good as none almost what reason is there? what inextricable perfection? . . . where his taste, where his smelling? where is begotten that terrible and great sound?” It nevertheless would have surprised the writer to know how much print and paper has been devoted to the mosquito since his day. Even the fall of the Roman Empire has been seriously attributed to their agency, as carriers of malaria.

Mosquitoes are a fairly large group of which over 2,000 species have been described—about 30 from Britain. They are found throughout the world from the tropics to the arctic circle. The most important genus as far as birds are concerned is *Culex*, although some species of *Aedes* and *Anopheles*, both found in this country, will sometimes attack

birds. *Culex* is an ancient genus, which already existed, as the fossil record proves, in the Oligocene period thirty million years ago. It is now mainly tropical or subtropical, only a few species penetrating into the temperate zone. Four of these are British, but only one, the most common and familiar of all mosquitoes, the house-gnat (*Culex pipiens*), is an important parasite of birds (Plate XXX). In India, Ross used the related *C. fatigans* for his world famous experiments proving the transmission of bird malaria by these insects.

Only the female house-gnat bites, and she does so principally at night. It is when swallows and martins gather in the reeds in communal roosts prior to migration (see Plate XXVI) that they are severely attacked, and mass infection with bird malaria frequently follows. In the southern seas these insects are said to cause entire colonies of pelicans to desert their nests. The behaviour of mosquitoes in the dark is difficult to observe unless they attack man himself, but recently an extremely ingenious invention has made this task much easier. Large numbers of the insect are captured and then sprayed with fine luminous adhesive dust. Subsequently they are released and their movements can be followed in the dark like aeroplanes with lights attached to their wings. It is not known if roosting birds are frightened by the pipe of a female mosquito. There is, however, some evidence that cattle have an inherited fear of the hum of the warble-fly (*Hypoderma bovis*) and an inherited fear of gnats might well have survival value in birds.

Mosquitoes are as a rule very fussy about the conditions in which they will mate. Some choose the evening before dark but only when the light intensity has fallen below 2.0 foot-candles. A bright light will put them off. As for the house gnat, it refuses to mate in a confined space. If the air is still the males swarm, just after sunset and again immediately after dawn, about six to nine feet from the ground to the leeward of some prominent object, like a high hedge or the stone coping on a roof. In the case of *Culex pipiens* about 50 to 100 males take part and the whole swarm moves rhythmically up and down—in the case of some other gnats it oscillates from side to side. The female is attracted by the hum of the swaying column and in the excitement her natural reserve is broken down and she is drawn into the swarm. She is then seized by a male, and the couple drop out of the dance and copulation takes place on the ground.

The house-gnat lays her eggs in the form of a boat-shaped raft which floats (Plate XXXd). In order to do so she stands on the surface

of the water, crosses her long hind legs near their extremities, and extrudes her eggs which are covered with adhesive cement, within the V-shaped mould thus formed. Each raft consists of 200 to 450 eggs and she may produce five or six rafts during her life. *Culex pipiens* lays on clean or foul water, in butts and tubs, tanks, wells, ditches, pond margins and stagnant puddles contaminated by farm manure or urine. Eggs are also deposited in pools in salt marshes providing they do not contain more than half sea-water.

Gnat larvae (Plate XXXc) are aquatic and sometimes occur in vast numbers. It was once estimated that 400,000,000 were present in two acres of Hampshire flood water, only a couple of inches deep. They feed by whirling minute particles of food into their mouths by oscillating a brush-like moustache, or by chewing up vegetable or animal matter—including one another if they get the chance. After moulting three times the larva pupates. The pupa is also aquatic and, like the larva, floats near the top of the water with its respiratory trumpets piercing the surface film.

The males hatch first. During the summer they dance their lives away and die when the cold weather sets in. Their mouthparts are poorly developed and they cannot suck blood and are limited to a diet of fruit juice and nectar. It is easy to distinguish a male from a female mosquito without the aid of a microscope as the male has feathery antennae. In the human species it is man that has a deep voice but in gnats conditions are reversed and the pipe of the male is several notes higher than that of its mate.

The female house-gnat requires a blood meal before she can lay fertile eggs and her chief victims are birds, although she will occasionally bite frogs and snakes and even mammals. In captivity her egg output is trebled if she is fed on bird's blood. Certain species of *Aedes* have been known to migrate thirty miles inland from the saline marshes where they breed, presumably in search of a blood meal. They subsequently return to the marshes to lay eggs. The distance covered is known accurately, owing to the re-capture of marked specimens. *Culex pipiens* will also supplement her diet by feeding on nectar, milk standing in pans, and even port wine. In the modern dairy the separator has deprived them of their chief source of milk, as a thick layer of cream on top appears to be an essential condition of feeding. Piercing the cream to get at the liquid beneath seems a satisfactory substitute for piercing the skin of a vertebrate animal to reach the blood below. When feeding

on flowers she will also pierce the involucre bracts in order to get at the honey. When the female is fully fed her voice drops in pitch from F to D. She is a voracious feeder and will ingest 1.2 milligrams of blood in a single meal although her own weight is only 1.4 milligrams. Small wonder that her voice becomes a trifle mellow.

Unlike the male, the female house-gnat survives the winter by hibernating in cellars, cool outhouses, dairies and cricket pavilions and living upon her own fat-body which is a reservoir of food. If she mates in the autumn she can store the sperm in her body and fertilise her eggs in the spring.

In Part II it was shown that different species of bird fleas are "zoned" according to the nesting habits of the host. Different species of mosquitoes also frequent fairly well defined elevations—a fact which is most noticeable when they swarm. Traps baited with living birds reveal that different genera and species are caught near the ground, in the lower and middle branches, and near the tops of trees. In nature there is probably a closer link with definite species of bird host than has hitherto been realised.

As carriers of disease female mosquitoes have no equal. Malaria, yellow fever, dengue and filariasis are among the maladies transmitted to man in the tropics. In Britain they transmit malaria and fowl-pox to birds and probably also filaria. They themselves have many enemies. Water-beetles, dragon-fly larvae, various small fish and newts feed voraciously on the immature stages. In the course of nine nights one newt (*Triton*) ate no less than 985 gnat larvae. Bats and birds, especially swallows and swifts, feed eagerly on the adults. Apart from one midge which sucks blood directly from gorged female mosquitoes instead of from the body of a mammalian host, they are free of insect parasites. This is remarkable when we consider the vast number of species which attack butterflies, moths, beetles and wasps, and so forth.

Naturally the best known parasite of the house-gnat is the malarial Protozoan, *Plasmodium relictum*, and its allies. Susceptibility to malaria appears to be hereditary in *C. pipiens*, and some strains are completely resistant. The egg production of infected females is greatly reduced and in this manner, as well as in a variety of other ways, it has a deleterious effect on the host. There are also numerous other fatal and harmful parasites of both larva and adult, ranging from Protozoa and Fungi to scarlet hydrachnid mites, so it must be admitted that mosquitoes themselves are not without their troubles.

Owing to its great economic importance the group as a whole has been intensively worked, and a vast literature has grown up around it. Unfortunately mosquitoes have proved difficult insects to study. Three hundred years ago Thomas Mouffet summed up the situation satisfactorily: "The distinction of gnats," he wrote, "is very perplex and obscure and has puzzled all the philosophers."

BLACK-FLIES (SIMULIIDAE)

The so-called black-flies, which are not always black, contrast with mosquitoes in a number of ways. They are smaller and dumpy, with short legs, and the female bites only by day. The larva and pupa, however, are similarly aquatic but they mostly inhabit swift running streams with highly aerated water and not stagnant pools.

The group contains approximately 500 species of which about 20 are British. Unfortunately very little is known about their blood-sucking habits in this country and much of the available information comes from observations made on similar species abroad.

The majority of species of black-fly attack mammals, but some confine their attention to birds, while a few bite both types of host indiscriminately. The best known bird black-fly in Britain, which is confined to the south and south-eastern parts of the country, is *Simulium venustum*. It will swarm on the heads and rumps of sitting hens and turkeys and drive them off their nests, and it will also force its way under the wings of young birds and suck their blood—sometimes with fatal results. The bite of the black-fly is much more painful than that of mosquitoes and its saliva decidedly toxic. At times they are responsible for the death of large numbers of cattle in eastern Europe. In America *S. venustum* is the carrier of a malaria-like parasite (*Leucocytozoon*) of wild ducks which it occasionally transmits to the domestic variety with fatal results. Another species is the vector of an allied Protozoan from the turkey. As *Leucocytozoon* is widespread among British wild birds (see p. 169) it is highly probable that black-flies are also carriers in Britain.

Only the female black-fly bites. The males are smaller and easily distinguished by their greatly enlarged eyes which almost meet on the top of their heads. Whereas the male mosquitoes attract the females by a communal dance, the male black-fly actively seeks his mate and is thus frequently found on or near the host. In some cases copulation takes place in nooks and crannies on the body of the mammal or bird

concerned. The female requires a blood meal before she can lay fertile eggs.

The eggs, which may number over 300, are deposited in jelly-like masses on the edge of streams or scattered over the water. In some cases the female skims above the surface laying an egg every time she dips her abdomen into the stream, and again at other times she crawls below the water to deposit her eggs on submerged vegetation and under stones.

The larva, which moults six times, has a fan-like structure round its mouth with which it sweeps minute organic particles down its throat. In order to be able to withstand a strong current it is provided with a posterior circlet of spines by which it can anchor itself in the upright position to stones and plants. In some streams there are very large numbers of these larvae. A count once revealed 734 to a square inch on a submerged branch. When the upper reaches of a stream begin to dry up, which often occurs in the case of swiftly running rills or rivulets, the larvae of some species migrate downstream.

The pupa is enclosed in a slipper-shaped silken cocoon spun by the larva. When the fly is ready to emerge it uses a sort of Davis-escape device. Air collects within the pupal skin until it finally bursts. The fly is then carried to the surface in a bubble of air, without even getting its feet wet—and darts away into the sunshine. Adult flies migrate many miles from their breeding haunts, possibly helped by the wind.

Birds destroy large numbers of black-fly. Chickens for example eat them greedily, and when they approach a barnyard fowl singly it is always a toss-up which will feed on the other. Aquatic birds also gorge on the larvae which they skim off submerged vegetation and stones.

Mosquitoes are carriers of various species of *Filaria*—nematodes which complete part of their development in the insect. Black-fly are also carriers of a related group of worms, *Onchocerca*. The larvae of these worms are confined to the connective tissues just under the skin of the infested mammal. They are consequently taken up by Simuliidae, which do not drill straight into the blood stream like mosquitoes but rasp a hole in the skin of the host. It has been claimed that the saliva of the black-fly attracts the worms.

Apart from Protozoa and nematodes there are several other parasites of these insects, but few, if any, are yet recorded from this country.

Although *Simulium venustum* is the best known of the bird black-flies in Britain, there are at least two other species, *S. latipes* and *S. aureum*,

which are far commoner and are distributed throughout England and Scotland. King Lear may have had the latter species in mind when he spoke of "the small gilded fly." The body of the female is covered in dense, gleaming, golden scaly hairs, and on the wing it resembles a little ball of light. It sucks the blood of geese.

BITING MIDGES (CERATOPOGONIDAE)

Midges suck the juices of flowers and pierce the wing-veins of dragon-flies, butterflies, moths and lace-wings, and many small insects are caught and devoured whole. One British genus only, *Culicoides* (Plate XXIX), of which some thirty species are found in this country, feeds on the blood of mammals and birds. The development of the parasitic habit in this family is therefore particularly easy to follow. Relatively little, however, is known about them or their life histories.

Midges are minute flies, only a few millimetres in length. The female alone sucks blood—generally at dusk or by night, but sometimes in blazing sunshine. The eggs are laid on moist soil or near water and the larva and pupa are aquatic or live in damp soil. Unlike those of gnats they can survive quite long periods out of the water without suffering any ill effects. Sometimes they breed in the liquid running from manure heaps, the sap seeping from gashes in trees or moist decaying vegetable matter. One Japanese midge which attacks hens, breeds in their dung.

There are no definite records of *Culicoides* biting birds in Britain although it is fairly certain that most of the species do so. In the United States large numbers of *C. biguttatus*, closely related to *C. fascipennis*, were found gorged with blood in the nests of crows and magpies. Although they are so small, midges are cruel and persistent biters. They do not fly in the wind, but they can soon take the romance out of a still summer evening. *C. impunctatus* is a major pest in the west of Scotland, "where its presence in conjunction with the kilt is said to have given rise to the Highland Fling."

HOUSE-FLIES (MUSCIDAE), BLUE-BOTTLES (CALLIPHORIDAE) AND NEST-FLIES (CARNIDAE)

Most of the house-fly group are not blood suckers, but the African tsetse flies (*Glossina*) attack both mammals and birds. The stable-fly

(*Stomoxys calcitrans*), which is widely distributed throughout the British Isles, is also occasionally found in birds' nests, and it is quite possible that if no mammals are available it finds sparrows and swallows satisfactory substitutes. The greatest numbers of the house-fly group, which are found either as obligate or occasional occupants of birds' nests, prey in the larval stage on other dipterous larvae or eat decaying animal and vegetable matter. They are not parasites of the birds themselves. The majority of the blue-bottle group are also parasitic in their larval stages on the larva and pupa of other insects. Many breed in decaying animal matter and sometimes they eat flesh and corpses. The larvae of flesh-flies (*Sarcophaga*) and the green-bottles and blue-bottles (*Lucilia* and *Calliphora*) and certain other genera are quite often found consuming the decomposing flesh in wounds on the bodies of birds. The original wound may have been inflicted by a blood-sucking insect. They are facultative parasites, and their presence is in the nature of a recurring accident. One genus however, the blue or green metallic flies (*Protonotaria*), are true ecto-parasites of birds in the larval stage.

The bird-bottle fly (*P. azurea*) feeds on nectar as an adult, and it can sometimes be seen around flowers in the sunshine (see tail-piece p. 5). The larvae live in the nest and at certain intervals attach themselves to the nestlings by their anterior end, which is modified to form a sucker with hooks in the centre. Although they sometimes kill the host they are frequently present in large numbers without apparently causing much harm. In one magpie's nest 373 larvae were counted, but the fledgelings seemed healthy. The species is quite common in Britain and has been recorded from a large number of birds, including the nightingale, redstart, skylark, meadow-pipit, and various tits, wagtails, crows, swallows and martins.

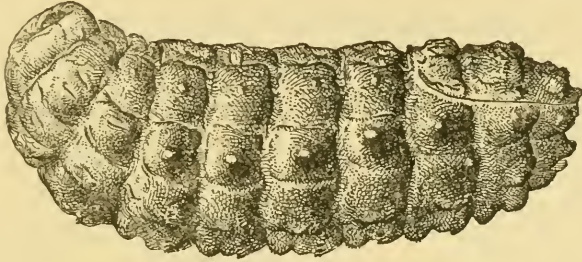
A frequent parasite of British birds with similar habits is the nest-fly (*Neottiophilum praeustum*). It is a large yellowish brown fly and the larva, which lurks in the lining of the nest, is a voracious blood-sucker. The anterior end is armed with two strong hooks which it thrusts into the flesh of the young bird while feeding. When fully gorged it drops back into the nest. Too many larvae in one nest kill the fledgelings and the female fly guards against this disaster by dispersing her eggs in several nests. The principal hosts are passerine birds and Basden has reared it commonly from nests of blackbirds, thrushes, finches, warblers, carrion-crow and the linnet; but it has also been taken occasionally from nests of the nightingale, tree-creeper, sparrow and hedge-sparrow.

One of the most interesting flies parasitising birds is *Carnus hemapterus*. It is a tiny, shining, black-bodied fly, only a few millimetres in length and it lives among the feathers of the host. The life-cycle is passed in the nest. The larva (according to Nordberg) is saprophagous and feeds on dead and decaying animal matter. Up to a few years ago it was thought that the adult was a blood-sucker, but the mouth-parts are not adapted for piercing and sucking and it is now considered more probable that it feeds on the fatty or waxy exudates from growing feathers. Both sexes of the fly are fully winged when they hatch, but after reaching a host—even if the distance covered is a few inches from the bottom of the nest to the back of a nestling—they break off their own wings, some distance from the base where there is a line of weakness, leaving a stump. After the wings are shed the abdomen becomes enormously distended owing to the abnormal growth of the fatty tissues. This curious condition is known as physogastry and it is usually developed by flies and beetles which are parasitic or symbiotic in ants' or termites' nests.

Carnus hemapterus has a wide distribution in Europe and America. Host-selection seems to depend on the type of nesting site rather than the species of bird. Tits, starlings, woodpeckers, and other hole-nesters are greatly favoured, but a wide range of host records exists which includes falcons, finches, warblers, crows, pigeons and swallows. It is not a common species in this country, although it is probably often overlooked, and has been bred from the nests of the starling, hedge-sparrow, barn-owl and blackbird. There are numbers of British species from the allied genus *Meoneura*, all of which are very small flies about one mm. in length. Sand-martins appear to be the host of *M. lamellata*, and a great variety of birds harbour *M. neottiophila* in their nests, including hawks, tits, woodpeckers, pigeons, finches, blackbirds, and carrion-crows.

The bird itself is an important enemy of flies but the various parasites which attack them are more important, especially in the larval stages. One type of mite eats the eggs of Muscidae, the adults hitch-hiking around on the body of the fly. There is also a formidable list of Protozoa (including the trypanosomes) and Fungi, of which flies are the known host. An exceptionally large number of pathological organisms are associated with Diptera owing to their unsavoury habits. Thus while feeding upon the excrement of birds they swallow the spores of *Coccidia*, the causative agent of so-called grouse disease, which is thus spread to other individual birds. They also swallow the eggs of tape-

worms of birds and disseminate them far and wide. Moreover they carry a truly remarkable number of bacteria about with them. Pains-taking Chinese workers calculated the grand total from a single house-fly and found 3,500,000 adhering to the outside and 30,000,000 to the inside of its body.



Parasitic larva of bot-fly, *Hypoderma bovis*, (x 3.5)

MITES (ACARINA)

They are so small that Epicurus said it was not made of Atoms but was an Atom itself . . .

THOMAS MOUFFET

THE MAJORITY of mites have roughly globular bodies, with their head and thorax fused, two pairs of mouth-parts and four pairs of legs in the adult stage. The larvae have only six legs when they hatch, but after a certain number of moults develop into nymphs with the full complement of legs. They are so small that it is necessary to have recourse to the microscope in order to see their structure. The number of species of free-living mites only outnumbers the parasitic mites by about three to one, and it is believed that parasitism must have arisen independently about a dozen times in the group. If ever an assembly of animals were pre-adapted to this particular mode of life it is the mites, not only on account of their minute size and varied feeding habits, but also because of their insatiable desire to wander about and creep into cracks and crevices. Except in a few families they are not greatly changed by their dependent existences. Mites living as ecto-parasites, however, even in distantly related suborders, develop striated cuticles. This is another case of parallel evolution which, like the development of combs on insects, appears to be the direct result of life in fur and feathers.

The best known group parasitising birds is that of the red mites (Dermanyssidae) which hide and breed in nests and under the bark of trees and creep out at night to suck the blood of the host. A common species in Britain is the swallow red mite (*Dermanyssus hirundinis*) which greatly resembles the common red mite of poultry (*Dermanyssus gallinae*), also widely distributed in the nests of many wild birds, including various passerines, gulls, and pigeons. *D. quintus* is a parasite confined to the green woodpecker, and *D. passerinus* from the greenfinch is an interesting

Irish record. All the red mites are true blood-suckers and when present in large numbers they may bleed the host to death. They are also carriers of relapsing fever of birds. *Fonsecaonyssus sylvarum*, also a type of red mite (Macronyssidae) which attacks poultry, pigeons and wild birds, has been found to be naturally infected with the virus of western equine encephalitis. Another related group sucks the blood in the nasal cavities of birds, such as sparrows, bullfinches, swallows, dippers, eider ducks and so forth. There are records from the Shetland Isles of *Rhinonyssus neglectus* from the purple sandpiper, *Sternostomum caldonicum* from the guillemot and *S. waterstoni* from the little auk, and several related species from various hosts.

Among the true feather mites the Analgesidae are the most familiar on birds, and over 150 species are known from Britain alone. These mites are not blood-suckers but feed upon the horny layers of the skin and the feathers. Some genera are found exclusively on the pinions (rectrices) of relatively large birds. Two well known examples are *Pterolichus ardeae* on the heron and *P. cuculi* from the cuckoo. Occasionally a species favours a circumscribed area of the pinions, such as the white portions of the wings of the nightjar, and is not to be found anywhere else. Certain other genera, notably *Syringobia* from various waders, including the sanderling and green sandpiper, and *Thecarthra* also, from plovers and gulls, inhabit the quills of some of the larger feathers and feed upon the pith. They seem to know when the moult is due, for they are never found in cast feathers. They lay their eggs in neat spirals inside the quill and if no male happens to be in the same feather with the females, they resort to virgin birth. The genus *Analges* and its allies contain mites which are found on all parts of the bird's plumage except the pinions. The specimen of *A. chelopus* illustrated on Plate XXXIb, was taken from the hedge-sparrow. The enormously enlarged third pair of legs of the male is a characteristic feature of these mites. They are not used for fighting but serve to lock the female in a firm embrace during copulation. In some species such as *Megninia strigis-otis* from the short-eared owl the male seems to stimulate the female by making passes over her with his huge legs and does not resort to force. In other cases (such as *Protalges attenuatus* from the barn-owl) his fierce love-making permanently dents her cuticle. These mites normally copulate precociously, before they are mature. If no female is available they pay a high price for their enforced virginity, for development is retarded or even arrested, and they fail to grow their

magnificent clasping legs—symbol of masculine virility in the acarine world. Another group of genera is found on the feathers of the wings, flanks and back of passerine birds. Some are confined to a single host and others occur on a wide variety, but the majority favour certain definite families and groups of birds such as finches, tits, crows or thrushes. Typical British species are *Trouessartia minutipes* which is peculiar to the house-martin, *Joubertia microphyllus* (Plate XXXIa) which is found on the chaffinch and tits, and *Proctophyllodes glandarius* which occurs on a wide range of hosts.

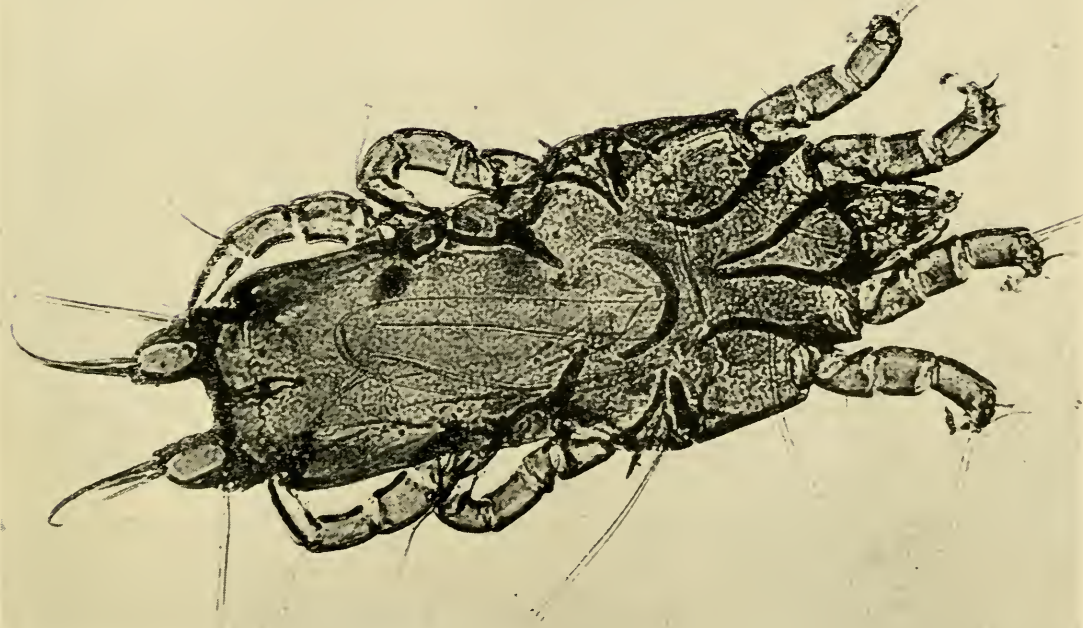
Certain wing mites (*Oustaletia pegasus*) found in the tropics on the hornbills (Bucerotidae) have the dorsal setae modified to form feather-like expansions. A superficial glance conveys the impression that they are winged, hence their Greek name.

Members of another group of the feather mites live next to the skin of the bird, at the base of the fine down feathers, and probably feed on scurf and skin débris. *Microlichus avus* from the jay and sparrow and *Epidermoptes bilobatus* from the fowl are typical examples.

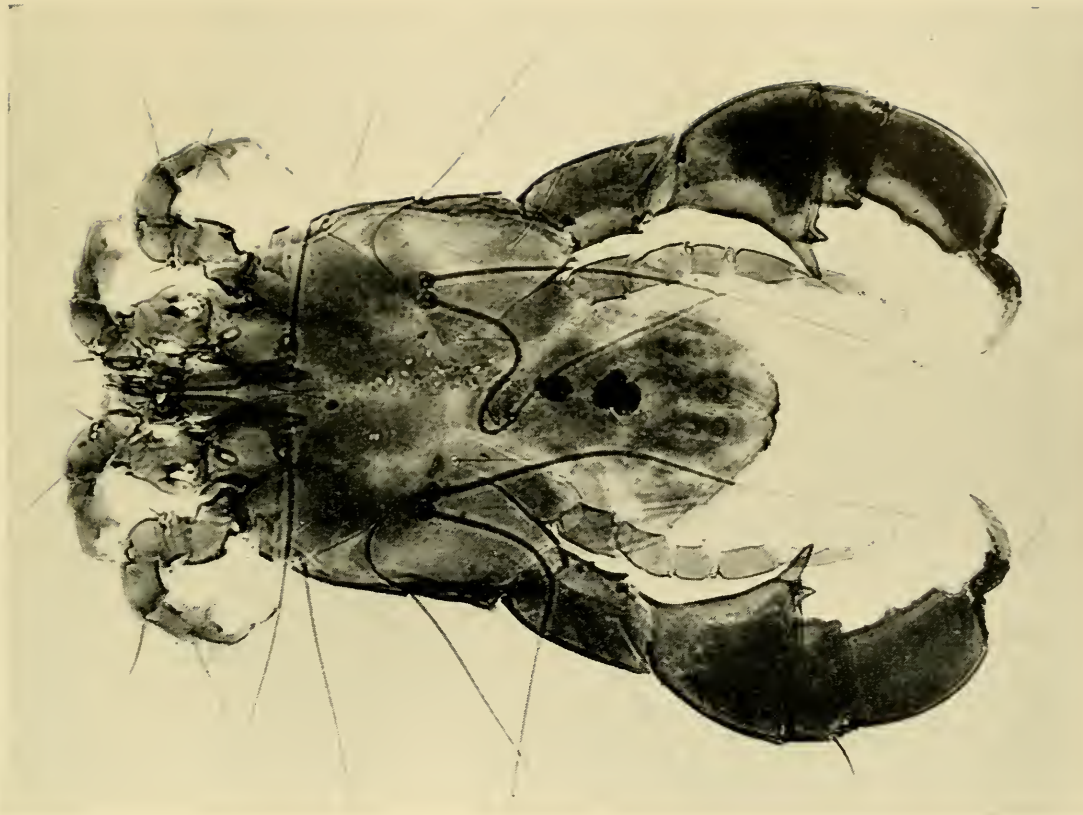
Although all true feather mites lay their eggs on the feathers, in some genera and species such as *Falculifer rostratus* from doves and pigeons and *Pterolichus obtusus* from the partridge, the second nymphal stage is passed in the fatty tissues beneath the skin of the bird. In the case of *Michaelichus bassani* from the gannet, the membranes lining the subcutaneous air-cells are selected, where the mite is often present in large numbers. The males of this species are generally asymmetrical; the only "normal" specimens have been found by Turk on gannets from Great Saltee Island.

Closely related to the itch mites are the lung mites (Cytolichiidae) which are found in the bronchial tubes and lungs of birds. Sometimes they invade the air sacs and even bone cavities in such numbers that the birds die of suffocation. Well known species in Britain are *Cytodites nudus* from the pheasant and turkey and *Laminosioptes cysticola* from poultry.

The true itch mites (Sarcoptidae) are best known as parasites of men and dogs and are the direct cause of scabies and mange, but some species also attack birds. Thomas Mouffet described them vividly, "always lying under the outward skin and creep under it as Moles do, biting it and causing a fierce itching." Familiar itch mites are the species which cause scaly leg and de-pluming mange in poultry, *Cnemidocoptes mutans* (see p. 228) and *C. gallinae*. As they pass their whole life beneath the skin they have no use for the adhesive



Arthur L. E. Barron
a. *Toubertia microphyllus*, female, from chaffinch



A. E. Botting
b. *Analgus chelopus*, male, from hedge-sparrow; the male shows enlarged claspng legs which are absent in the female



Arthur L. E. Barron

a. Nymph, ventral surface (× 16)



W. T. Tams

W. T. Tams

b. Engorged adult from head of a willow-warbler, (× 5.1), ventral surface and dorsal surface

suckers on their feet, or the long tactile hairs which are characteristic of most ectoparasitic mites, and these structures are missing in *Cnemidocoptes*. In addition their legs are very reduced and the mouth-parts greatly modified.

An interesting family of mites is the Cheletidae, members of which are predacious and hunt the true feather mites in the bird's plumage. Some have abandoned this symbiotic way of life and have turned parasite. The species of the genus *Syringophylus* live inside the quills of pigeons and poultry and their bodies have become greatly elongated and profoundly modified in shape to suit their long narrow habitat. In this way they resemble the quill mites of the Analgesidae, which are also slim and elongated. The quite unrelated and abundant hair-follicle mites (Demodicidae), which are parasites of mammals, show a similar type of adaptation; they have long cylindrical bodies and their legs are reduced to mere stumps.

The genus *Harpyrynchus* is also truly parasitic. They live in the feather follicles of passerine birds which they enlarge to form tumours about the size of peas. These are located chiefly on the flanks and wings of the host. The females never emerge from these tumours and only the immature stages are "free". In shape they form a great contrast to *Syringophylus*. Far from being long and narrow they are almost circular with stumpy legs reminiscent of the itch mites. Sometimes colonies of *Harpyrynchus* destroy the follicular bulbs over large areas of the birds' bodies, thus causing a sort of feather mange.

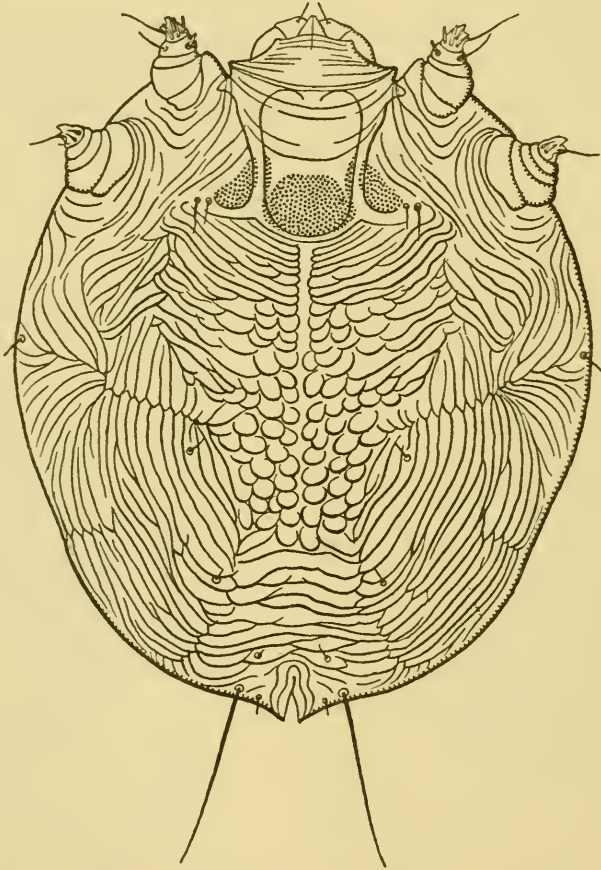
The Laelaptidae are essentially parasites of mammals, especially the small rodents, but a few species are found upon birds. *Eulaelaps novus* appears to be confined to the sand-martin, and *Ptilonyssus nudus* is recorded from the song thrush and various small passerines in Britain.

The brilliantly coloured harvest mites (Trombidiidae) are parasitic in the larval stages although free-living and predacious as adults and nymphs. They are often found in great numbers on game-birds, thrushes and other ground-loving species. They attach themselves to the skin, which they pierce, and feed on lymph.

Mites of the family Tyroglyphidae, known as cheese mites owing to their predilection for that particular delicacy, are often found in birds' nests. They feed chiefly on decaying organic matter, but some are predatory or parasitic. During development many species pass through a dispersal stage known as a "hypopus nymph". The egg hatches as usual into a six-legged larva, which in turn sheds its skin and becomes

an eight-legged nymph. At this stage the subsequent moult produces the hypopus. This form is devoid of mouth parts and cannot feed. The legs are reduced and several adhesive discs or suckers are developed on the ventral surface. It is solely adapted to phoresy or passive dispersal by some arthropod carrier. It is these hypopus nymphs which are found hitch-hiking on fleas (see p. 103), flies, ticks and even on the wings of moths. They are never parasitic at this stage and use the adult insect merely as a means of transport. Nevertheless in large numbers they can cause the death of the transport host.

In the adult form the bodies and secretions of mites are toxic, at any rate to man, and possibly to other animals. So-called grocer's itch and miller's itch are really forms of acute dermatitis (sometimes accompanied by fever, asthma, vomiting and other symptoms) produced by contact with flour and grain heavily infested with mites.



Itch mite, *Cnemidocoptes mutans*, occurring on various birds
(x 176)

TICKS (IXODOIDEA)

Ticks are really only large mites which may reach a length of half an inch or more when gorged. There are about 300 different species in the world and as a group they are not really successful. Sometimes, however, a single species is present in fairly large numbers. It was estimated that in certain parts of the U.S.A. there were 2,800,000 feeding ticks to the square mile, parasitizing the snow-shoe hare and ruffed grouse, but this is nothing compared with certain mites which may number several thousand to the square inch.

A few species are confined exclusively to birds, although a fairly high proportion feed on both mammals and birds and in their larval stages some regularly attack ground-nesters, such as larks and plovers.

There are two groups of ticks which have adopted rather different types of lives. Members of the family Argasidae, which are tough and leathery with gorgeously embossed integuments, live and breed in nests and burrows, and feed at night when the bird or mammal returns to rest. They engorge very rapidly and therefore do not have to leave the habitation of the host. They are found mostly in warm and tropical countries and in the rigours of the British climate they seek out a species like the domestic pigeon, which lives in sheltered dove-cotes. Members of the other family of ticks, the Ixodidae, which have a dorsal plate or scutum on their backs, are not nest dwellers and depend for food on a chance meeting with the host as it wanders about in the fields and woods. They engorge slowly and therefore spend a considerable amount of time actually attached to the bird's body. The fully fed female of the most familiar British species, the sheep tick, *I. ricinus* (Plate XXXII) looks like a shiny blue pea sticking firmly to the skin of the host. The mouth-parts are deeply embedded in the flesh and on account of the recurved spines (Plate XIIId) which anchor the rostrum in position it is extremely difficult to dislodge. This a typical adaptation to the parasitic mode of life and impressed the early naturalists. Thomas Mouffet wrote, "For Tykes will sometimes enter deep into the skin with their nose, that you can hardly pull them out but with the loss of their heads and they seldom wander but they bite cruelly and make themselves a hollow place and there they stand fast." In addition to the spined rostrum (Plate XIIId), ticks have suckers between their claws which assist them in clinging to the host, especially before they become fixed and in their larval stages.

The lives of the Ixodidae are far more precarious than those of the Argasidae—a fact which is reflected in their greatly increased egg output, the females laying in thousands instead of hundreds.

Ticks are the great exponents of the gentle art of waiting. An adult can wait from four to seven years for a meal and even a young larva will survive six months without feeding. The great food reservoirs (for the host's blood) in their branching intestines makes this extraordinary endurance feat possible. Both sexes sometimes wait many months for a mate and finally when they come together copulation can last over a week.

On emerging from the egg the larva has only six legs and is known as a seed tick. It has to wait for a passing host in order to obtain the first blood meal. Subsequently it drops to the ground or back into the nest and moults into an eight-legged nymph. Again it has to wait for the host and another blood meal, after which it once more drops to the ground and moults, this time emerging as a fully mature tick (Plate XXXIIb). Yet another wait for the host follows.

The familiar sheep tick (*Ixodes ricinus*), feeds equally well on a large variety of mammals including stoats, red deer, rabbits, squirrels, mice and even hibernating hedgehogs. In fact it will attack any warm-blooded animal with which it comes into contact. It has been recorded from many birds, and favours ground-feeding and ground-nesting species like grouse, larks and meadow-pipits, but it has also been taken from the long-eared owl, whinchat, redwing, blackbird, rook, lapwing, chaffinch—altogether from 47 different British birds.

It is generally located on the head of an avian host, attached near the eye or the angle of the mandibles, where it cannot be pecked off. After engorging for a few days on the bird the female drops off to lay her eggs, but an unfertilised female is incapable of finishing her meal and remains attached, sometimes for weeks and months until found by the male, who quickly puts an end to her dreary repast.

Copulation between ticks is most peculiar. The male enlarges the female sex orifice with his rostrum—a surgical operation which takes a considerable time—and then with the aid of his mouth-parts introduces a packet of his own sperm inside the female. Soon afterwards he dies.

In most Ixodidae it is the male which actively seeks the female, but sometimes the rôles are reversed. Again there are those curious cases where no male has ever been found and the eggs develop parthenogenetically. In rare instances the males, which are dwarfed, are parasitic upon the females, and suck the host's blood via the body of their mates.

There are several *Ixodes* which are confined to birds. A cosmopolitan species, widely distributed in the nests of sea birds is the guillemot tick (*I. uriae*). In Britain it is recorded from gannets, fulmars, guillemots, puffins, curlews and so forth, from many coastal districts including Devon, Yorkshire, the Farne Islands, St. Kilda and Shetland. On a narrow ledge of cliff 400 feet above the sea and frequented during the breeding season by tens of thousands of sea birds, Hewitt observed a pair of *I. uriae* copulating beneath a stone, with four or five males standing by waiting their turn. The scene was described in a graphic correspondence with Wheeler at the end of the last century, and makes the reader sigh for the days when naturalists still found time to cultivate letter writing as an art.

Another species which parasitises sea birds is the shag tick (*I. univavatus*) which is confined to cormorants and shags and has been collected near Plymouth, the Scilly Isles, the Cheddar Gorge and also certain locations in Scotland and Ireland. *I. canisuga* is taken constantly from the nest of the sand-martin in Britain, and continental writers consider it is a separate species confined to this bird. Occasional records from other bird hosts include *I. caledonicus* from crows, ravens, rock-doves and a Greenland falcon from Scotland; *I. brunneus*, which is confined to bird hosts in Europe, Africa and North America, and has been found once in England on an owl; and *I. passericola* which was discovered by Turk on a Cornish house-sparrow nesting under the eaves of his own house. There is also one record of *Haemaphysalis cinnabarina* from the stone-curlew, and *Hyalomma marginatum* taken off a migrating rose-coloured pastor on Fair Isle.

It is interesting to note that in the U.S.A. when the numbers of the snow-shoe hares are at low ebb the tick population of *H. leporis-palustris* depends almost entirely on the ruffed grouse (*Bonasa umbellus*) as an alternative host.

The best known British example of the Argasidae, is the pigeon tick (*Argas reflexus*). It lives in dove-cotes and pigeon lofts, although the first record in this country was made from specimens caught in Canterbury Cathedral. At one time it was considered peculiar to "the dark recesses of this time honoured fane." When pigeons are not available it attacks other birds, such as sparrows and chickens.

Ticks are very dangerous parasites. Their saliva which they pour into the flesh of the host can be highly toxic, and the bite of one tick may kill the host. Even their eggs contain poisonous substances which

can prove fatal to birds. Blindness sometimes follows attachment in the region of the eye, and the flesh of the bird becomes "pulpy" and semi-liquid in the immediate vicinity of the tick. Many fatal diseases of mammals are carried by ticks and both the pigeon tick and fowl tick (*A. persicus*) are vectors of fowl relapsing fever. The causative agent is a spirochaete (*Borrelia anserinum*), which undergoes development in the body cells of the tick. Many birds are susceptible to this fatal disease which is passed on in the eggs of the tick. The larvae are thus already infected at birth.

Some birds, besides the "delousers" mentioned in Chapter 3 destroy large numbers of ticks. Jackdaws have been seen feeding avidly on the guillemot tick and in many places chickens are run in with cattle and sheep to keep the pastures free of them. They are also eaten by ants and are parasitised by small Hymenoptera which lay their eggs in the bodies of young nymphs which are then consumed alive by the developing insects.

TONGUE-WORMS (PENTASTOMIDA)

The tongue-worms in the adult stage inhabit the nasal fossae and respiratory tract of vertebrates—chiefly reptiles. They feed on blood and slimy exudates. The only species known from birds is found in the air sacs (see Fig. 4 (1) p. 196). The larval form, which is ingested in the egg stage, invades the viscera of a much wider range of vertebrates which act as intermediate host, but there are only a few stray records from birds.

These curious parasites appear like worms—cylindrical, blind and pale. The body, which is generally a few centimetres in length, is often divided into rings but these do not correspond to any internal segmentation. Two pairs of retractile hooks which superficially resemble cats' claws, and are thought by some to be vestigial appendages, are placed on either side of the mouth. Respiration is cutaneous. The sexes are separate. The females are larger than the males and may have over a million eggs developing simultaneously in their ovaries.

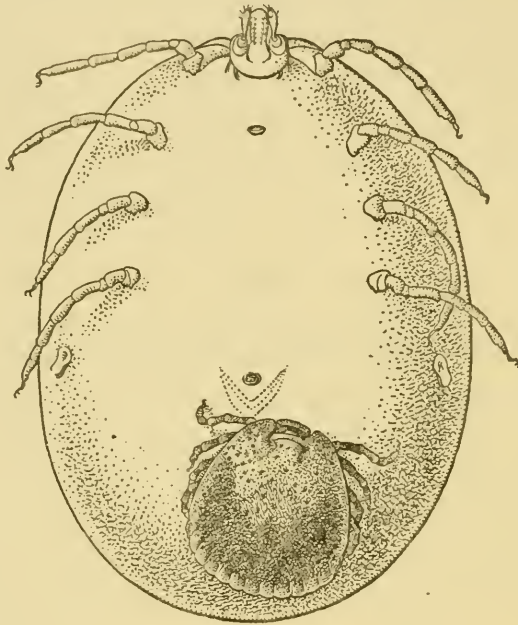
As we have said, the chief hosts of tongue-worms are reptiles, which include some of the largest forms, such as the boa-constrictors, pythons and crocodiles. Related species from certain genera parasitising crocodiles and various large snakes, are found in widely separated

parts of the globe, with large areas in between where they are altogether absent. These two facts suggest that the Pentastomida is a group of great antiquity, a supposition which is supported by the morphology of the tongue-worms themselves. The single species which in its adult stage parasitises birds, *Reighardia sterna* (order Cephalobaenida), is placed in a genus and family of its own. It has not yet been recorded from Britain but as three out of the five known hosts are on the British list it seems highly probable that in due course it will be found here. The species has been collected from the common tern in Italy, North America and China, from the ivory gull in Greenland, and the glaucous gull from Lapland. The bird tongue-worm is therefore widely distributed, but in this case the discontinuity may be more apparent than real, as collectors of pentastomes are rather rare and widely distributed themselves. The intermediate host is not known, but a fish of the herring group seems a reasonable guess. On the other hand nymphal stages have been found in the veins of the common tern, which suggests that development could be direct, without the help of an intermediate host.

There is a single record of a larval form found in a bird on the British list, namely *Armillifer armillatus* from the honey-buzzard in Sweden. This species is a parasite of pythons in the adult stage, but like many of the spiny-headed worms it apparently has the power of encapsulating in a variety of hosts if ingested accidentally and has also been found at this stage in man, leopards and dogs !

The great interest of the tongue-worms lies in the fact that they are so modified, apparently by their parasitic mode of life, that no agreement has been reached with regard to their correct place in the animal kingdom. At one time or another they have been classified with the flat-worms, and the roundworms—in fact with all the major groups of parasitic worms. To-day (1946) they are placed with the Arachnida in the *Zoological Record*. Chandler (1946), however, considers them to be a separate and aberrant class of arthropods. Baer (1946) states that the tongue-worms are now attached to the annelids or segmented worms. Heymons, who is probably the greatest authority on the group, cautiously suggests that they occupy a position somewhere between the arthropods and the annelids. Their life-cycle, which involves an intermediate host, is certainly reminiscent of the parasitic worms. The first larval stage when it emerges from the egg, on the other hand, has two pairs of vestigial legs and resembles a mite. Some authors regard these legs as atrophied appendages of the arthropod pattern, while others

argue that they represent degenerate parapodia of the polychaete type. In many cases when the adult parasite has been modified beyond recognition and reduced to a pallid worm-like organism, the larvae provide the answer and prove they are cirripedes, copepods or molluscs as the case may be. But in this instance the larvae, like the adults, have suffered such a profound change that their present structure merely presents a series of unanswerable conundrums, which have so far kept the zoologists guessing.



Female tick, *Aponomma* sp. (x 8)
with parasitic male attached.

CHAPTER 13

MICRO-PARASITES

For who hath despised the day of small things?
ZECHARIAH 4:10

MODERN PLUMBING stands between us and daily intimacy with tapeworms and lice, but most of us are still familiar with the effects of the microscopical parasites, the bacteria, fungi and viruses. Sooner or later we contract some infectious or contagious illness, a cold in the head, boils, ringworm or a more serious disease like measles. The unlucky ones may develop tuberculosis or catch infantile paralysis. Birds are also victims of these microscopic and ultra-microscopic organisms, but unless they initiate diseases which also affect man, either directly or indirectly, little is known about them. The average individual is unaware that sparrows also suffer from colds in the head and that wood-pigeons and starlings may contract tuberculosis.

BACTERIA

Bacteria, which are usually classified as plants, have been described by Gardner as minute cells, consisting of semi-liquid protoplasm, surrounded by a flexible protoplasmic membrane. They lack a cell-nucleus comparable to the structure common to Protozoa or higher organisms, although evidence has accumulated which suggests that there is a nuclear apparatus in many respects analogous to those characteristic of multicellular plants and animals. In form bacteria may be spherical or spheroid (*Coccus*), or rod-shaped, either blunt or tapering (*Bacillus*, *Bacterium*), or twisted and shaped like a corkscrew (*Spirillum*, *Vibrio*). All the motile types possess flagella which are extremely difficult to see even with a high powered microscope. They

act as locomotor organs and also help to churn up the nutritive medium in which the organism lives.

Bacteria usually multiply by binary fission. The cell lengthens to almost twice its normal size, a septum is formed and it then splits transversely into two halves. After division the cells sometimes adhere to one another, forming aggregations or chains. Some bacteria produce spores, a process which might be described as transformation rather than reproduction, since no increase in numbers is involved. The spore stage is probably a resting phase in which the bacterial cell is more resistant to unfavourable external conditions. *Bacillus anthracis*, the causative agent of anthrax, can remain alive on fields in the spore stage for several years and resist boiling for ten minutes ! The cyst stage in certain parasitic Protozoa and worms is somewhat reminiscent of spore formation in bacteria.

Owing to their minute size it is difficult to describe these organisms adequately by morphological characters alone and many bacteria must be distinguished by their biochemical and physiological functions and the symptoms they produce in the host. Reactions to dyes and the body fluids of various animals are also of great importance for the purpose of identification. Their classification, Topley points out, is based largely on chemical structure rather than the gross architecture of the cell. Most free-living bacteria are saprophytes, but many commensals and most of the symbiotic and parasitic forms obtain their nourishment by decomposing or breaking down living cells or body fluids into a form which they can assimilate and synthesise into protoplasm. The harmful effects on the host are due to the poisonous substances which bacteria produce. These give rise to the various symptoms and lesions which are characteristic of certain diseases. One of the best known groups attacking both birds and mammals is the genus *Mycobacterium* (family Mycobacteriaceae). They are so-called "acid-fast" bacteria, that is to say, once stained with carbol-fuchsin they resist decolorisation by mineral acids. They are slender, immobile, rod-shaped organisms which reproduce by simple fission and do not form spores. They are notorious as the causative agent of tuberculosis, although some species are harmless saprophytes and inhabit odd media, such as butter, smegma and the moist surface of timothy grass. Different types of *Mycobacterium* are responsible for avian and mammalian tuberculosis but birds and man do not infect one another. Cows, however, seem to contract both types in addition to one of their own. Various species of

wild birds suffer from tuberculosis. In the U.S.A. it has been recorded from sparrow, crows, cow-birds, pheasants, the sparrow-hawk and barn-owl. In Britain the disease is most frequently met with in gregarious birds such as starlings, rooks, sea-gulls and wood-pigeons. This is scarcely surprising, since avian tuberculosis is passed from bird to bird by contact, or by the accidental ingestion of freshly contaminated faeces or the exudate from the lungs. In the case of barnyard fowl, which are also liable to contract the illness, old birds are more susceptible than young birds. The disease is initiated by way of the digestive tract, not the lungs, and ulcerative lesions can form in the liver, spleen, intestines, bone marrow, ovaries, lungs, air-sacs and in fact most tissues. There is no rise in temperature but a characteristic symptom is the gradual wasting away of the body, associated with extreme exhaustion. Affected birds may die within a few months or may survive for several years.

Another well-known group of bacteria which attack both birds and mammals is the genus *Salmonella* (family Bacteriaceae), the causative agent of typhoid and paratyphoid fever in man, and pullorum disease and fowl typhoid in birds. These bacteria are primarily intestinal parasites. They are rod-shaped motile organisms with numbers of flagella distributed indiscriminately over the surface of the cell. All are Gram negative, that is to say, they do not retain Gram's stain if decolorised by ethyl alcohol or acetone.

Birds are particularly susceptible to *Salmonella* and no less than forty species have been described from the fowl in the U.S.A. alone. A few are host-specific, but many attack a wide range of warm-blooded animals. Pullorum disease (*S. pullorum*) has been recorded from several wild birds including the bullfinch, chaffinch, goldfinch and certain pigeons. Sparrows, quail, pheasants and bitterns are also susceptible to experimental infection. This is by far the most important disease of birds which is transmitted via the egg. On poultry farms large numbers of chicks may be infected by contact with contaminated excreta or the down in incubators, or by contaminated food or water in brooders. Nevertheless the chief vehicle of infection is certainly the egg. In virulent epidemics the death rate of affected chicks may reach 90 per cent. or more and pullorum disease has been the cause of huge losses to the poultry industry. Various other bacteria of the paratyphoid group have been isolated from wild birds ranging from teal to siskins. Duck eggs are a recognised source of *Salmonella* food poisoning in man.

The spirochaetes are classified by some zoologists as Protozoa and by others as bacteria. The electron microscope has shown recently that at least some spirochaetes possess long filamentous processes. Therefore the chief feature which was supposed to distinguish them from bacteria—motility without flagella—seems to have been disposed of. Spirochaetes are active colourless thread-like organisms which can move with equal ease either backwards or forwards. There is a central filament or axis around which the body is wound like a spiral staircase round the newel. The number of spirals varies but is constant for each species. Spirochaetes reproduce by transverse fission and there is apparently no sexual process. The best known and most notorious genus is *Treponema* which includes the causative agents of syphilis, yaws and relapsing fever. One species, *T. anserinum*, parasitises birds and is the cause of relapsing fever in geese and other farmyard fowl on the Continent. It has not been recorded from wild birds in Britain, but it is known to infect species such as the little owl, snipe, sparrow and crow which are on the British list. Syphilis is spread from one individual to another by contact of infected surfaces, but relapsing fever of both man and birds is spread by blood-sucking arthropods. The chief carriers of avian spirochaetes—of which there may be several distinct species—are ticks of the genus *Argas*, but red mites (*Dermanyssus gallinae*) can also act as vectors. The spirochaetes are taken up during a blood meal and in the case of the tick invade the various tissues of the body including the salivary glands. They also enter the eggs, perhaps as many as thirty to one egg, and the disease is thus inherited by succeeding generations of ticks.

Not unnaturally the bacteria which infect birds have been studied chiefly in poultry. When a particular disease is recognised in chickens and ducks, particularly if it is the cause of financial losses, it is worked on fairly intensively and as a result it is often subsequently tracked down in wild birds. This has been the case with so-called fowl cholera* (*Past-*

*It is worth drawing attention to the perverse popular names given to the diseases of poultry, which might well have been designed especially to confuse the ordinary parasitologist. Thus the term "fowl cholera" is applied to a disease allied to the plague or pest, and not even distantly related to cholera of man. Therefore the true cholera which attacks birds has to be called a "vibrio infection." The term "fowl pest" is reserved for a disease caused by a virus, which has nothing whatsoever in common with *Pasteurella pestis*, the causative agent of plague in man. The well known and relatively innocuous disease of children known as chicken pox, has on the other hand, nothing to do with chickens, nor does it attack birds, and it is not a true pox.

eurella avisepctica), anthrax (*Bacillus anthracis*), vibrio infection (*Vibrio metchnikovi*), infectious coryza (*Haemophilus gallinarum*) and various other diseases caused by the *Streptococcus* and *Staphylococcus* type of bacteria, apart from those already mentioned. Nevertheless the bacterial diseases of wild birds, particularly in Britain, are virtually unknown.

The organisms described above are all parasites with a marked pathological effect on the host. There are, however, numerous bacteria which constitute the normal flora of an animal's body. Some of these are harmless commensals, others are parasites which have no noticeable effect except in certain special circumstances when they become dangerous, and some are definitely beneficial to the host and are thus more correctly labelled symbionts. There is considerable evidence, for example, that certain bacteria in the intestines of mammals and birds synthesise proteins, vitamins and possibly essential amino-acids which are then used by the host. Some of the invertebrate parasites of birds apparently depend on the presence of the bacteria associated with the alimentary canal, for they cannot survive without them. It is always more difficult to study the beneficial rather than the harmful bacteria, for the effects of the former are so much less dramatic. In a few cases, such as the deep sea fish with luminous organs, the relationship is fairly obvious. The fish possess definite hollow structures, generally situated on some part of the head, supplied with specialised secretory glands. The bacteria are present in the water and filter into these special organs from outside. Once they have gained access they find themselves in the presence of a perfect nutrient medium secreted by the glands in which they luxuriate and multiply rapidly. The highly phosphorescent areas which result from these dense aggregations of luminous bacteria serve the fish as recognition marks, warning signals, or lures to attract their prey. Very few symbiotic relationships between bacteria and vertebrates present such a clear cut picture as this, but it is nevertheless highly probable that they do in fact exist between birds and the microscopical organisms which live in their bodies. This case must not be confused with the occasional records of luminous bacteria on the plumage of owls which cause the birds to glow faintly and have given rise to many terrifying ghost stories. This luminescence is due to the accidental presence of saprophytic forms which are commonly found growing on dead meat and fish. The owls acquire them temporarily from the carcass on which they have been feeding.

THE VIRUSES

The viruses are a group of organisms which are nearly all too small for the eye to perceive even with the aid of a microscope, although they can sometimes be photographed with the aid of the electron microscope. Their presence is revealed only when they stimulate some noticeable reaction in the host. They have never been cultivated outside the living cell, and the exact nature of a virus is a matter for speculation. They may be minute micro-organisms somewhat resembling very small bacteria, progressively degraded by a parasitic form of life which they have pushed to the utmost limits of specialisation. On the other hand there is another theory supported by some powerful evidence, which suggests that viruses are not living organisms at all but chemical substances—huge nuclear proteins which multiply by so-called autocatalysis. Like bacteria and parasitic Protozoa the viruses can reach their hosts by contact between infected individuals or contaminated materials including food and water, or by insect carriers; some are airborne and others infect their hosts by unknown means.

At least one virus disease, psittacosis, sometimes called ornithosis, apparently possesses a certain news value. Consequently when a keeper in the parrot house at the zoo contracts it or an old lady with budgerigars dies of the infection, the British public learn of the occurrence along with the latest murder story and the football results. The causative agent is a virus which invades and destroys the reticulo-endothelial cells, giving rise to clinical symptoms resembling influenza but often complicated by pneumonia. It is rather larger than the ordinary filterable viruses and falls mid-way between them and the Rickettsia-like bacteria. Parrots are on the whole more susceptible than other birds, but pigeons, finches, gulls, ducks, pheasants and fulmars also suffer from the disease. In the years 1933 to 1937, there were autumn epidemics of pneumonia among the human inhabitants of the Faeroe Islands, the cause of which was traced by Rasmussen to a widespread infection among juvenile fulmars which were used by the islanders to supplement their ordinary diet. Nearly six times as many women as men were infected and it was assumed that they inhaled the virus along with a fine dust which is liberated when birds are plucked. During the war it was discovered that carrier pigeons in Britain were not infrequently infected with psittacosis, but there were no clinical symptoms and it was a type which did not apparently attack man. It

is probable that wild birds in Britain are also subject to the disease.

In 1948, Dane recorded a severe epidemic among the manx shearwaters on Skomer Isle. Hundreds of juvenile birds died in outbreaks which occurred in two consecutive breeding seasons. The causative agent was a virus and the visible symptoms included blisters on the webs of the feet, inflammation of the eyes which led to blindness, and extreme exhaustion sometimes accompanied by unnatural extension of the legs. Some similar symptoms had been observed in three juvenile herring-gulls which died on nearby Skokholm Isle, and it seems probable that the disease is not confined to shearwaters. Ducks have been infected experimentally.

A world-wide virus disease of chickens is popularly known as fowl-pox. The organism concerned is related to the virus of small-pox and cow-pox. In the days before vaccination, chickens which contracted the disease were regarded with grave apprehension, as they were considered a possible source of human epidemics, but it is now known that fowl-pox is not transmissible to man. Moreover several different types of pox are known which attack birds—fowl-pox, pigeon-pox and canary-pox. Pigeons are resistant to fowl-pox, but chickens contract a very mild form of the disease if exposed to pigeon-pox, which then renders them immune to the deadly form of their own variety. In the same way an attack of cow-pox immunises man against small-pox. A pigeon-pox vaccine is now used widely to protect chickens against the disease. Various mosquitoes are proved carriers of fowl-pox. They mechanically transmit the virus from one bird to another. The house-gnat remains infective for 58 days after feeding on a diseased bird. It is remarkable that some strain of the virus has not become acclimatised to man, since it must continually be introduced into his body by this insect. The same applies to the avian *Plasmodium*. Canary-pox is also a disease of wild sparrows in the United States and several outbreaks among them have been studied. Quail, grouse, pheasants, partridges and pigeons are also subject to natural infections of avian pox of one type or another. The disease almost certainly occurs in wild birds in Britain.

There are of course other viruses recorded from birds, apart from the three selected above; for example, the causative agents of Rous sarcoma, fowl paralysis, fowl leukaemia and fowl pest. In Italy a previously unknown virus has been recorded from wild thrushes and another from owls in the United States. No doubt many others await discovery and investigation in wild birds in Britain.

FUNGI

Fungi are plants without chlorophyll which live as saprophytes, parasites, commensals or symbionts. All the species attacking birds and mammals are facultative parasites which pass from a saprophytic mode of life because conditions happen to favour the change. Fungi attacking other plants are often obligatory parasites and strictly host specific.

The parasitic fungi of birds are microscopic organisms and the reader will be disappointed if he expects to see a robin with a large mushroom sprouting under its wings or from between its toes. The host's reactions to viruses and bacteria are visible to the naked eye and one can see pockmarks and boils. Similarly, fungi are responsible for obvious lesions, such as the red patches of ringworm, but the causative organism has to be sought and examined with the aid of a microscope. The general appearance and colour of colonies of fungi grown in the laboratory are however of great importance for the purpose of identification.

A typical parasitic fungus consists of filamentous branching threads or hyphae, with a tough chitinous outer covering, collectively forming a mycelium, which ramify through the tissues of the host. These filaments absorb the decaying substances or solutions in which they are immersed and can also secrete various enzymes which assist them in the process of decomposing organic matter. Fungi reproduce either by a sexual or asexual process. They give rise to spores which are extremely long lived or resistant and can germinate after a resting period of 20 years or more.

In many respects fungi resemble bacteria. In some forms the mycelium breaks down and forms chains of cells, or fragments into separate cells, and in these stages it is virtually impossible to distinguish them from bacteria. Conversely in some classifications, certain bacteria are placed among the fungi and the mycelium is described as "rudimentary or absent."

Diseases which result from attacks by fungus are known collectively as the mycoses. A great variety parasitises man and in his *Précis de Parasitologie* Brumpt considers them sufficiently important to assign them 429 pages out of a total of 2,064. Some of these species also attack birds. Favus, which is a chronic mycosis of the skin, is produced by various members of the genus *Achorion*. Thrush, a mycosis of the



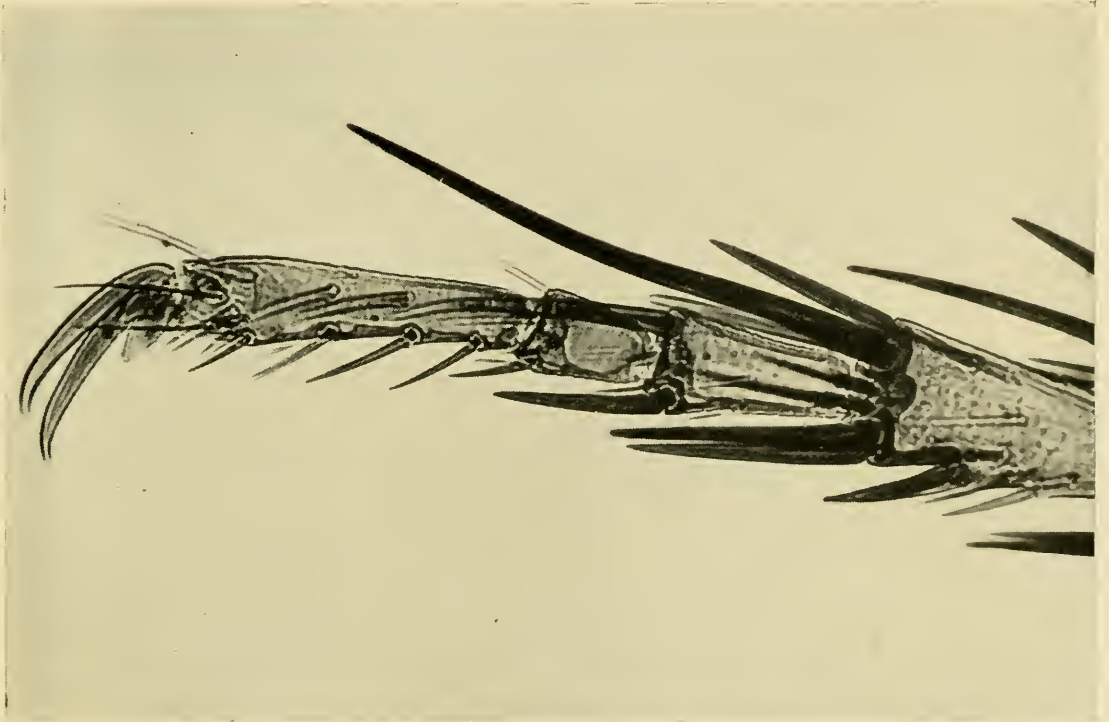
S. C. Porter

a. Common house-martin flea, *Ceratophyllus hirundinis*, male at rest ($\times 16$)



S. C. Porter

b. Common house-martin flea, *C. hirundinis*, about to feed ($\times 16$)



Arthur L. E. Barron

c. Terminal portion of leg of shearwater flea, *Ornithopsylla laetitiae* ($\times 205$)



Eric Hosking

a. Cormorants breeding in a colony: colonial nesting favours a high rate of infection with bacteria as well as fleas and other ectoparasites



Morrey Salmon (by flashlight)

b. Shearwater at entrance to its burrow: host of the most interesting British bird flea, *Ornithopsylla laetitiae*, only known from the British Isles. This bird is attacked by a fatal virus disease

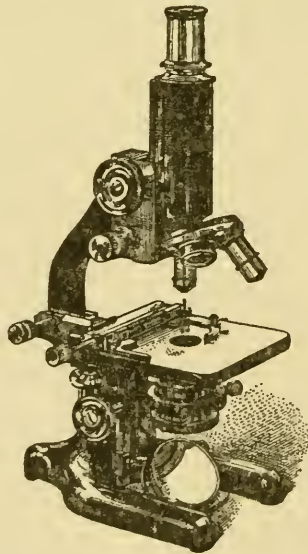
mouth and intestinal tract, is due to infection with the genera *Monilia* and *Oidium*. Perhaps the best known fungus parasitising birds is *Aspergillus fumigatus* (see tail-piece Chapter 1, p. 10), which is localised in the respiratory tract. The spores of this plant are widely distributed in nature and the birds inhale them with dust or pick them up with mouldy food or water. They form colonies in the lungs and air passages and some birds are highly susceptible to the bacteria-like toxins they produce. Several allied species are known and sometimes multiple infections occur when *Penicillium* and *Mucor* moulds are found in association with *Aspergillus*. We have frequently observed mycosis in wild wood-pigeons from all parts of Britain and Dane records *A. fumigatus* in the air sacs of the manx shearwater.

As we have seen in the preceding chapters, fungi are also most useful to birds since they are hyper-parasites of many species of arthropods and helminths which parasitise avian hosts. One of the best known genera is *Empusa* (Entomophthoraceae) of which various species cause a fatal disease in mosquitoes (including the house-gnat) and other Diptera such as blow-flies, house-flies, and midges, and also in mites. Large numbers attack roundworms at all stages of their development. Some extremely interesting fungi, such as the genera *Dactylaria* and *Dactyella* (Hyphomycetales), capture certain parasitic nematodes alive during their free-living stages. They are snared by means of loop-shaped portions of the mycelium, each of which operates on the lines of a sphygmomanometer. Contact with the prey causes the loops to swell suddenly and constrict round the worm which is held fast and ultimately consumed.

There is a curious and obscure group of parasites, the Sarcosporidia, members of which are located in the striated muscles of mammals and birds. At one time they were classified as Protozoa but are now considered to be fungi. Surface feeding ducks are the most heavily infected group, but they have been recorded from 28 species of birds from eight different orders. The larger forms of the parasite can be seen as little white streaks in the striated muscles which give the fibres a "wormy" appearance. When removed from the tissues each resembles a minute colourless spindle. The body is divided into chambers, which, in fully developed specimens, are filled with sickle-shaped spores. The life-cycle of *Sarcocystis* is not properly understood, although there is some evidence that infection can occur after ingesting urine and faeces from animals with the disease. On the Continent avian sarcosporidiosis

has been recorded from several common birds on the British list such as the blackbird and sparrow, and there seems little reason to doubt that it will eventually be found in this country.

The relationship which exists between parasitic fungi and bacteria is one of the greatest interest. In many cases these two types of organism compete with one another in the same environment. Often the presence of bacteria in a culture of fungi arrests its development, but in other cases they seem to exert a beneficial influence. Certain Staphylococci, for example, stimulate the growth of *Achorion*, and in the presence of bacteria (but not in pure cultures) *Aspergillus* produces spore-bearing perithecia. On the other hand it is now known that extracts of certain fungi have a powerful antibiotic or lethal effect on various bacteria. In 1913 Vaudremer showed that a filtered extract of *Aspergillus fumigatus* inhibited the growth of tubercle bacilli. In recent years penicillin has been extracted from various species of *Penicillium* (especially *P. notatum*) and has proved the most powerful antibiotic ever known. An extract from another fungus, *Streptomyces griseus*, now known as streptomycin, also exerts a powerful lethal effect on certain bacteria, among them species such as the tubercle bacillus, which is not affected by penicillin. The secretions of fungi have consequently provided one of the great discoveries of the age.



CHAPTER 14

THE FAUNA OF BIRDS' NESTS

. . . this bird
Hath made his pendant bed and procreant cradle :
SHAKESPEARE

BIRDS' NESTS, as Waterston remarked with masterly understatement, must make lively nurseries. It is the really snug nests, built under eaves or placed in holes, like those of martins and jackdaws, which provide the offspring with an early insight into the grim realities of life. Even migration must seem a picnic in comparison with the tortures of nestling days. Young wood-pigeons, which squat precariously on a flimsy raft high up in the branches, have a very easy time in comparison, and could well look back with nostalgic regret on the period of pigeons' milk passed among the swaying tree tops.

The inhabitants of birds' nests, other than the rightful owners, are chiefly arthropods. Insects and mites predominate, although ticks, pseudo-scorpions, spiders and an occasional centipede, wood-louse, or free-living nematode may also be present. In Finland, Nordberg studied the fauna of 56 species of birds' nests, from which he recorded no less than 529 different kinds of arthropods. Beetles accounted for 118 species and mites another 228. The rest consisted of bugs, flies, fleas, ticks, feather lice, moths, springtails, earwigs, book-lice and a few parasitic Hymenoptera and spiders. A number of permanent obligate ecto-parasites, such as the feather lice, occasionally wander off the host, possibly in the process of transferring themselves to the nestlings, and are found in the nest, but they are not true nidicoles, as their proper habitat is the host's body. In addition, about a third of the species found in birds' nests are purely casual or accidental visitors. Another large category includes species which frequent various micro-habitats that afford conditions similar to those of nests. Thus many beetles which

are found in nests in holes are equally numerous in holes without nests. There are also many common plant-eating mites and insects which are passively introduced along with moss and lichen and other vegetable nesting material. These flourish in a wide range of bird habitations, and, in cases such as the mite, *Oribata geniculatus*, can become dominant species, but they are in no way peculiar to this type of habitat. Despite the large proportion of wanderers, accidental visitors, occasional and casual residents, and constant if independent inhabitants, there remains quite a high proportion—say between 20 and 25 per cent.—of the species present, which at one stage or another of their life-cycle are obligate nidicoles and dependent on nests. Of these a few are host-specific, and are found only in the nests of one species, or of a group of related species of birds, but many are catholic in their tastes.

Various factors influence and determine the fauna of birds' nests, and our knowledge concerning them is ridiculously small, but one or two generalisations can be made with confidence. Nests which are built in holes, and which are returned to and re-occupied year after year, contain on an average a larger number of individual nidicoles and a greater variety of species than other nests. In this respect the host itself seems to be less important. Thus the wood-pigeon has the smallest nest fauna of any British bird so far examined, both as regards numbers and variety, and the closely related stock-dove, which generally nests in holes, has the largest. Needless to say there are many exceptions. The crow family as a rule have revoltingly verminous nests, and the carrion-crow with about 80 species recorded can boast a richer fauna than most hole dwellers. The type of nest, whether it is domed or flat, or just a scrape, massive or flimsy, constructed of mud or moss, stick or stones, sea-weed or sand, naturally influences the nest fauna. The site chosen, the age of the nest, whether it has contained young, its distance from the ground, the proximity to water or human habitations or other birds' nests is also important. The habits of the host, particularly its choice of food, which to a great extent determines the nature of the débris within the nest, have a considerable bearing on the species of arthropods found there. Thus a beetle, *Trox scaber*, which chiefly feeds on old bones and hides, is characteristic of owls' nests and one would not look for it under a sitting firecrest or blackcap.

The population of a bird's nest is not, of course, stable. The various nidicoles have different requirements of food, temperature, humidity or light; and this will influence which species occur in specific nests, in

which part of the structure and at what period of their history. Thus within the nest itself there may be different levels at which various species are more abundant than at others. For example, in a great tit's nest, out of a total of 3,469 arthropod inhabitants, 490 were found in the lining, 2,277 in the middle layers and 702 in the outer structure. In a flycatcher's nest the position was reversed and out of a total of 1,568 specimens no less than 840—over half—were found in the lining, and the smallest numbers were present in the middle layer, where, in the tit's nest, they reached a maximum. An observer once saw fly larvae—up to that moment completely hidden—seethe to the surface of the lining when droppings fell, and eagerly devour them. The nest is occupied however, for only a very brief period and most populations—especially if the larvae and adults of each group are counted together—reach a maximum density during two or three days when the young are about to leave or have just flown. Quite a large assortment of arthropods overwinter in immature or adult stages in the nest.

The habitations of the Hirundinidae (martins and swallows) probably harbour the most interesting nidicoles of any group of British birds, although several others, such as the jackdaw, starling and stock-dove have a larger assortment. The crows as a family, have a richer though less distinctive nest fauna.

A conspicuous inhabitant of house-martins' and occasionally other birds' nests is the swallow bug (*Oeciacus hirundinis*, Plate XXXVIb). We have already remarked (p. 16) that martins and men probably shared cave dwellings in prehistoric times and they may both have acquired this group of parasites in their former habitat. Very few birds are preyed on by bugs. One of their essential requirements is a permanent dwelling house, for during the day they hide in cracks and crevices—in which they also lay their eggs—and only creep out at night for a blood meal. There is one other bird bug in Britain, *Cimex columbarius*, which is a parasite of the domestic pigeon. In all probability it is a sub-species of the human bed-bug (*C. lectularius*, see Plate XXXVIa) which has passed accidentally on to pigeons and chickens since their domestication by man, and has now become morphologically distinct. Fertile hybrids can be obtained by crossing the two forms. The bugs which infest wild birds can only survive if the host is the type which returns to its old nest. Moreover the nest itself must remain fairly dry during the host's absence. In the United States the barn-swallow (*Hirundo rustica erythrogaster*) and purple martin (*Progne subis*), and the oven-bird

(*Furnarius rufus*) in South America, harbour related species of bugs. The majority of other bugs (Hemiptera) are plant suckers, but they are to a certain extent preadapted to an ecto-parasitic mode of life, as they are flattened dorso-ventrally and have piercing mouth-parts. Many free phytophagous bugs show a tendency to winglessness, and in some species one sex has wings and the other has not (p. 52). Some of the assassin bugs (Reduviidae) which normally prey on other insects, have become voracious blood suckers and are often found in birds' nests in America. Only one family, the species of which live on bats, have evolved into true permanent obligate ecto-parasites.

An Anthocorid bug, *Lytocoris campestris*, is a cosmopolitan species also found in house-martins' nests in Britain. It is a predator which sucks mites and the pupae of fleas but since it has also been known to feed on human blood its activities in the nest are not beyond suspicion. It probably competes with the pseudoscorpions—arthropods looking like miniature crayfish—which hunt and eat mites. One in particular, *Chelifera cancroides*, is a constant species in the nests of swallows and martins. It is a great hitch-hiker (see p. 18) and is carried to new feeding grounds attached to various insects, especially flies, which it clasps firmly with its huge pincer-like claws.

Swallows, house-martins, and also house-sparrows and to a lesser degree flycatchers, which in Britain nest so frequently on man-made buildings, often harbour certain nidicoles for which they and their human neighbours can blame one another. Thus five indigenous species of dermestid beetles are found in their nests and except for *Dermestes murinus*, which is common in the habitations of various birds of prey, these are only rarely recorded from other wild birds' nests in Britain. Both larva and adult of *D. lardarius* and *D. murinus* feed on stored products such as dried and smoked fish and meat, cheese, dried milk, bones, dried insects and so forth. To a certain extent *D. lardarius* is predacious and if present in large numbers occasionally attacks and kills nestling birds. It has been known to bore into the wing bones of young pigeons and eat them alive. In nests these beetles also feed on dried insect remains, which seem to be a favourite food, for in nature dermestids are also found commonly in wasps' and bees' nests and caterpillar webs. *Attagenus pello*, another dermestid found in the same birds' nests as the previous species, feeds on nectar as an adult, but the larva favours a diet of feathers, dead insects, furs, skins, woollen carpets, grain and cereal products. These beetles are scarcely

welcome guests, but there are several groups of Coleoptera which prey on the parasites of the birds, especially fleas and their larvae, and can therefore be regarded as symbiotic partners. Foremost of these are rove beetles (Staphylinidae) and histerid beetles (Histeridae). The former family is extremely interesting (see p. 50), since many species have become adapted to life in nests—of colonial and gregarious insects as well as of mammals and birds—all over the world. In this country the genus *Microglotta* is the most noteworthy. The insects feed on fleas and their larvae. It seems possible that the species in birds' nests such as *M. nidicola* and *M. pulla* can only breed at a temperature between 36° and 40°C.—in other words when the parent birds are brooding. Although these beetles often remain in deserted nests and wander into ants' nests, they apparently do not breed there and Heim de Balzac suggests that high temperatures are necessary to bring about the maturation of the gonads. In Britain *M. nidicola* is confined to nests of the sand-martin and is found in about 70 per cent. of their burrows—sometimes more than fifty specimens in one nest. Other species recorded from this country are *M. picipennis*, apparently confined to buzzards' nests in Britain, but found in those of a variety of birds of prey on the continent, and *M. gentilis*, which favours owls' nests.

A wide range of hosts seems suitable for *M. pulla*, which has been recorded from the habitations of many birds, but shows a predilection for those of tits. There are of course various other rove beetles associated with birds' nests, of which perhaps *Atheta nidicola* and *A. nigricornis* are the most characteristic. Although recorded from martins' they are more commonly met with in other nests. Spittle has found both in the nests of the heron and carrion-crow along with a third species, *A. trinotata*, which unlike the previous pair is not predacious but parasitic upon anthomyid fly larvae and pupae. One species, *A. oloriophyla*, was first found in 1933 in a swan's nest and has not been recorded since. Other typical genera are *Philonthus* (*P. fuscus* seems confined to birds' nests) and *Aleochara*. Of the Histeridae the genus *Gnathoncus* is a voracious eater of fleas in all stages of development. Curiously enough it is absent from the martins' nests, which have the highest flea population known (see p. 109). It is possible that it has a liking for certain species, e.g. the hen flea (*C. gallinae*), but not for others. A wide variety of nests harbour *G. punctulatus*, (see tail-piece Chapter 7) and in Finland it is a constant and sometimes dominant species in the nests of the house-sparrow, great tit and similar birds which are usually

infested with the hen flea. Two other species, *G. nidicola* and *G. buyssoni*, are recorded from owls' and hawks' nests in Britain. Sometimes the adults develop a perverted taste and chew the feet of sitting birds. However *Gnathoncus* is generally modestly represented compared with its prey. A flycatcher's nest harboured 170 specimens, a great tit's 58, a chaffinch's 34, and 14 were taken by Spittle from an owl's nest. Three other British histerids found in birds' nests are *Dendrophylus punctatus*, *D. pygmaeus*, and *Hister merdarius*. In addition to the predatory beetles there are numbers which perform a useful function by scavenging in the nests of their hosts. We have already mentioned the beetles *Trox scaber* and *T. scabulosa* which are very common in nests of birds of prey where they feed on bones and hides. Over 100 specimens have been recorded from one nest. Beetles of the family Lathridiidae, such as *Enicmus minutus*, which feed on fungi both as adults and larvae, are frequent occupants of a wide range of birds' nests, and act as scavengers. About 40 species of beetles have been recorded from hirundinid nests in northern Europe, but the jackdaw can probably boast the greatest attraction for Coleoptera. Over 50 species have been recorded from its nest alone. Nordberg, by a somewhat abstruse calculation, found there were 280 beetles per cubic decimetre of jackdaw nesting material! Few birds, however, harbour a host-specific beetle. Probably the only avian host in Britain thus distinguished is the sand-martin.

Even more peculiar is the fact that the sand-martin is parasitised by a host-specific tick, *Ixodes canisuga*. As we have seen (p. 229) ticks are rarely host-specific—and in this respect, as well as many others, the sand-martin is unique among British passerine birds. The mite fauna of birds' nests is extensive, consisting of species which are parasites of the host or other nidicoles, or are scavengers and plant eaters. The martins have several species which are peculiar to them.

Certain clothes moths are also found in birds' nests; *Tinea pellionella* is a common species in martins' and sparrows' nests. The larva feeds on the lining but it also chews up expensive materials such as carpets, fur coats and cushions in the houses on which the birds have built their nests. A predator of the larva, the window fly (*Scenopinus fenestralis*) has occasionally been recorded from nests. Another related moth, *T. lapella* (see tail-piece of Chapter 2, p. 19), is an obligate commensal of certain passerine birds like the hedge-sparrow and thrush. The larva also feeds on feathers, and although there are presumably many other sources of keratin available this moth has up till now been found only in nests, and

is far more closely linked with this habitat than the previous species. The commonest moth in swallows' and martins' nests in England is *Hofmannophila pseudospretella* and it has also been bred by Basden from nests of the barn-owl, wren and starling. The larvae are scavengers and will feed on faeces, dead nestlings and even addled eggs. Two other moths, *Monopis rusticella* and *M. ferruginella*, are also commonly associated with nests of many birds in this country. There are, however, in Britain, no true symbiotic moths comparable with the species usually present in the nest of the Australian golden-shouldered parrakeet (*Psephotus chrysopterygius*). The larva of this moth lives unobtrusively in the bottom of the nest, and, like a well-trained nurse-maid, not only tidies up the nursery, but with meticulous care cleans the droppings off the nether limbs of the nestlings.

Chief among the scavengers are the fly larvae. As we have seen in Chapter 12, some of these have become true ecto-parasites on the nestlings and some facultative parasites, but there remains a fair number, such as species of *Fannia*, *Anthomyia*, *Hydrotaea* and *Phaonia*, which, as a rule, feed on refuse in the nest, although at times they may be semi-predacious. A few species also parasitise other dipterous larvae. Occasionally the magnificent metallic corpse-feeder *Cynomyia mortuorum* is found in nests, and probably the larvae are not above suspicion as facultative parasites. True parasites of nestlings are the larvae *Protocalliphora* and *Neottiophilum*, which are dealt with in Chapter 11 (p. 221). *Carnus* and *Meoneura* are thought to be ectoparasitic as adults, but their larvae probably live as scavengers in the nest. There are also some groups of flies, Phoridae, Helomyzidae and others, which occur quite frequently and are vegetable refuse eaters, but are also found in carrion, dung and fungi. There are also a few Hymenoptera which parasitise the larvae of fleas, flies and moths, and are no doubt extremely useful to the birds.

Generally each bird or group of birds has a characteristic nidicolous fauna, in which certain species are found more frequently than others or in larger numbers. In martins' nests in Britain, fleas are the dominant and most important group (see p. 80). They are present in over 80 per cent., and their numbers are greater and their species more varied in these than in other birds' nests. Flies are the next most important group, followed by moths. Here, however, there is a divergence between the fauna of the ground nesting sand-martin and the house-martin and swallow. Moths are an important group in

the latter's nests, but uncommon in the former's, where mites take their place as a dominant group.

It will have become evident from this brief account, mainly of the fauna of martins' and swallows' nests, that the bird-lovers who carefully preserve their habitations from one year to another also unintentionally preserve the louse-flies, fleas, mites and bugs over-wintering as larvae and pupae or hibernating in the nest, which are directly responsible for bringing hours of pain, misery, disease or even death to the nestlings in the following spring. Under these circumstances it seems astonishing that birds returning from their winter quarters, especially those which feed on insects, do not rid their own nests of nidicoles before reoccupying them. They are, however, creatures of habit and inflexible instincts. Hedge-sparrows and other species (see p. 261) will let their own young die of starvation if they are shifted from the inside to the edge of their nests. In such a position they are not recognised as nestlings and are not fed. It is possible that birds do not associate food-hunting with the nest, but in its presence respond to a strong instinct to be unobtrusive and quiet, and to disturb it as little as possible. They may not, therefore, recognise the nidicoles as food. Furthermore, these arthropods may be highly unpalatable. The smell of bed-bugs does not suggest that they would form an attractive breakfast. On the other hand, recent visual observations made on rooks during sexual display and courtship in the rookery *in winter* show that they obtain a considerable amount of food from their nests. The photograph on Plate XXXVII of a whitethroat is a source of speculation. What, in fact, is it doing? Removing faeces from the nest or routing out nidicoles? Possibly birds do destroy numbers of these arthropods. In any case it is an aspect of bird behaviour about which little, if anything, is known and it should prove yet another interesting and fruitful source of study.

CHAPTER 15

SKUAS

Sailing on obscene wings athwart the noon . . .

SAMUEL TAYLOR COLERIDGE

INCIPIENT or casual clepto-parasitism among birds can be seen by anyone who visits the Serpentine on a cold winter afternoon and watches the gulls and diving ducks.

Children often throw large chunks of bread into the water which are hastily seized by the tufted ducks. While they are attempting to swallow these unwieldy pieces the gulls dash at them and try to harry them or startle them into dropping the bread into the water. The ducks frequently dive to escape from the gulls, which hover over the water and pounce again immediately after the ducks surface. Quite often, owing to their wonderful powers of flight, their dash and persistence, the gulls manage to appropriate the bread for themselves. This behaviour is the result of the unnatural conditions prevailing on the Serpentine, where all the birds are crowded together round an artificial source of food, but it proves how, in certain circumstances, species which are not normally clepto-parasites can modify their behaviour in that direction. A more curious episode of this type was once observed in the farmyard. A cockerel, with great dash and daring, rushed up to a cat and seized and swallowed the mouse with which it was playing.

The only real British bird clepto-parasites are the skuas, but it is perhaps worth mentioning one or two foreign species which have developed a slightly different form of the same habit.

The American wigeon (*Anas americana*)—a rare vagrant in Britain—associates with coots and robs them of the weeds which they obtain by diving under water but subsequently bring to the surface to eat. This is probably an extension of a commensal relationship similar to that which exists between our wigeon and brent geese.

A stranger form of clepto-parasitism is practised by certain tropical thrushes (Turdidae), particularly of the genus *Alethe*, which are often referred to as "ant-birds." They have developed the habit of following parties of driver ants and, in addition to catching insects which may be flushed by foraging columns, they actually rob the ants of the prey which they are carrying. In the Belgian Congo, Chapin once observed small parties of thrushes and bulbuls (Pycnonotidae) waiting alongside a forest road and robbing the ants when they were forced to expose themselves to view in the open while crossing from one side of the road to the other. The frigate-birds (Fregatidae), of which there are five species, are related to our gannets and cormorants. They range over the tropical seas, sailing around throughout the day on motionless wings, sometimes rising to great heights until they are mere specks in the sky. At sundown they return to the shore and roost communally in convenient trees. They never settle on the water and this particular aversion may well be one of the factors contributing to the development of the clepto-parasitic habit. If there are shoals of pelagic fish within sight they swoop down and take their choice almost without ruffling the surface of the sea. If such prey is scarce they pursue other birds and force them to disgorge their food, either from their beaks or their crops.

The skuas are brown, gull-like birds, which range across the northern and southern oceans at all distances from the shore, spending most of their lives at sea, and unlike the frigate birds do not return to land to roost. They, also, obtain a large proportion of their food by robbing other birds. There are four native species, but of these only the great skua and the arctic skua breed in Britain. The long-tailed skua and pomatorhine skua are passage migrants and seasonal visitors.

The great skua is essentially a maritime bird and is rarely seen inland. It is a little larger than a herring-gull, dark brown in colour, with a white patch at the base of the primary wing feathers. In the spring it resorts to elevated moorlands and rough hilly pastures near the sea, where it breeds in colonies. The nest is little more than a scrape lined with heather and moss. As a rule it lays two eggs, which are usually olive-grey or reddish-brown with dark brown spots and blotches. Both sexes incubate the eggs and when the young hatch the male provides their food while the female broods them.

Most of this food is obtained by piracy. The great skua pursues a number of different species of sea birds, chiefly gulls—even those which are larger than itself, such as the greater black-backed gull. It attacks

with great dash and agility and, with quick stoops and swerves, worries and frightens the quarry until it abandons its catch in mid-air or disgorges its last meal. Very often the skua, with a graceful aerial dive, catches the fish, or whatever the prize may be, before it falls into the sea. Meinertzhagen noticed that skuas in the Shetlands adopt a special method of robbing gannets. They seize the tip of the gannet's wing, causing it to crash into the sea and flounder helplessly in the water. The skua only lets go when the gannet has disgorged. At other times the skua seizes the gannet by the tail and tips it up into the water.

The arctic skua, which is the commonest British species, is a smaller bird and easily distinguished by the two long straight feathers projecting from its wedge-shaped tail. These are clearly seen on Plate XXXVIIIa. Its upper parts are uniformly brown, but the breast varies considerably and is sometimes almost white. Its habits are similar to those of the great skua, although in stormy weather it is more often seen inland. The arctic skua also obtains its food principally by piracy. It concentrates more on the smaller gulls, such as the kittiwakes and terns, but it also pursues puffins and guillemots. When the skua has selected a victim it follows it with great persistence, turning and twisting with amazing agility and chasing it relentlessly until the food is dropped. It then catches it with a single stoop and swallows it in mid-air. Despite their piratical habits the skuas are all capable of capturing their own prey. Apart from fish and other marine organisms they kill and eat a wide range of young birds and some adults, devour eggs and carcasses and various insects including beetles and dragon-flies. They also take small mammals at their breeding haunts, and have even been known to kill lambs.

CHAPTER 16

THE EUROPEAN CUCKOO

And these are they which ye shall have in abomination
among the fowls . . .

LEVITICUS 11 : 13

THERE ARE about 200 different species of cuckoo, but only one breeds in Britain—the European cuckoo (Plate XXXVIIIb). The ancient Hebrews were possibly deceived by its hawk-like appearance and, for this reason, may have prohibited it, along with the nightjars and the owls, as an article of diet.* Most casual observers to-day who catch sight of a cuckoo beating along open hedgerows, or gliding out of a thicket or copse, mistake it for a bird of prey. It must be admitted that in silhouette, colouring, size and flight it is superficially very like a sparrow-hawk. Compared with some of its foreign relatives it is a drab bird. The upper parts and breast are blue-grey and the remaining under-parts whitish with dark bars. The legs and feet are yellow. In Asia, India and Africa many cuckoos are brilliantly coloured—bright metallic green, purple, bronze, golden and pied. Quite a large proportion of the American species—most of which are not parasitic—are terrestrial birds, which rarely use their wings, but can put on an amazing turn of speed running across country or through dense undergrowth.

The song of the male cuckoo is too well known to require description, but in these days of specialisation many naturalists are unaware that the female of the species does not “cuckoo” at all, but has a soft bubbling call—rather like a sudden rush of water through a narrow-necked bottle. Almost everything about the European cuckoo is peculiar, even its diet. Hairy caterpillars constitute its favourite food—a form of nourishment which no other bird would touch—and their hairs become imbedded in the cuckoo’s gizzard so that it appears to be lined with

* According to the Authorised Version.

dense fur. This diet is an inherited rather than an acquired taste, which develops once the cuckoo has left the care of its foster-parents—no matter what form of food it has previously received from them.

When the cuckoo returns from its winter quarters in Africa, the female selects a territory for herself, preferably in rather open country. Sometimes she returns to the same area several years running. In the case of the European cuckoo the territory is a few acres in extent, but in some African species such as the small golden cuckoo (*Lampromorpha caprius*), which victimises colonial-nesting weavers, it may be restricted to one tree. She defends this territory against all other female cuckoos parasitising the same fosterer as herself. Although successful invasions sometimes occur it is unusual to find two female cuckoos in the same area laying in the nests of the same species of small bird. Individuals parasitising other hosts are tolerated. Occasionally a young bird which has failed to establish a territory of her own will roam across country, laying at random in any available nest she can find.

The male cuckoo also establishes a territory, but in the case of the British species it rarely coincides with the territory of any particular female. He favours wooded areas or the edge of small copses rather than open country. The cuckoo's relations with the opposite sex are distinctly casual and very promiscuous. Sometimes numerous males gather when they hear a female's amorous bubbling and she may copulate with one, two, or all of them. At other times one particular male may seek her out persistently and thus give the impression that they are permanently paired. Again, a male bird may haunt several adjacent territories, bestowing his favours freely on all the female owners.

The female cuckoo hunts systematically for the nests of her victims, which are generally small passerine birds—chiefly those which feed on insects. Quite often though, the linnet, which is a seed eater, is chosen. When she locates a pair building she begins a careful and prolonged vigil, observing the behaviour and movements of the future fosterers from a point of vantage and sometimes gliding down to examine the nest at close quarters. The visual stimulus thus received appears to excite ovulation and the cuckoo's egg reaches maturity and is ready for laying about five days later, in fact shortly after the fosterers have themselves begun to lay.

Most birds deposit their eggs early in the morning, but the cuckoo does so in the early afternoon, a period at which the parent birds—

providing their clutch is incomplete—are most likely to be absent. She glides over the selected nest several times and then quickly alights in it and lays one egg directly into the nest—the entire action occupying no more than five seconds. Subsequently she destroys one or more of the fosterer's eggs, either by throwing them out or by crushing and eating them. Sometimes she carries one a considerable distance in her beak before disposing of it. When the cuckoo deposits her egg in a small domed nest with a side entrance it is impossible for her to enter and lay in the usual manner. The egg is then forcibly projected into the aperture from the bird's cloaca while she hovers immediately over the nest—a feat which might excite envy in an Olympic athlete. Some hold the view that on certain occasions it is first laid on the ground, picked up in the cuckoo's beak and then dropped into the nest. Whether this sometimes happens is a matter of acute controversy. The majority of eggs (if not all) which are seen being carried by cuckoos are not their own, but eggs of the fosterers which they are about to destroy.

If conditions are favourable and there are enough breeding pairs of the right species of fosterer present, with incomplete or just completed clutches, the female cuckoo will continue laying eggs at intervals of about forty-eight hours until between fourteen and twenty have been deposited. One female parasitising meadow-pipits has been known to lay twenty-five eggs in one season. There are, however, rarely enough nests available in a single territory to make such a feat possible, although the cuckoo is able to keep several under observation simultaneously. On occasion she will destroy a whole clutch in order that a particular nest should be in a suitable condition to receive one of her eggs at a later date. Some species such as the great spotted cuckoo lay several eggs in the same nest, but the European cuckoo almost always distributes her eggs singly.

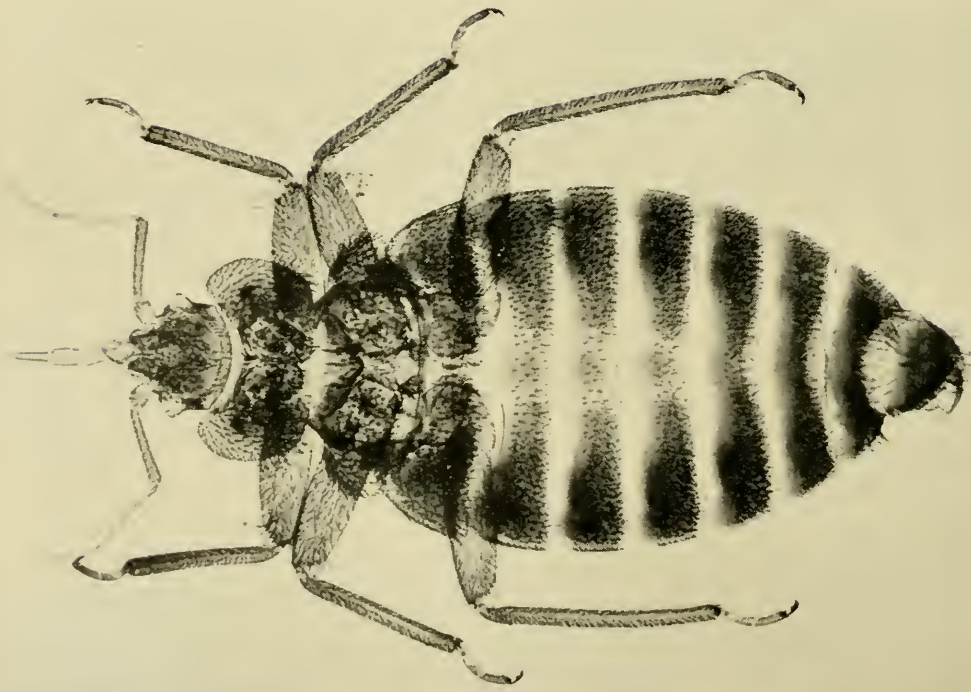
It is now a well-established fact that there are strains or "gentes" of the European cuckoo which, throughout their lives, parasitise only one particular species of small birds. In Britain there are relatively few regular hosts. The main fosterers used are the meadow-pipit, the robin, the pied wagtail, the hedge-sparrow, the reed-warbler and the sedge-warbler. In Germany a favourite host is the red-backed shrike, which is rarely, if ever, attacked in Britain. In Finland, on the other hand, the most popular fosterers are the redstart (which is rarely parasitised in Germany), the wheatear, the whinchat and the pied flycatcher, all of which lay blue eggs. In Finland 68 per cent. of cuckoos' eggs are blue,



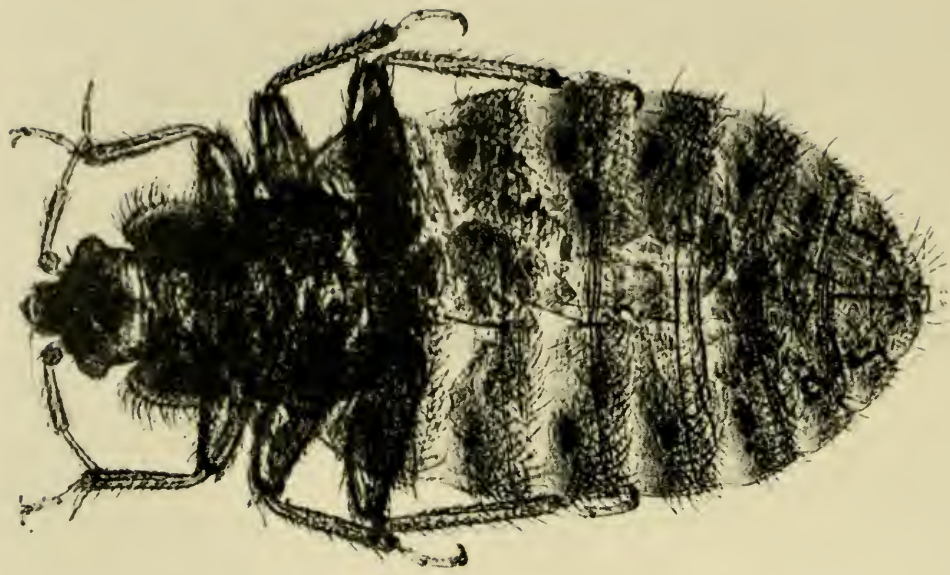
Plate XXXV

Eric Hosking

Sand-martin at nest burrow: this long and sandy burrow, excavated by the sand-martin for its nest and to which it returns year after year, harbours an unusually interesting parasitic and commensal fauna, of which certain species are exceptionally abundant and host-specific



J. G. Bradbury
a. Bed-bug *Cimex lectularius* (× 10)



Arthur L. E. Barron
b. Swallow-bug, *Oeciacus hirundinis* (× 20)

whereas in England they are almost all of the spotted type. The number of eggs laid by individual cuckoos depends to a certain extent on the species of host favoured. Thus, in Germany "red-backed shrike" cuckoos lay fewer eggs than "robin" cuckoos, for the breeding season of the former host is much shorter. Sometimes, when nests are scarce or an accident occurs, a cuckoo is compelled to lay in any nest she can find. Also some cuckoos are eccentric and select unusual hosts and others fail to establish a territory and have to lay at random in a wide variety of nests. Thus, over fifty hosts have been recorded from Britain alone, but nevertheless, the overwhelming majority of cuckoos in this country lay their eggs in the nests of the five or six regular fosterers mentioned above. It is, however, not known *why* a female cuckoo selects a certain specific fosterer for her initial laying, and generally continues to select similar fosterers throughout her period of reproductive activity. Why does a "meadow-pipit" cuckoo in Britain, for example, regularly select the nests of meadow-pipits rather than other small birds in which to lay her first egg? This is one of the unsolved mysteries of the cuckoo's life history. One possible explanation is that she has a strong inclination to parasitise the same species by which she herself was reared. Much of the recent work on bird behaviour has shown that certain sights and sounds and general situations can act as stimuli which release inborn and well formed patterns of behaviour. Thus it is quite possible that the plumage and song of birds exactly similar to those which reared her and the general appearance of their nest "rings a bell," and acts as a "releaser" of this type (habitat imprinting which in this case might be called host imprinting), and thus stimulates the female cuckoo to foist her eggs upon them rather than any other species. But this is pure conjecture.

The eggs of the species as a whole are very variable both in regard to colour and markings, but all the eggs from one individual bird are similar. The various strains or gentes of cuckoos, such as "wagtail" cuckoos and "pipit" cuckoos, have developed eggs which, to a greater or lesser degree, resemble the eggs of the regular fosterers.

Many small birds have an inherited fear and dislike of the adult cuckoo. They will mob it and drive it off in the same way in which they attack birds of prey. Pliny wrote: "They know how all birds hate them for even very little birds are readie to war with them." Some interesting experiments could be done with models and stuffed specimens to try to determine by what features the cuckoo is recognised.

If the intended foster parents surprise the cuckoo near their nest they make frantic efforts to drive her away, buffeting and pecking her in a courageous manner. The cuckoo never fights back—it would certainly not be in her interest to injure the future foster parents of her own chick—but she is very persistent and even if driven off returns time and again and generally succeeds in laying her egg in the chosen nest. Sometimes one or more males accompany the female and try to divert the fosterers' attention while she quickly and furtively deposits her egg. Chance has remarked that at times the victims behave as if they were mesmerised by the cuckoo. Some pairs of meadow-pipits which he had under observation appeared to welcome her attentions and seemed to fly up to her as she sat watching their activities and "virtually invite her" to their nest. He also noted that sometimes after a cuckoo had laid her egg the fosterers would at once begin to brood, although their own clutch was not yet complete, as if the visitation was regarded in the nature of an honour conferred upon them. At any rate it can be said that the presence of the cuckoo is a disturbing and exciting influence, which can upset the normal rhythm of their behaviour.

A frequent result of the cuckoo's visit to a nest is its desertion by the intended fosters. One of the adaptations to brood-parasitism is the development of eggs resembling those of the fosterers, but in the case of the European cuckoo the adaptation is by no means perfect and the birds often notice the strange egg and remove it, build over it or merely abandon the nest. Some species of bird desert much more readily than others and consequently keep the cuckoo at a safe distance. Many warblers, for instance the chiffchaff and wood-warbler, will abandon their nests if a fight has taken place, and Capek found that 77 per cent. of cuckoos' eggs which had been placed in the nest of the latter species were destroyed, whereas in the same district the common redstart accepted and reared all but five per cent.

It has already been explained that the cuckoo tries to lay her egg either before the fosterer's clutch is complete, or immediately upon completion. In this she succeeds in about 70 per cent. of her layings. The young cuckoo develops more rapidly than the foster nestlings and hatches out one to four days before them if brooding had not commenced prior to the introduction of the cuckoo's egg into the nest. Correct timing is of great importance, for the parasite is thus given several days' start, a definite advantage over the rest of the brood.

While the young cuckoo is still blind and mute, at the tender age of about ten hours, it develops a sudden and powerful impulse to eliminate all the other inmates of the nest. The touch of any object, whether it is an egg or a nestling, seems to cause it intense discomfort, possibly even pain, and it forthwith attempts to rid itself of the intolerable presence. There is a small highly sensitive cavity on its back in the region of the synsacrum into which it attempts to roll the offending egg or nestling. Eventually, at the cost of a protracted, exhausting and hideous struggle, it succeeds in hoisting its burden to the side of the nest and ejecting it over the side. This is repeated until the young cuckoo remains as the sole occupant of the nest. Three and a half to four days after hatching when the plumage begins to grow, it becomes less sensitive and the all-powerful desire for solitude fades away. The dorsal cavity, which now no longer serves any useful purpose, is gradually obliterated.

It is a curious fact that the parent birds do not become agitated by the disappearance of the rest of the clutch and do not appear to notice the absence of their own young. They never attempt to feed them if they lie starving on the ground and sometimes will even remove one from the edge of the nest if the cuckoo has failed to heave it well over the side—as if it were a piece of unwanted rubbish. It appears that small passerine birds entirely fail to recognise their own young at this stage of development if they are not in their proper place—i.e. well and truly in the bottom of their nest.

Not all species behave like the young European cuckoo and eject the eggs and young from the nest. In some cases, for example, in the genus *Eudynamis*, the young brood-parasite is reared together with the nestlings of the foster parents. The general colouring of the young cuckoo's plumage somewhat resembles that of the fosterers' young—black when crows and starlings are the host and brown if the other nestlings are brown, too. They are consequently less conspicuous and tone in with the rest of the brood. In another group of parasitic birds, the African widow-birds (*Vidua*), this resemblance to the fosterers' young is developed to an amazing degree—even down to such details as the distinctive specific markings inside the gape.

When it is about twenty-one days old the young of the European cuckoo leaves the nest, which has often, by this time, become too small for it. Cuckoos which are reared in wrens' nests, for example, present a most extraordinary sight bulging out of the entrance hole—often back-side foremost. Before the young cuckoo starts on the long migration to

Africa the foster parents continue to feed it for a further period of about two weeks. This is an extremely arduous task which also incidentally exposes them to various enemies in a manner which would not occur with their own unobtrusive young.

Attention has already been drawn to the fact that sometimes the female cuckoo appears to mesmerise her victims. As a nestling the young cuckoo also produces an unusually exciting effect and not only do the fosterers exert themselves madly to satisfy its hunger, but even strange birds feel drawn to come and feed it. This also occurs during the period after the young cuckoo has left the nest, but still requires feeding. Pliny noticed this peculiar effect on the foster mother: "She joyeth to see so goodly a bird toward : and wonders at herself that she hath hatched and reared so trim a chick." This power of psychological stimulation is probably yet another important biological adaptation, which, like the extraordinary characteristics already mentioned, has become necessary owing to the cuckoo's peculiar and difficult mode of life.

ADAPTATION OF THE CUCKOO'S EGGS

We have already mentioned that the colour and markings of the cuckoo's eggs resemble, to a greater or lesser degree, those of the foster birds chosen to rear their young. This fact has always aroused interest and also considerable controversy. For a long time it was thought that the female cuckoo knew the colour of her own eggs and could select a clutch which they matched, or could, through some physiological reflex, even *control* the colour of her own eggs. It has also been maintained that the female cuckoo mates with the fosterer—a fact which, it was claimed, explains not only the colour of her eggs but their small size, and the derivation of the middle English term "cuckold"!

Recently, investigations, particularly painstaking observations in the field, have thrown considerable light on the whole problem, but it must be admitted that uncertainty still exists concerning much of the cuckoo's private life. Great progress was made in unravelling the tale when it was discovered that individual female cuckoos always lay the same coloured eggs with the same characteristic design. Another discovery which showed how selection worked was the proof obtained from innumerable careful field studies and many experiments, that the small

passerine birds which are the chosen hosts recognise the cuckoo's egg as something undesirable. Subsequently they frequently destroy it or desert the nest in which it has been laid. It is not, of course, suggested that the birds know the egg is a cuckoo's egg—what disturbs them is an egg in some way different from their own and this sense of disharmony prompts them to eject it or to begin to build a new nest altogether. In these circumstances those eggs which resemble the fosterer's or vary in the same direction, and consequently do not arouse anxiety or antagonism in the host, have the best chance of survival and development. In this way selection gradually produces eggs more and more like those of the foster parents. In the same manner elimination by natural enemies produces plovers' eggs and terns' eggs which almost exactly resemble the ground they nest on. In the latter case they have to be concealed from egg thieves, while in the case of the cuckoo the host constitutes the principal enemy. This theory, of course, assumes that the various deviations from the original egg-type are fixed by heredity. The genetics of the cuckoo's egg have not been investigated, but at any rate it is known that egg-shell colour in the domestic fowl is transmitted independently and equally by either sex. Some species of cuckoo like the Indian hawk cuckoo (*Hierococcyx varius*) and all the species of the genus *Clamator*, such as the red-winged crested cuckoo (*Clamator coromandus*) have developed eggs which mimic the host's in every detail, so that even an experienced ornithologist can be deceived. Sometimes the texture of the shell or a small difference in weight reveals the truth, but at times it is virtually impossible to tell which is the brood parasite's egg.

Such a high degree of specialisation naturally restricts the cuckoo in question to one or two closely related species of host, which is always a dangerous position for a parasite to adopt. The advantage of a wide circle of fosterers probably explains why the cuckoos, once embarked upon parasitism, diverged to hosts with eggs unlike their own, which were primitively white or pale bluish green.

There are one or two questions which immediately spring to mind after reading the foregoing account. It has been mentioned that some birds are much more willing to accept the cuckoo's egg than others. The hedge-sparrow, which we know was a favoured host in Shakespeare's day, will brood almost anything foisted upon it from cuckoos' eggs to pebbles. Nor does it attack the adult cuckoo. It is not surprising, therefore, to find that as no selection takes place, no blue-type egg has been developed by the cuckoo parasitising this species. Why then has

the cuckoo not become entirely fixed to complacent fosterers? A possible answer to this question may be that there are very few uncritical fosterers; such birds are quickly over-parasitised and greatly reduced in numbers and then, owing to their scarcity, the cuckoo is forced to lay in other available nests. Therefore selection does not, in the long run, favour the choice of uncritical hosts. It would appear that the type of mimicry found in the European cuckoo is only developed if fosterers exist which are neither too discriminating nor too complacent.

As we have seen, there are strains or "gentes" of the European cuckoo which favour different hosts in different districts. It is assumed, and in some cases proved, that these birds return to breed in the areas where they were originally hatched. The strains are to some extent isolated both geographically and ecologically. Why then has the European cuckoo not broken up into a number of distinct subspecies or species? Stresemann believes that promiscuous sexual behaviour results in a considerable amount of crossing between the gentes, which consequently works against speciation.

Colour and markings are not the only adaptations displayed by the cuckoo's eggs. In the case of the European cuckoo, which parasitises small birds, the eggs are relatively tiny, weighing one thirty-third only of the parent bird. On the other hand, the great spotted cuckoo (*Clamator glandarius*), a rare vagrant in Britain, which parasitises crows and magpies, lays eggs which are larger than normal, namely one eleventh of her own weight.

The egg shells are also heavier and tougher than those of the host's eggs. The hasty manner in which laying takes place and the projection into nests with side entrances, not to mention the occasional transportation in the bird's beak, sets a premium on shell-toughness. It may also prove useful in cases where the fosterers make abortive efforts to eject the egg—for they generally begin this operation by trying to peck a hole in it. The eggs, as in all known brood parasites, develop more rapidly than those of their hosts.

Despite the amazing number of adaptations displayed by the cuckoo the mortality rate of its young is very high. Capek records that out of 237 cuckoos' eggs laid, only 62 per cent. were hatched—but if he could have taken into consideration those eggs which had been immediately destroyed or built over by the fosterers the actual proportion of failures would undoubtedly have proved considerably higher.



Plate XXXVII

Whitethroat removing parasites?

Eric Hosking



Eric Hosking

a. Arctic skua: a food robber or cleptoparasite



Eric Hosking

b. Cuckoo: a brood-parasite fed by its foster-parent, a pied wagtail: this relationship favours the transfer of parasites to new hosts

As for the young cuckoos which actually hatch, 43 per cent. die before they are twenty days old.

It is hardly surprising, therefore, that only a small number of species have travelled successfully along such difficult and hazardous paths and that we find brood-parasitism is relatively a rare phenomenon among birds. Nevertheless it has arisen independently in several unrelated families, and is found among American starlings or hang-nests (Icteridae), African weaver-birds (Ploceidae), honey-guides (Indicatoridae, which are closely related to woodpeckers), ducks (Anatidae) and cuckoos (Cuculidae). Within the last family the habit has probably been developed several times over as it is highly unlikely that all the parasitic cuckoos known to-day are descended from a single parasitic ancestor. Some knowledge of these related forms is useful for a proper understanding of the European cuckoo.

Brood-parasitism has probably originated in several different ways. An important factor in the development of the habit must be the impulse, manifest in a number of birds, to use or usurp the nests of other species. In Britain it is a commonplace occurrence for sparrows to drive out martins and swallows, and to raise their young in the vacated nests. Stock-doves will make use of old magpies' nests and starlings breed in cavities excavated by woodpeckers. Such examples could be multiplied almost indefinitely.

Transitional stages between this casual seizing of other birds' nests and the total loss of nest-building instincts can be followed in some of the cow-birds (*Molothrus*). The bay-winged cow-bird (*Molothrus badius*) occasionally builds her own nest and broods her own young. More frequently she usurps the nests of other birds, which she repairs or alters and ejects or builds over any eggs which may already be present. Quite often several females take a fancy to the same nest and lay in it—one female only, however, incubates the multiple clutch. A close relative, the screaming cow-bird (*M. rufo-axillaris*), has progressed considerably farther in the same direction and is an obligate brood parasite. The female neither builds a nest, nor takes any interest in the welfare of her young. She lays her eggs either singly or in twos or threes almost exclusively in the nests of her close relative, the bay-winged cow-bird. In fact she has become dependent on the latter species for survival and is only found within the same geographical area. In addition to the acquired habit of usurping nests, the cow-birds manifest a progressive weakening of the protective territorial instinct of the males.

It is probably a combination of these two factors which is responsible for the origins of brood parasitism in this genus.

Among cuckoos we find there is the same tendency. The majority of the American species build their own rather simple nests in the forks of trees or on the ground. One or two species, however, such as the yellow-billed cuckoo (*Coccyzus americanus*)—which is a rare vagrant in Britain, recorded in this country on about fourteen occasions—frequently usurp other birds' nests in which they lay and incubate their own eggs. Again others, such as the ani (*Crotophaga ani*) lay in mutual or communal nests. Obviously, in the cuckoo family as well as in the cowbirds, nest-seizing is an important step in the development of the parasitic habit, although in the case of many cuckoos there is no slackening of the territorial instinct—at least on the part of the female bird.

Every countryman knows that a china egg placed in a hen's nest will encourage her to lay. It is quite possible that the parasitic habit in certain birds originally arose from an exaggeration or perversion of this psychological response. Thus, a female with an egg in her oviduct, on catching sight of an incomplete clutch, would be seized with an uncontrollable urge to lay then and there, even in another bird's nest. Among ducks and geese, which build open nests on the ground, it is not uncommon for two females of the same or different species to lay in one nest—the original owner incubating and rearing the brood. At Mývatn in Iceland, where up to twelve species of duck breed in an identical habitat and in a similar style, there is much "adventitious parasitism" of this type. It is particularly marked in the case of the long-tailed duck. One South American duck (*Heteronetta atricapilla*) is an obligate brood parasite, which lays her eggs principally in nests of other ducks but also in those of various ground nesting species such as gulls, waders and coots. It is quite likely that visual stimulation plays a big part in determining her actions. When the brooding drive is uppermost some gulls will attempt to "incubate" golf balls, tins or even suitably shaped cakes if they are placed in their nests. It is, therefore, surprising that brood parasitism is not found in this type of colonial bird. Certain species of weaver-birds which are also colonial nesters have in fact exploited this situation. A less numerous species mingles with the main colony and surreptitiously introduces its eggs into suitable nests.

Notwithstanding the very strong brooding instinct shown by many birds, this drive can be easily lost if it is not maintained by natural selection. For instance a fact with which most countrymen are familiar

is the difficulty experienced to-day in obtaining a broody hen. Chickens, during the past few years, have been selected chiefly for their egg-laying capabilities and the great majority of chicks are hatched in incubators. Without deliberate intention broodiness has been "bred out" of most strains of domestic fowls, and if by chance a broody hen is needed to rear a covey of wild partridges, a long tour in a car from farm to farm is required in order to locate one. The common complaint of twenty years ago that "the hens have stopped laying and have gone broody" is now as much a thing of the past as a sirloin of beef or a hansom cab.

If a bird therefore embarks upon a series of chance layings in nests other than her own, it is not difficult to see how a large number of eggs will possess better survival value than the instinct for incubating and brooding, and the latter characteristic will be speedily eliminated.

Most parasitic birds are sexually promiscuous, either polygamous or polyandrous, or both. This loose way of living, particularly when it is associated with a loss of parental instinct on the part of the male, seems to be connected with the development of the parasitic habit. In some cases, for example in the cow-birds, it appears as a consequence rather than a cause of the parasitic mode of life. Further information is required about the biology of brood-parasites, but it seems certain that the habit is almost always associated with various types of promiscuous sexual relationships.

Brood-parasites—by whatever routes they may have developed the habit—seem to possess certain characteristics in common. Their eggs, for example, always develop at a quicker rate than those of the host. The advantage of hatching before the foster nestlings appears to be extremely important, if not essential, for their survival. The European cuckoo hatches two days before the host, and the cow-birds from one to four days, even when the closely related species of cow-bird fosterer is concerned. A widely spread habit among the females of brood-parasites is the removal or destruction of at least one egg of the foster bird. The eggs themselves are frequently modified in certain well defined directions. Thus, the shell is much tougher in the case of the parasite's egg. This is even true of the two related cow-birds referred to above. The size and weight of the eggs and the colour and pattern of the shell frequently tend to resemble those of the fosterer. Some brood-parasites lay eggs which are superficially indistinguishable from those of their host. Well known examples of this phenomenon are recorded from

weaver birds, cow-birds and cuckoos. Deliberate destruction of the eggs or nestlings of the fosterer by the young of the brood-parasite is known among cuckoos and honey guides. The former heave them out of the nest and the latter are thought to peck them to death. Parasitic cow-birds achieve the same object by a more subtle method. They manage by importuning the foster parents to get most of the food for themselves and the rightful young eventually die of under-nourishment and debility.

Successful brood-parasitism, like successful ecto-parasitism, seems to impose development and specialisation along certain lines. Therefore, in widely separated groups of birds, located in opposite sides of the globe we find these striking examples of parallel development.

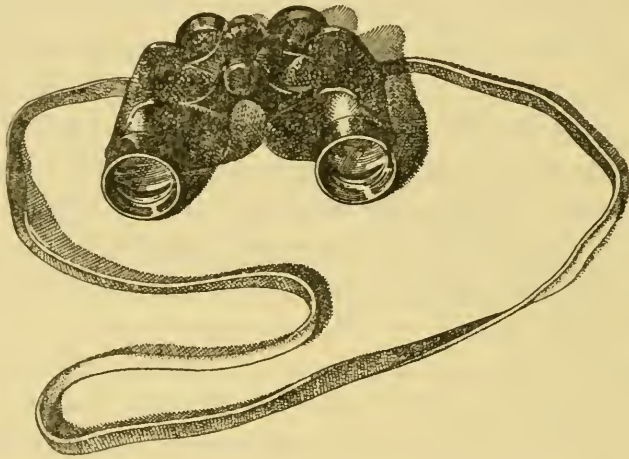




Plate XXXIX

Eric Hosking

House-martins collecting mud for their nests: a louse-fly can be seen crawling on the back of the bird nearest the camera.

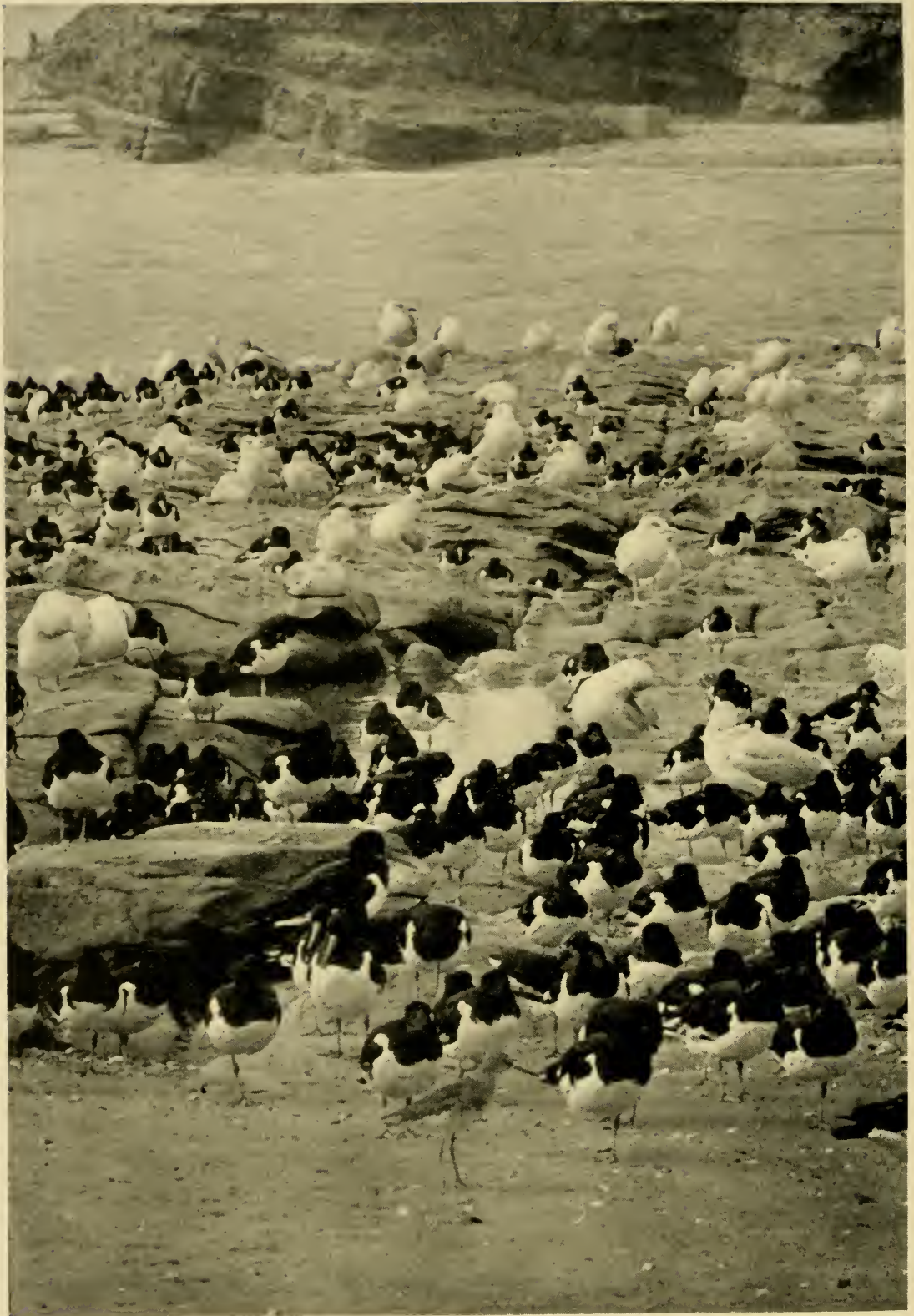


Plate XL

Eric Hosking

Birds congregating on the sea shore: this type of habitat and the conditions shown here favour a high infection rate with Trematodes

BIBLIOGRAPHICAL APPENDIX

ONLY A FEW books have been written which are concerned with the study of parasites in general (see below) and none has been published in this country. Moreover, the great majority of such books are limited to the description of the parasites of man and domestic animals, and chief stress is laid on their medical and veterinary importance. The outstanding textbook of this sort is Brumpt's *Précis de Parasitologie* (6th edition, Paris, 1949), which is over 2,000 pages in length and illustrated with 1,305 text figures. It is written in the French language. Although the book deals exclusively with the parasites of man, it is so comprehensive that a general idea of the morphology, life-cycles and classification of all the major parasitic groups can be obtained from this monumental work.

There are no books in any language dealing exclusively with the parasites of birds. The nearest approach is a recent publication edited by Biester and Schwarte, *Diseases of Poultry* (Iowa, 1948). Consequently, the general reader and the ornithologist who may now be interested are left to struggle with the scattered literature to the best of their ability.

In Britain, France, Germany and the United States there are scientific periodicals devoted exclusively to parasitology—which can be read in the libraries of the British Museum (Natural History), the Science Museum and the Zoological Society—and with the aid of the subject indexes at the end of the volumes the papers dealing with bird parasites can be sorted out and studied.

The scientific publications in such journals generally contain references to previous papers and various books dealing with the same subject, which helps the reader in tracking down further information. In addition to these journals there are various publications designed specially to assist the zoologist in keeping abreast of current literature, published both here and abroad. These consist of classified abstracts, classified lists of titles and authors, in conjunction with copious subject indexes. The geographical distribution of the animals in question is

sometimes given in detail, so that British fauna can be separated from the rest.

There are several famous series of zoological treatises, such as the *Cambridge Natural History*, which set out to survey the animal kingdom group by group. It is of the greatest importance to consult the four main series of this type (see below) no matter in which group of parasites the reader may be interested. Some of the volumes are now quite out of date but others are recent and first class—for example, Stresemann's *Aves* (*Handbuch der Zoologie*, 1934).

For the study of every group of parasites it is of course useful to find an up-to-date and reliable textbook, particularly one which supplies a good, but not necessarily detailed, classification of the group concerned. In many cases no such book exists and the unfortunate non-specialist is then left to flounder. Below, the authors have endeavoured to suggest, chapter by chapter, what literature will prove helpful if the reader wishes to embark on a more serious study of the parasites in question. (Unless otherwise stated the papers are written in English.) Some of the publications have been suggested partly on account of their valuable bibliographies, and these have been marked with an asterisk.

Throughout the text the reader will find an occasional reference to an author or to a paper which does not appear in the relevant list in the Bibliographical Appendix. However, the full reference to these authors and their publications will be found in the papers indicated by an asterisk. Thus, for Chapter 7, references to the numerous works of Jordan and Rothschild will all be found in *Pulgas* by A. M. da Costa Lima and C. R. Hathaway, *A Synopsis of the British Siphonaptera* by N. C. Rothschild or *Katalog der palaearktischen Aphanipteren* by J. Wagner, which contain copious bibliographies.

Most of the literary quotations in the text are so well known that it seems unnecessary to refer to their source. The particular translations of Pliny and Mouffet from which we have quoted so liberally are, however, especially attractive, and these references are consequently given below.

HOLLAND, PHILEMON (1601). *The Historie of the World commonly called the Naturall Historie of C. Plinius Secundus*. Trans. P. Holland.

MOUFFET, THOMAS (1658). *The Theater of Insects*. English translation in *The History of Four-footed Beasts and Serpents*. Edited by John Rowland.

PART I
INTRODUCTION AND CHAPTER 1*

Most important periodicals concerned exclusively with
parasites

Parasitology. Cambridge 1908—

Journal of Parasitology. Urbana, Ill. 1914—

Zeitschrift für Parasitenkunde. Berlin 1928— (chiefly in German).

Annales de Parasitologie humaine et comparée. Paris 1922— (chiefly in French).

Rivista de Parassitologia. Rome 1937— (chiefly in Italian).

†*Experimental Parasitology*. New York 1952—

Most useful abstracts and indexes (in English) for use by
the parasitologist

Zoological Record. London.

Biological Abstracts. Philadelphia.

Review of Applied Entomology. (Series B) *Medical and Veterinary*. London.

Helminthological Abstracts. St. Albans, England.

Main Zoological Treatises

Cambridge Natural History. London.

Handbuch der Zoologie (Kükenthal und Krumbach) (in German).

Bronns Klassen und Ordnungen des Tierreichs. Leipzig (in German).

Traité de Zoologie. Paris (in French).

General books on parasitism

BAER, J. G. (1946). *Le Parasitisme*. Lausanne (in French).

BAER, JEAN G. (1951). *Ecology of Animal Parasites*. University of Illinois Press, Urbana.

BRUMPT, E. (1949). *Précis de Parasitologie*. Paris (in French).

CAULLERY, M. (1922). *Le Parasitisme et la Symbiose*. Paris (2nd edition, 1950) (in French).

*CHANDLER, A. C. (1930). *Introduction to Parasitology*. (9th edition). Revised 1955. London and New York.

GRASSÉ, P. P. (1935). *Parasites et Parasitisme*. Paris (in French).

HEGNER, R. W., ROOT, F. M., AUGUSTINE, D. L. and HUFF, C. G. (1938). *Parasitology*. New York.

LAPAGE, GEOFFREY (1951). *Parasitic Animals*. Cambridge Library of Modern Science.

PEARSE, A. S. (1942). *Introduction to Parasitology*. Springfield, Ill.

RILEY, W. A. (1945). *Introduction to the Study of Animal Parasites and Parasitism*. Minneapolis.

† All items thus marked have been added in the third edition (1957).

Books on the bird host

- *BIESTER, H. E. and SCHWARTE, L. H. (1943). *Diseases of Poultry*. (2nd edition). Revised 1948. Iowa, U.S.A.
- Catalogue of the Birds in the British Museum*. 27 vols. London.
- †GRASSÉ, PIERRE-P. (editor) (1950). *Oiseaux. Traité de Zoologie, XV*. Paris (in French).
- PETERS, J. L. (1931—). *Check-List of Birds of the World*. Cambridge, Mass.
- ROMANOFF, A. L. and A. J. S. (1948). *The Avian Egg*. London and New York.
- STRESEMANN, E. (1927-1934). *Aves*: in Kükenthal and Krumbach, *Handbuch der Zoologie*. Bd. 7, Hft. 2. Berlin and Leipzig (in German).
- WITHERBY, H. F., JOURDAIN, F. R. C., TICEHURST, N. F., TUCKER, B. W. (1938-1941). *The Handbook of British Birds*. Vols. I-V. London.

NOTE: The lists of parasites given for each species of bird in Niethammer's *Handbuch der deutschen Vogelkunde I-II*, Leipzig 1937-1938 is totally unreliable and it is best to ignore this part of the publication. An accurate compilation of records of the parasites of British birds—providing that in all cases the source of the record is given—would be quite invaluable.

CHAPTERS 2 AND 3. COMMENSALISM AND SYMBIOSIS

There are no books which deal specifically with commensalism and symbiosis among birds, but the following papers should be consulted and the various references listed in their respective bibliographies should also be read and studied. If added information is required about particular species of birds, for instance the buff-backed heron, or the sheath-bills, it is advisable to consult accepted ornithological authorities such as Bannerman (*Birds of Tropical West Africa*, Vols. I-V, London, 1930), or Murphy (*Oceanic Birds of South America*, Vols. I & II, New York, 1936). One or two papers have been published recently dealing specifically with the peculiar habit known as phoresy.

Commensalism and Symbiosis

- †ALLEE, W. C., EMERSON, A. E., PARK, O., PARK, T., and SCHMIDT, K. P. (1949). *Principles of Animal Ecology*. 837 pp. Saunders, Philadelphia.
- *BAKER, E. C. STUART (1931). Nesting associations between birds and wasps, ants or termites in the Oriental Region. *Proc. Ent. Soc. London*, 6: 34-37.
- BUCHNER, P. E. C. (1930). *Tier und Pflanze in Symbiose*. Berlin (in German).
- †DAVENPORT, DEMOREST (1955). Specificity and behavior in symbioses. *The Quart. Rev. of Biol.*, 30: 29-46.
- †DURANGO, S. (1949). The nesting associations of birds with social insects

- and with birds of different species. Extracted and translated in *Ibis*, 91: 140-143.
- FISHER, J. and HINDE, R. A. (1949). The Opening of Milk-bottles by Birds. *British Birds*, 42 : 347-357.
- HARVEY, E. N. (1940). *Living Light*. Pp. xvi + 328 col. frontisp. and 88 figs. Princeton.
- LYNES, H. and VINCENT, J. (1939). The White-rumped Swift *M. caffer* beginning to breed under the eaves of houses. *Ostrich* (Pretoria), 10 : 75-84.
- MOREAU, R. E. (1933). The food of the Red-billed Oxpecker, *Buphagus erythrorhynchus* (Stanley). *Bull. Ent. Res. London*, 24 : 325-335.
- *MOREAU, R. E. (1942). The nesting of African Birds in association with other living things. *Ibis*. (14), 6 : 240-263.
- MYERS, J. G. (1935). Nesting associations of Birds with social insects. *Trans. Ent. Soc. London*, 83 : 11-22.
- NELSON, T. H. (1882). Small birds carried by Cranes in their migrations. *The Zoologist*, 60 : 73.
- Supplement to the report of the twelfth annual meeting of the American Society of Parasitologists. Report of the Committee (1937). *Journal of Parasitology*, 23 : 325-329.
- See also *The Handbook of British Birds* (Witherby) under the individual species referred to in the text.

Phoresy

- †BEQUAERT, J. C. (1953). The Hippoboscidae or Louse-flies (Diptera) of Mammals and Birds. *Ent. amer.*, 32: 163-174.
- †SMIT, F. G. A. M. (1953). Transport of Mallophaga by Fleas. *Parasitology*, 43: 205-206.
- VACHON, M. (1947). Nouvelles remarques à propos de la phorésie des Pseudoscorpions. *Bull. Mus. Hist. Nat.* (2), Paris (in French), 19 : 84-87.
- WARBURTON, C. (1928). *Ornithomyia avicularia* (Diptera Hippoboscidae) as the carrier of Mallophaga, with some remarks on phoresy in insects. *Parasitology* (Cambridge), 20 : 175-178.

CHAPTERS 4, 5 AND 6

THE EFFECT OF PARASITES ON THE HOST

THE EFFECT OF PARASITISM ON THE PARASITE

THE ORIGINS OF PARASITISM AND THE EVOLUTION OF PARASITES

Relevant material will be found in all the books on the general aspect of parasitism quoted above. The following publications should also prove interesting.

- BALL, G. H. (1943). Parasitism and evolution. *Amer. Nat.* 77: 345-346.
- †BECKER, ELERY R. (1953). How parasites tolerate their hosts. *Journal of Parasitology*, 39: 467-480.
- BODENHEIMER, F. S. (1938). *Problems of Animal Ecology*. Oxford.
- Evolution, Essays on Aspects of Evolutionary Biology* (1938). Edited by G. R. de Beer. Oxford.
- ELTON, C. S. (1930). *Animal Ecology and Evolution*. Oxford.
- GIARD, A. (1911-1913). *Oeuvres diverses* (2 Vols.). Paris (in French).
- GOLDSCHMIDT, R. (1940). *The Material basis of Evolution*. California and London.
- HALDANE, J. B. S. (1932). *The Causes of Evolution*. London.
- HUXLEY, J. S. (1940). *The New Systematics*. Oxford.
- *HUXLEY, J. S. (1942). *Evolution, The Modern Synthesis*. London.
- †LACK, DAVID (1954). *The Natural Regulation of Animal Numbers*, 343 pp. Oxford.
- MAYR, E. (1942). *Systematics and the Origin of Species . . .* New York.
- METCALF, M. M. (1929). Parasites and the aid they give in problems of taxonomy, geographical distribution and paleogeography. *Smithson. Misc. Publ.* 81. No. 8.
- ROTHSCHILD, N. C. (1917). Convergent development among certain ectoparasites. *Proc. Ent. Soc. (London)*, 1917: 141-156.
- SHIPLEY, A. E. (1926). Parasitism in evolution. *Sci. Progr. (London)*, 20: pt. II, 637-661.
- SMITH, THEOBALD, (1934). *Parasitism and Disease*. Princeton.
- STUNKARD, H. W. (1929). Parasitism as a biological phenomenon. *Scient. Monthly*, 28: 349-362.

PART II

INTRODUCTION AND CHAPTERS 7 AND 8 FLEAS AND FEATHER LICE

In order to study any particular order of insects it is necessary to have at hand certain books dealing with general entomology. Fortunately, several first class textbooks on the Insecta have been written in English.

Fleas (Aphaniptera): A satisfactory classification of the families will be found in Hopkins & Rothschild (1953). *An Illustrated Catalogue of the Rothschild Collection of Fleas (Siphonaptera) in the British Museum (Natural History)*, I, but in this first volume only the Pulicoidea are dealt with in detail. The species of purely economic interest are

adequately classified by Jordan in Smart's *Insects of Medical Importance*. The external morphology of the flea is admirably dealt with by Snodgrass, 1945 (see below). With regard to the fauna of Britain, the most up-to-date paper is still that of Rothschild published in 1915, but shortly a section by F. G. A. M. Smit dealing with fleas will appear in the series *Handbooks for the Identification of British Insects*, published by the Royal Entomological Society of London. This will save the unfortunate beginner a hunt through the papers listed in bibliographies and a search through the *Zoological Record* for British records.

Feather lice (Mallophaga) : There is no satisfactory classification of the feather lice in existence. The best account of their biology will be found in Hopkins' paper which deals principally with the Mallophaga of mammals. It has an excellent bibliography.

General Entomology

- BRUES, C. T. (1946). *Insect Dietry. An account of the food habits of insects*. Cambridge, Mass. Harvard Univ. Press.
- FORD, E. B. (1945). New Naturalist Series, 1. *Butterflies*. London.
- IMMS, A. D. (1925). *A General Textbook of Entomology*. (3rd edition, revised 1934) London.
- IMMS, A. D. (1947). New Naturalist Series, 8. *Insect Natural History*. London.
- SMART, J. (1943). *A Handbook for the Identification of Insects of Medical Importance*, with chapters on fleas by K. Jordan and arachnids by R. J. Whittick. London. Brit. Mus. (Nat. Hist.). Revised edition 1948.
- SNODGRASS, R. E. (1935). *Principles of Insect Morphology*. New York and London.
- *STEINHAUS, E. A. (1946). *Insect Microbiology*. New York and London.
- *WIGGLESWORTH, V. B. (1939). *The Principles of Insect Physiology*. (3rd edition 1947). London.

Fleas (Aphaniptera)

- ALLAN, RONALD M. (1950). Fleas (Siphonaptera) from birds in North-East Scotland. *The Scottish Naturalist*, 62 : 33-41.
- BUXTON, P. A. (1932). Studies on the biology of fleas. *London Naturalist*, 1932 : 39-42.
- BUXTON, P. A. (1932). The climate in which the rat-flea lives. *Ind. Jour. Med. Res.* 20 : 281-297.
- BUXTON, P. A. (1938). Quantitative studies on the biology of *Xenopsylla cheopis* (Siphonaptera). *Ind. Jour. Med. Res.* 26 : 505-530.
- *COSTA LIMA, A. M. DA, and HATHAWAY, C. R. (1946). Pulgas. *Monografias do Instituto Oswaldo Cruz*. Rio de Janeiro, Brasil. (This paper contains a most important bibliography).

- †DUNNET, G. M., & ALLAN, R. M. (1955). Annual and regional variation in the flea populations of nests of the house-martin *Martula u. urbica* (L.) in North-east Scotland. *Ent. mon. Mag.*, 91: 161-167.
- HIRST, L. F. (1925). Plague Fleas, with special reference to the Milroy Lectures, 1924. *Jour. Hyg.* 24: 1-16.
- †HOPKINS, G. H. E., & ROTHSCHILD, M. (1953). *An Illustrated Catalogue of the Rothschild Collection of Fleas (Siphonaptera) in the British Museum (Natural History)*, 1, London.
- IOFF, I. G. (1941). The ecology of fleas in connection with their epidemiological importance. Pyatigorsk. *Ordzhonik Kraev. Izd.* 116 (in Russian).
- JORDAN, K. (1926). On *Xenopsylla* and allied genera of Siphonaptera. *Verh. III. Internat. Ent. Kongr.* (Zürich), 1925: 593-627.
- JORDAN, K. (1929). On some problems of distribution, variability and variation in North American Siphonaptera. *Trans. 4th Int. Cong. of Ent.* (Ithaca, 1928), 489-499.
- JORDAN, K. (1942). On *Parapsyllus* and some closely related genera of Siphonaptera. *Eos.* (Madrid), 18: 7-29.
- MITZMAIN, M. B. (1910). Some new facts on the bionomics of the California rodent fleas. *Ann. Ent. Soc. Amer.* 3: 61-82.
- *ROTHSCHILD, N. C. (1915). A synopsis of the British Siphonaptera. *Entom. Mag.* (London), 51: 49-112. (important references for early records).
- ROTHSCHILD, M. (1948). Bird fleas collected by Miss Theresa Clay, Colonel Richard Meinertzhagen and Captain W. H. Pollen in the Island of Ushant, Brittany, France, with a Note on the Distribution of *Ceratophyllus borealis* Rothschild (1907). *Entom.* 81: 84-95.
- ROTHSCHILD, M. (1951). A collection of fleas from the bodies of British birds, with notes on their distribution and host preferences. *Bulletin of the British Museum (Natural History)*, Entomology, 2: no. 4, in press.
- †ROTHSCHILD, M. (1955). The distribution of *Ceratophyllus borealis* Rothschild, 1906, and *C. garee* Rothschild, 1902, with records of specimens intermediate between the two. *Trans. Royal Ent. Soc.*, 107: 295-317.
- SHARIF, M. (1936). The life history, the biology and the anatomy of the early stages of the rat-flea, *Nosopsyllus fasciatus*, Bosc. *Abstr., Diss. Univ. Cambridge*: 29-30.
- †SMIT, F. G. A. M. (1954). *Lopper. Danmarks Fauna* 60: 125 pp. Copenhagen. (In Danish).
- †SMIT, F. G. A. M., and ALLAN, R. M. 1955. Variation in the seventh sternum of females of the House-Martin flea *Ceratophyllus farreni* Rothschild, with remarks on synonymy. *The Entomologist*, 88 (1101): 41-46.
- †SMIT, F. G. A. M., and ROTHSCHILD, M. (1955). Two new subspecies of fleas (Siphonaptera) from the British Isles, with a discussion on their distribution. *Trans. Royal Ent. Soc.*, 107: 341-372.

- SNODGRASS, R. E. (1946). The Skeletal Anatomy of fleas (Siphonaptera), *Smithson Misc. Coll.* 104: no. 18, 1-89.
- STRICKLAND, D. (1914). The biology of *Ceratophyllus fasciatus* Bosc., the common rat-flea of Great Britain. *Jour. Hyg.* 14: 129-142.
- *WAGNER, J. (1930). *Katalog der palaearktischen Aphanipteren*. Vienna: F. Wagner, 55. (The subsequent additions to this catalogue must not be overlooked).
- WAGNER, J. (1939). Aphaniptera. In *Bronns Klassen und Ordnungen des Tierreichs*, Vol. 5, Abt. 3, Buch 13, Teil f., 114.
- WATERSTON, J. (1910). On some habits and hosts of bird Ceratophylli taken in Scotland in 1909; with description of a new species (*C. rothschildi*) and records of various Siphonaptera. *Proc. Roy. Phys. Soc. Edin.* 188: 73-91.
- WIGGLESWORTH, V. B. (1935). The regulation of respiration in the flea *Xenopsylla cheopis* Roths. (Pulicidae). *Proc. Roy. Soc.* 118: 397-419.

Feather lice (Mallophaga)

- CHISHOLM, A. H. (1944). The problem of "Anting." *Ibis*, 86: 389-405.
- DENNY, H. (1842). *Monographia Anoplurorum Britanniae*. London.
- GIEBEL, C. G. (1874). *Insecta Epizoa*. Leipzig. (in German).
- *HOPKINS, G. H. E. (1949). The host-associations of the lice of mammals. *Proc. Zool. Soc. London*, 119: 387-604.
- HOPKINS, G. H. E. and CLAY, T. (1952). *A check-list of the Mallophaga*. British Museum (Natural History).
- *KELER, S. (1938). Übersicht über die gesamte Literatur der Mallophagen. *Z. angew. Ent.* 25: 487-524.
- PIAGET, E. (1880). *Les Pédiculines*. Leyden. (in French).
- PIAGET, E. (1885). *Les Pédiculines. Supplément*. Leyden. (in French).
- REDI, F. (1668). *Esperienze intorno alla generazione degli insetti fatti*. Florence. (in Italian).

PART III

CHAPTER 9, PROTOZOA

Wenyon's textbook is an all time classic. Although necessarily out of date in certain respects (for example, further important discoveries have been made concerning the life-cycle of malaria during the last few years), it can still form the basis of any research on the Protozoa. *Bird Malaria* (although the host check list is unreliable), is a book which should also be read in conjunction with this chapter.

- †BAKER, J. R. (1955 personal communication: part in press). The blood protozoa of British birds.
- †BUXTON, P. A. (1955). *The Natural History of Tsetse Flies*, 816 pp., 47 pls., London.
- COLES, A. C. (1914). Blood parasites found in mammals, birds and fishes in England. *Parasitology*, 7 : 17.
- HEWITT, R. (1940). *Bird Malaria*. Amer. Hygiene Monogr. Ser. No. 15. Baltimore.
- HUFF, CLAY G. and COULSTON, FREDERICK. (1944). The development of *Plasmodium gallinaceum* from sporozoite to erythrocytic trophozoite. *J. Infect. Dis.* 75 : 231-249.
- JAMES, S. P. and TATE, P. (1938). Exo-erythrocytic schizogony in *Plasmodium gallinaceum* Brumpt. 1935. *Parasitology*, 30: 128-139.
- JAMES, S. P. (1939). The incidence of exo-erythrocytic schizogony in *Plasmodium gallinaceum* in relation to the mode of infection. *Trans. Roy. Soc. Trop. Med. and Hyg.* 32 : 763-769.
- KUDO, R. R. (1946). *Protozoology*. (3rd edition). Springfield, Ill.
- SHORTT, H. E., MENON, K. P. and SEETHARAMA IYER, P. V. (1940). The forms of *Plasmodium gallinaceum* present in the incubation period of the infection. *Ind. J. Med. Res.* 28 : 273-276.
- WENYON, C. M. (1926). *Protozoology*. Vols. I and II. London.

CHAPTER 10, WORMS (VERMES)

There is no textbook in the English language concerned with parasitic worms as a whole. Sprehn's *Lehrbuch der Helminthologie*, a German publication, deals with all four main groups and is the best of its kind. Various medical and veterinary helminthologies are however available, several of which are written in English. The worms as a whole comprise an enormous group and it is preferable to consider the various classes separately. Unfortunately no satisfactory classification of the flukes has been compiled up to date. The tapeworms and roundworms are admirably dealt with by Fuhrmann and the Chitwoods. Since Meyer's monograph on the spiny-headed worms, van Cleave has suggested a modified classification and the reader is advised to hunt up his various papers on this group which have the advantage of being written in English. Two lists of helminths by Baylis from British vertebrates are very useful. One of the most urgent requirements in the field of helminthology is a compilation describing the known life-cycles of parasitic worms, together with lists of their intermediate hosts.

General books and papers on Worms

- BAYLIS, H. A. (1928). Records of some Parasitic Worms from British Vertebrates. *Ann. Mag. Nat. Hist.* (10), 1 : 329-343.
- BAYLIS, H. A. (1939). Further records of Parasitic Worms from British Vertebrates. *Ann. Mag. Nat. Hist.* (11), 4 : 473.
- † BRAND, THEODOR VON (1952). *Chemical Physiology of Endoparasitic Animals*, 339 pp. New York.
- DOLLFUS, R. P. (1946). Parasites (animaux et végétaux) des Helminthes. *Encyclopédie Biologique*. 27. Paris. (in French).
- FAUST, E. C. (1929). *Human Helminthology ; a Manual for Clinicians, Sanitarians, and Medical Zoologists*. Philadelphia and London.
- NEVEU-LEMAIRE, M. (1936). *Traité d'helminthologie médicale et vétérinaire*. Paris. (in French).
- SPREHN, C. E. W. (1932). *Lehrbuch der Helminthologie. Eine Naturgeschichte der in deutschen Säugetieren und Vögeln schmarotzenden Würmer unter besonderer Berücksichtigung der Helminthen des Menschen, der Haustiere und wichtigsten Nutztiere*. Berlin. (in German).

Roundworms (Nematoda)

- CHITWOOD, B. G. and M. B. (1937—last published 1948). *An introduction to nematology*. Baltimore (Monumental Printing Co.) Washington, D.C. (A good skeleton classification will be found in Part I, Section 1, p. 49).
- GRAM, E. B. (1927). Bird parasites of the Nematode suborders Strongylata, Ascaridata and Spirurata. *Bull. U.S. Nat. Mus.* 140 : 1-465.
- DOUGHERTY, ELLSWORTH C. (in press). Evolution of zooparasitic groups in the phylum Nematoda, with special reference to host-distribution. *Journal of Parasitology*, 37 : no. 4.

Spiny-headed worms (Acanthocephala)

- MEYER, A. (1933). *Acanthocephala. Bronns Klassen u. Ordnungen des Tierreichs* Leipzig. 4 (Abt. 2 Buch 2 Lfg. 2) 333-582. (in German).

Tapeworms (Cestoda)

- † BAER, JEAN G. (1954). Révision taxinomique et étude biologique des Cestodes de la famille des Tetrabothriidae. *Mémoires de l'Université de Neuchâtel*, 1, 121 pp. Neuchâtel (in French).
- FUHRMANN, O. (1931). *Vermes Amera. Cestoda*. in Kükenthal und Krumbach. *Handbuch der Zool.* 2, Teil 2. Berlin, 257-416. (in German).
- FUHRMANN, O. (1932). Les tenias des oiseaux. *Mém. Inst Univ. Neuchâtel* 8 : 1-381. 147 figs. (in French).
- LARSH, JOHN E. (1951). Host-parasite relationships in cestode infections, with emphasis on host resistance. *Journal of Parasitology*, 37 : no. 4, 343-352.

Flukes (Trematoda)

- DAWES, B. (1946). *The Trematoda*. Cambridge.
- FUHRMANN, O. (1928). *Trematoda*. In Kükenthal und Krumbach, Handbuch d. Zool. Berlin, 2, Part 2. 1-140. (in German).
- LARUE, GEORGE R. (in press). Host-parasite relations among the digenetic trematodes. *Journal of Parasitology*, 37 : no. 4.
- †NICOLL, W. (1923). A reference list of the trematode parasites of British birds. *Parasitology*, 15 : 151-202.

Leeches (Hirudinea)

- †MANN, K. H. (1954). *A key to the British Freshwater Leeches with notes on their ecology*. Freshwater Biological Association Scientific Publication No. 14, 21 pp.
- †MANN, K. H. (1955). The Ecology of the British Freshwater Leeches. *The Journal of Animal Ecology*: 24, (1): 98-119.
- HARDING, W. A. (1910). A revision of the British Leeches. *Parasitology*, 3 : 130-201.

CHAPTER II, FLIES (DIPTERA)

Apart from the general books on insects, the volumes mentioned below are of great assistance and have provided most of the data for this chapter. Bequaert's monograph on the louse-flies is a masterpiece, and Séguy provides useful lists in both his papers. Mattingly's paper is invaluable for the determination of the mosquitoes.

- *BATES, MARSTON, (1949). *The Natural History of Mosquitoes*. New York.
- †BEQUAERT, JOSEPH C. (1953). The Hippoboscidae or Louse-flies (Diptera) of Mammals and Birds. Part 1 : Structure, Physiology and Natural History. *Entomologica Americana*, 32 (new series): 1-209, & 33: 211-442.
- †COE, R. L., FREEMAN, PAUL, & MATTINGLY, P. F. (1950). *Handbooks for the identification of British Insects*, IX, part 2, Diptera 2. Nematocera : families Tipulidae to Chironomidae : pp. 1-216, London.
- EDWARDS, F. W., OLDROYD, H., & SMART, J. (1939). *British Blood-sucking Flies*. London.
- KEILIN, D. (1924). On the Life-history of *Anthomyia procellaris* Rond, and *A. pluvialis* L., hibernating in nests of birds. *Parasitology*, 16 : 150-159.
- MARSHALL, J. F. (1938). *The British Mosquitoes*. London.
- †OLDROYD, H. (1949). *Handbooks for the identification of British insects*, IX, part 1, Diptera 1. Introduction and key to families : pp. 1-49. London.
- SÉGUY, E. (1946). Diptères ornithophiles in *Encycl. Ent. Ser. B* 2, 10 : 118-132 (in French).

† This list refers to records from birds on the British list, not British birds, as the title suggests.

- †SÉGUY, E. (1950). La Biologie des Diptères. *Encycl. ent. Ser. A*, 26, 609 pp. (in French).
- †TATE, P. (1954). Notes upon the biology and morphology of the immature stages of *Neottiophilum praeustum* (Meigen, 1926) (Diptera: Neottiophilidae) parasitic on birds. *Parasitology*, 44: 111-119.

CHAPTER 12, MITES AND TICKS (ACARINA)

The recent French publication *Traité de Zoologie* (see below), gives a good general account of the mites and ticks, in French, a useful classification (p. 879), and a selected bibliography. One of the outstanding contributions to the knowledge of ticks is Nuttall's and Warburton's series of papers. Portions of the monograph are necessarily out of date but nevertheless it should be read from cover to cover. A magnificent monograph on the Analgesoidea (feather mites) has been published by Dubinin, unfortunately in Russian. Recent papers on British ticks can be found in *Parasitology*. Various papers on parasitic mites have been published by Turk (in English) and the reader is advised to look these up.

Heymons' monograph on the tongueworms (Pentastomida) is first class. Unfortunately it is in German and there is no equivalent in English.

- *ANDRÉ, M. (1949). Ordre des Acariens. Grassé *Traité de Zoologie*. Tome 6: 795-892, Paris (in French). (A useful classification will be found on p. 879).
- †BAKER, E. W., & WHARTON, G. W. (1952). *An Introduction to Acarology*, 465 pp., New York.
- *HEYMONS, R. (1935). *Pentastomida. Bronns Klassen und Ordnungen des Tierreichs*. Bd. 5, Abt. IV. Buch 1. Leipzig (in German).
- NUTTALL, G. H. F., WARBURTON, C., COOPER, W. F. and ROBINSON, L. E. (1908-1926). *Ticks, A Monograph of the Ixodoidea*. Pts. 1-4, London.
- †RADFORD, CHARLES D. (1949-50). The mites (Acarina) parasitic on mammals, birds and reptiles. *Parasitology*, 40: 366-394.
- †RADFORD, CHARLES D. (1952-53). The mites (Acarina: Analgesidae) living on or in the feathers of birds. *Parasitology*, 42: 199-230.
- VITZTHUM, H. GRAF (1929). Milben, Acari. *Tierwelt Mitteleuropas* Bd. III. Lfg. 3. (in German).

CHAPTER 13, MICRO-PARASITES

Bacteria and Viruses: Topley and Wilson's textbook is the all-time classic in this field, and in every respect is beyond praise. (For a classification of bacteria see Vol. I, p. 310). Various pertinent chapters in the *Diseases of Poultry* (see above) are also useful especially for tracking down obscure papers.

Fungi. The best available textbooks dealing with fungi are in French (see below). The species described in Dollfus' compilation are of the greatest interest in view of the importance of the nematode parasites of birds.

- BRUMPT, E. (1949). *Précis de parasitologie*. Vols. I and II. Paris. (for fungi see pp. 1607-2039). (in French).
- DANE, SURREY D. (1948). A disease of Manx Shearwaters (*Puffinus puffinus*). *J. Animal Ecol.* 17: 158-164.
- DOLLFUS, R. (1946). Parasites (animaux et végétaux) des Helminthes. *Encyclopédie Biologique*. Paris.
- FLOREY, H. W., CHAIN, E., HEATLEY, N. G., JENNINGS, M. A., SANDERS, A. G., ABRAHAM, E. P. and FLOREY, M. E. (1949). *Antibiotics. A survey of Penicillin, Streptomycin, and other antimicrobial substances from fungi, actinomycetes, bacteria, and plants*. 2 Volumes. Oxford University Press, London, New York and Toronto.
- GARDNER, A. D. (1931). *Microbes and Ultramicrobes*. London.
- LANGERON, M. (1945). *Précis de mycologie*. Paris. (reprinting, new edition promised for 1950).
- †POULDING, R. H. (1952). Five cases of Aspergillosis in immature gulls. *Ibis*: 94, No. 2, pp. 364-366.
- SMITH, K. M. (1940). *The Virus; Life's Enemy*. Cambridge (reprinted with appendix 1948).
- *TOPLEY, W. W. C. and WILSON, G. S. (1929). *Principles of Bacteriology and Immunity*. (3rd edition). Revised by G. S. Wilson and A. A. Miles 1946 (in two vols.), London.
- URBAIN, A. and GUILLOT, G. (1938). Les aspergilloses Aviaires. *Rev. Path. Comp. Hyg. Gen.* no. 503, 27 pp. (in French).

CHAPTER 14, THE FAUNA OF BIRDS' NESTS

There are, unfortunately, no general papers in English dealing with the fauna of birds' nests, and it is to be hoped that someone will soon supply the missing volume. Large numbers of scattered papers in various entomological journals (such as the *Entomologists' Monthly Magazine*, the *Entomologist*, etc.) contain isolated records of beetles, flies, fleas and other insects from nests of British birds, but an up-to-date comprehensive review covering all the groups concerned is urgently required. Chapter 14 has been compiled from both published and unpublished notes generously supplied by Mr. Basden, Dr. China. Mr. Donisthorpe, Dr. Hinton, Mr. Spittle and Dr. Turk.

The following publications should prove useful :

- † ARMSTRONG, E. A. (1953). Nidicoles and Parasites of the Wren. *Irish Nat. J.* 11 : 57-64.
- HEIM DE BALSAC, H. (1938). Commensalisme ornithophile de Coléoptères Staphylinides; son déterminisme par exigences thermiques de maturation des gonades. *C.R. Acad. Sci. Fr.*, (Paris), 207 : 644-646. (in French).
- HINTON, H. E. (1945). *A Monograph of the Beetles associated with Stored Products*. Vol. I. London.
- JOHNSON, C. G. (1939). Taxonomic characters, variability and relative growth in *Cimex lectularius* L. and *C. columbarius* Jenyns (heteropt. Cimicidae) *Trans. R. Ent. Soc.* (London), 89 : 543-568.
- JOY, N. H. (1932). *A practical handbook of British beetles*. London. 2 vols.
- NORDBERG, S. (1936). Biologisch-oiklogische Untersuchungen Über die Vogelnidicolen. *Acta Zoologica Fennica* 21, Helsingfors. (in German).
- Ogilvie, C. M. (1949). Observations in a rookery in winter. *Brit. Birds*, 42 : 65-68.
- SEGUY, E. (1946). Diptères ornithophiles in *Encycl. Ent. Sér. B2*, 10 : 118-132. (in French).
- † USINGER, R. L., & FERRIS, G. F. (in press). *The Family Cimicidae (Hemiptera Heteroptera)*.

CHAPTERS 15 AND 16, SKUAS AND CUCKOOS

The account of the skuas is taken principally from the chapter relating to this group in Witherby and chapter 16 is based entirely upon Stresemann's account of the cuckoo. The latter is probably the best short summary up to date (see below). The other books mentioned in the bibliography should be read and studied since they give a good picture of the field work carried out in connection with the cuckoo. Mr. H. N. Southern has kindly allowed us to read some notes from his paper on the European cuckoo which should be published shortly.

Skuas

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- MURPHY, R. C. (1936). *Oceanic Birds of South America*. Vols. I and II. American Museum of Natural History. New York. (pp. 1006-1033 for Stercorariidae).
- WITHERBY, H. F., JOURDAIN, F. R. C., TICEHURST, N. F., and TUCKER, B. W. (1941). *Handbook of British Birds*. Vol. V. (pp. 122-137, for *Stercorarius*).

Cuckoos

- BAKER, E. C. S. (1942). *Cuckoo problems*. London.
- CHANCE, E. P. (1940). *The truth about the Cuckoo*. London.

- FRIEDMANN, H. (1928). Social parasitism in birds. *The Quart. Rev. of Biol.* (Baltimore), 3 : 554-569.
- FRIEDMANN, H. (1948). *The parasitic cuckoos of Africa*. Washington Academy of Science, Monogr. No. 1.
- *STRESEMANN, E. (1927-1934). *Aves*: in Kükenthal and Krumbach, *Handbuch der Zoologie*, Berlin and Leipzig. (pp. 417-427 and 818-819 for Cuculidae). (in German).
- THORPE, W. H. (1945). The evolutionary significance of habitat selection. *J. Anim. Ecol.* 14 : 167-170.

INDEX OF POPULAR AND SCIENTIFIC NAMES

Main Sections are in heavy type

- Acanthocephala, *see* Spiny-headed Worms
- Acarina, *see* Mites
- Achorion* (Fungi), 242
- Acoelus vaginatus* (Tapeworm), 194
- Actinomyces rhodii* (Fungus), 20
- Actornithophilus* (Feather Lice), 121, 133
- Actornithophilus patellatus*, *see* Curlew Quill Louse
- Acuaria* (Roundworms), 184
- Acuaria hamulosa* (Gizzard Worm), 185
- Acuaria laticeps* (Roundworm), 184
- Acuaria spiralis* (Roundworm), 185
- Aedes* (Mosquitoes), 214, Pl. XXX (211)
- Aedes geniculatus* (Mosquito), 165
- Alaudidae (Larks), 165
- Alcedoecus* (Feather Lice), 150
- Alcedoffula* (Feather Lice), 150
- Aleochara* (Rove Beetles), 249
- Alethe* (Thrushes), *see* Ant-birds
- Alpine Chough (*Pyrrhocorax graculus*), 89, 95
- Alpine Hare (*Lepus timidus*), 87, 89
- Amabilia* (Tapeworms), 194
- Amblycera (Feather Lice), 122, 123, 132, 139, 147-156, Pl. XXII (131)
- American Sand-Martin Flea (*Ceratophyllus riparius*), 86
- American Wigeon (*Anas americana*), 253
- Amoebidae (Protozoa), 174
- Amphibians, 161, 188
- Amyrsidea* (Feather Lice), 156
- Analges chelopus* (Mite), 225, Pl. XXXI (226)
- Analgesidae, *see* Feather Mites
- Anas americana*, *see* American Wigeon
- Anaticola* (Feather Lice), 132, 141
- Anatoecus* (Feather Lice), 132, 141
- Ancistrona* (Feather Lice), 128, 153
- Anodonta* (Freshwater Mussels), 30
- Anomotaenia* (Tapeworms), 193
- Anomotaenia arionis* (Tapeworm), 194
- Anomotaenia constricta* (Tapeworm), 193
- Anomotaenia nymphaea* (Tapeworm), 194
- Anopheles* (Mosquitoes), 214
- Anoplocephalidae (Tapeworms), 197
- Anoplura, *see* Sucking Louse
- Anseriformes (Ducks, Geese, Swans), 43, 130, 131, 141, 152-153, 163, 174, 183, 195, 199, 205
- Ant-birds (*Alethe*), 254
- Anthocorid Bug (*Lyctocoris campestris*), 248
- Anthomyia* (Flies), 251
- Ants, 13, 14, 25, 26, 49, 50, 51, 55, 103, 126-128, 197, 254
- Apatemon gracilis* (Fluke), 206
- Aphaniptera, *see* Fleas
- Aploparaksis filum* (Tapeworm), 195
- Aploparaksis furcigera* (Tapeworm), 195
- Apodiformes (Swifts), 150
- Aporina delafondi* (Tapeworm), 197
- Aponomma* sp. (Tick), fig. p. 234
- Aquanirmus* (Feather Lice), 153
- Arctic Fox, 194
- Arctic Hare, 92
- Arctic Skua (*Stercorarius parasiticus*), 15, 110, 213, 254, 255, Pl. XXXVIII (265)
- Arctic Tern (*Sterna macrura*), 15, 135
- Ardeicola* (Feather Lice), 152
- Ardeiphilus* (Feather Lice), 152

- Argas* (Ticks), 238
Argas reflexus, see Pigeon Tick
Argas persicus, see Fowl Tick
 Argasidae (Ticks), 39, 229, 231
Armadillium vulgare, see Wood Louse
Armillifer armillatus (Tongue-Worm), 233
 Arthropods, 19, 48, 63, 150, 163, 172, 178, 243, 245
Arhythmorhynchus longicollis (Spiny-headed Worm), 190
Ascaridia galli (Roundworm), 183
Ascaris (Roundworms), 180
Ascaris lumbricoides (Roundworm), 44
 Ascaroidea (Roundworms), 183
Asellus aquaticus, see Hog Slater
Aspergillus fumigatus (Fungus), 243, Fig., p. 10
 Assassin Bug (*Rhodnius prolixus*), 20
 Assassin Bugs (Reduviidae), 248
Atheta nidicola (Rove Beetle), 249
Atheta nigricornis (Rove Beetle), 249
Atheta oloriphyla (Rove Beetle), 249
Atheta trinotata (Rove Beetle), 249
Attagenus pellio (Beetle), 248
Aucheromyia sp., see Floor Maggots
 Auklet (*Ptychorhamphus aleuticus*), 90
 Auks (Alcae), 130, 183, 195
 Australian Black Swan (*Chenopsis atrata*), 194
Austromenopon (Feather Lice), 153
 Avian Malaria (see also *Plasmodium*), 2, 7, 33, 36, 164, 165, 215
 Avocet (*Recurvirostra avosetta*), 160, 173

Bacillus, see Bacteria
Bacillus anthracis (Bacterium), 236, 239
 Bacteria, 29, 36, 120-121, 22, 235-239
 Bacteriaceae (Bacteria), 237
Bairamlia fuscipes (Hymenoptera), 103
Balfouria monogama, 39
 Bald Eagle (*Haliaeetus leucocephalus*), 125
 Barnacle Goose (*Branta leucopsis*), 14-15
 Barnacles (Cirripedia), 47
 Barn-Owl (*Tyto alba*), 21, 184, 222, 225, 236, 251, Pl. VI (23)
 Barn-Swallow (*Hirundo rustica erythrogaster*), 247
 Bat, 62, 97, 111, 217
 Bat Flea, 84, 94
 Bay-winged Cow-bird (*Molothrus badius*), 265
 Bearded Tit (*Panurus biarmicus*), 110
 Beaver, 62
 Bed-bug (*Cimex lectularius*), 2, 53, 121, 247
 Bee-eater (*Merops apiaster*), 12, 150
 Bee-eaters (*Merops* sp., see also Carmine Bee-eater), 12
 Bees [and Wasps], 13, 26, 27, 55
 Beetles (Coleoptera), 2, 45, 51, 52, 246, 248-250
Bilharziella palonica, see Duck Blood-Fluke
 Bird-bottle Fly, see *Protocaliphora azurea*
 Birds of Prey, 14, 15, 24, 94, 183, 188, 190, 249
 Bittern (*Botaurus stellaris*), 152, 237
 Blackbird (*Turdus merula*), 85, 165, 169, 171, 181, 185, 189, 221, 222, 230, 240, Pl. IV (15)
 Black-flies (Simuliidae), 49, 169, 185, 211-212, 218-220
 Black-headed Gull (*Larus ridibundus*), 15, 17, 206
 Black-necked Grebe (*Podiceps nigricollis*), 15
 Black-necked Stilt (*Himantopus mexicanus*), 194
 Black-throated Diver (*Colymbus articus*), 197
 Black-winged Stilt (*Himantopus himantopus*), 194
 Black Redstart (*Phoenicurus ochrurus*), 112
 Bladder Snail (*Physa* sp.), 18
 Blennies (*Blennius*), 202
 Blow-flies (Diptera), 243
 Blue Tit (*Parus coeruleus*), 18, 25, 111, 169
 Bluebottles (Calliphoridae), 211-212, 220-223, 55
 Boa-constrictors, 232
 Boreal Flea (*Ceratophyllus borealis*), 110-111, 87, 94
Borrelia anserinum (Spirochaete), 232
 Brambling (*Fringilla montifringilla*), 169
 Bream (*Abramis brama*), 195
 Brent Goose (*Branta bernicla*), 12, 46, 253
 Brook Trout (*Salvelinus fontinalis*), 195
Bruelia (Feather Lice), 150
 Buff-backed Heron (*Ardeola ibis*), 24
 Bugs (Hemiptera), 3, 7, 41, 48, 52, 120, 245, 247, Pl. XXXVI (259)
 Bulbuls (Pycnonotidae), 12, 254
 Bullfinch (*Pyrrhula pyrrhula*), 225, 237
 Bumble-bee (Hymenoptera), 136, 293
 Buntings (*Emberiza*), 165
 Bustards (Otididae), 13
 Butterfish (*Pholis*), 202
 Butterfly, 43, 68, 70, 73, 87, 109, 114, 136, 220
 Buzzard (*Buteo*), 14, 15, 173, 186, 189, 249

Calliphora (Flies), 221
 Calliphoridae (Flies), 220
 Camel, 171, 178
Campanulotes (Feather Lice), 154
 Canary, 4, 36, 211
 Canary-pox (Virus disease), 241
 Capercaillie (*Tetrao urogallus*), 183
Capillaria (Roundworms), 186
Capillaria annulata (Roundworm), 186
Capillaria columbae (Roundworm), 186
Capillaria contorta (Roundworm), 186
Capraiella (Feather Lice), 150
 Caprimulgiformes (Nightjars), 150

- Carcinus maenas*, see Shore Crab
- Carduiceps* (Feather Lice), 154
- Carminic Bee-eater (*Merops nubicus*), 13
- Carnidae (Flies), **220-223**
- Carnus hemapterus* (Nest-fly), 7, 41, 222
- Carrion-Crow (*Corvus corone*), 101, 112, 127, 181, 184, 193, 195, 222, 249
- Cat, 6, 76, 93, 94, 194, 253
- Cat Flea (*Ctenocephalides felis*), 76, 93
- Calatropis verrucosum* (Fluke), 202
- Cattle, 7, 22, 24, 25, 215, 218, 232
- Centipede, 181, 245
- Centrorhynchus aluconis* (Spiny-headed worm), 189
- Centrorhynchus teres* (Spiny-headed worm), 189
- Ceratophyllidae (Fleas), 95
- Ceratophyllus* (Fleas), 70, 91, 94, 95, 99, 107
- Ceratophyllus borealis*, see Boreal Flea
- Ceratophyllus diffinis* (Flea), 101
- Ceratophyllus farreni*, see Farren's House-Martin Flea
- Ceratophyllus fringillae*, see House Sparrow Flea
- Ceratophyllus gallinae*, see Hen Flea
- Ceratophyllus garei*, see Duck Flea
- Ceratophyllus hirundinis*, see Common House-Martin Flea
- Ceratophyllus lunatus* (Flea), 95
- Ceratophyllus niger* (Flea), 111
- Ceratophyllus riparius*, see American Sand-Martin Flea
- Ceratophyllus rossittensis*, see Crow Flea
- Ceratophyllus rusticus*, see Scarce House-Martin Flea
- Ceratophyllus styx*, see Sand-Martin Flea
- Ceratophyllus vagabunda*, see Vagabond Flea
- Ceratopogonidae (Flies), **220**
- Cestoda, see Tapeworms
- Cestodaria (Tapeworms), 194
- Chaffinch (*Fringilla coelebs*), 148, 169, 171, 226, 230, 237, 250
- Charadriiformes (Plovers, Waders, Gulls, Auks, see also Waders), 154-155, 130, 133, 140, 163
- Cheese Mites (Tyroglyphidae), 227, 228
- Cheletidae (Mites), 28, 227
- Chelifer cancroides* (Pseudoscorpion), 248
- Cheu-can (*Pteroptochus rubecula*), 92
- Chicken Louse (*Menacanthus stramineus*), 44, 125
- Chiff-chaff (*Phylloscopus collybita*), 260
- Chilomastix gallinarum* (Protozoa), 173, Fig. 2e p. 162
- Chough (*Pyrrhocorax pyrrhocorax*), 89
- Chough Flea, see *Frontopsylla frontalis* and *Frontopsylla laetus*
- Ciconiiformes (Storks, Herons and Bitterns), 152, 130, 141
- Ciconiphilus* (Feather Lice), 152
- Cimex columbarius*, see Pigeon Bed-bug
- Cimex lectularius*, see Bed-bug
- Citellophilus* (Fleas), 92
- Citellus* (Ground Squirrel), 92
- Clam (Mollusc), 205
- Clegs (Tabanidae), 11, 25, 171
- Cliff Swallow (*Petrochelidon albifrons*), 14, 169
- Cnemidocoptes gallinae* (Mite), 226
- Cnemidocoptes mutans* (Mite), 226, Fig. p. 228
- Coccidia (Protozoa), **161**, 222
- Coccus* (Bacterium), 161, 235
- Cochlosoma anatinis* (Protozoa), 173
- Cockle (Mollusc), 205
- Cockroach, 73, 184
- Coleoptera, see Beetles
- Collyriculum faba* (Fluke), 39
- Coloceras* (Feather Lice), 154
- Colpocephalum* (Feather Lice), 135
- Columbicola* (Feather Lice), 123
- Columbicola columbae*, see Common Pigeon Louse
- Columbiformes (Pigeons and Doves), 154, 163, 226
- Colymbiformes (Divers), 153
- Colymbus* (Divers), 195
- Common Eider (*Somateria mollissima*), 110
- Common Gull (*Larus canus*), 17, 206
- Common House-martin Flea (*Ceratophyllus hirundinis*), **108**, Pls. XVII (98) and XXXIII (242) 68, 72, 85, 86, 92, 94, 101
- Common Louse-fly (*Ornithomyia avicularia*), 213, Pl. IX (34)
- Common Pigeon Louse (*Columbicola columbae*), 123
- Common Periwinkle (*Littorina littorea*), 31, 202, 204, Pl. XXVIII (179)
- Common Rat Flea (*Nosopsyllus fasciatus*), 68-70, 72-75, 84
- Common Sandpiper (*Actitis hypoleucos*), 194
- Common Tern (*Sterna hirundo*), 135, 233
- Contracecum* (Roundworms), 183
- Contracecum spiculigerum* (Roundworm), 183
- Coot (*Fulica atra*), 54, 156, 182, 184, 253, 266
- Copepoda (Fish lice), 3, 23, 47, 54, 194, 195
- Cormorant (*Phalacrocorax carbo*), 133, 147, 153, 189, 254, Pl. XXXIV (243)
- Cormorants (Phalacrocoracidae), 121, 147, 153, 183, 196, 231
- Corn-Crake (*Crex crex*), 110, 205
- Coraciiformes (Kingfishers etc.), 150, 163
- Corvus splendens* (Crow), 164
- Corynosoma* (Spiny-headed Worms), 189, Fig. 4 (196)
- Corynosoma strumosum* (Spiny-headed Worm), 189
- Corynosoma tunitae* (Spiny-headed Worm), 189
- Corynosoma turbidum* (Spiny-headed Worm, Fig. 4 (196)
- Cotugnia* (Tapeworms), 197

- Cotylurus cornutus* (Fluke), 206
 Cows, 16, 17, 20, 21, 24, 173
 Cow-birds (*Molothrus*), 10, 24, 265, 267, 268
Craspedonirmus (Feather Lice), 153
Craspedorrhynchus (Feather Lice), 140
Crataerina pallida, see Swift Louse-fly
 Crested Tit (*Parus cristatus*), 43, 112
 Crocodile, 23, 232
 Crocodile Bird (*Pluvianus aegyptius*), 23
 Crossbill (*Loxia curvirostra*), 172
Crotophagus ani, see Tick Bird
 Crow Flea (*Ceratophyllus rossittensis*), 46, 101, **III**, 113
 Crows (Corvidae), 101, 111, 124, 184, 189, 221, 222, 226, 231, 238, 261, 264
 Crustacea, 188, 190, 194, 195, 207
Cryptocotyle jejuna, see Red-shank Fluke
Cryptocotyle lingua, see Herring-gull Fluke
Ctenocephalides felis, see Cat Flea
Ctenophthalmus agyrtes, see Field-Mouse Flea
 Cuckoo (*Cuculus canorus*), 5, 9, 10, 36, 37, 38, 110, 126, 135-136, 189, 225, **256-268**, Pl. XXXVIII (265)
 Cuckoo Head-lice (*Cuculoecus latifrons*), 126, 136, 156
Cuculotogaster (Feather Lice), Pl. XXIII (146)
 Cuculiformes (Cuckoos), 151, 163
Cuculiphilus (Feather Lice), 136
Cuculoecus (Feather Lice), 126, 136
Cuculoecus latifrons, see Cuckoo Head-lice
Culex fatigans (Gnat), 215
Culex pipiens, see House-gnat
 Culicidae (gnats, mosquitoes), **214-218**
Culicoides (Midges), 220
Culicoides biguttatus (Midge), 220
Culicoides fascipennis (Midge), 220
Culicoides impunctatus (Midge), 220
Culicoides obsoletus (Midge), Pl. XXIX (210)
Cummingsiella (Feather Lice), 154
 Curlew (*Numenius arquata*), 3, 42, 121, 129, 130, 183, 194, 231
 Curlew Quill Louse (*Actornithophilus patellatus*), 121
 Cyclophyllidea (Tapeworms), 194
Cyclops serrulatus (Copepod), 195
Cyclops strenuus (Copepod), 195
Cyclops viridis (Copepod), 195
Cynomyia mortuorum (Fly), 251
Cypria ophthalmica (Ostracod), 195
Cytodites nudus (Mite), 226
 Cytolichiidae (Mites), 226
 Dace (*Leuciscus leuciscus*), 195
Dactylaria (Fungi), 243
Dactylella (Fungi), 243
Daphnia (Water Fleas), 184
Daphnia pulex (Water Flea), 184
Dasypsyllus (Fleas), 90, 91, 95
Dasypsyllus gallinulae, see Moorhen Flea
 Davaineidae (Tapeworms), 197
 Deer, 212, 230
Degeeriella (Feather Lice), 151
 Demodicidae (Mites), 227
Dendrophylus punctatus (Beetle), 250
Dendrophylus pygmaeus (Beetle), 250
Dennyus (Feather Lice), 121, 125
Dennyus truncatus (Feather Louse), 121, 125
 Dermanyssidae (Mites), 224
Dermanyssus gallinae (Mite), 224
Dermanyssus hirundinis (Mite), 224
Dermanyssus passerinus (Mite), 224
Dermanyssus quintus (Mite), 224
Dermatobia hominis (Warble Fly), 212
Dermestes lardarius (Beetle), 248
Dermestes murinus (Beetle), 248
Diaptomus gracilis (Copepod), 195
Diaptomus vulgaris (Copepod), 195
Dilepis undula (Tapeworm), Pl. XXVII (178)
Diphyllobothrium (Tapeworms), 194
 Diplomonadida (Protozoa), **173-175**
Diplophallus polymorphus (Tapeworm), 194
Diplostomum spathaceum (Fluke), 206
 Dipper (*Cinclus cinclus*), 114, 225
 Diptera, see Flies
 Diving Petrel (*Pelicanoides urinatrix*), 91
 Dogs, 12, 45, 98, 125, 223, 226
 Domestic animals, see also Mammals, 16, 21-23, 24, 25, 171, 173
 Dominican Gull (*Larus dominicanus*), 91
Dorcadia dorcadia, see Roe-deer flea
 Doves, see Columbiformes
 Dragonfly (*Libellula quadrimaculata*), 136, 204, 220, Fig. p. 198
 Drosophila (*Dicruridae*) 25
Drosophila, see Small Fruit Fly
 Duck (Anatidae), 39, 41, 49, 85, 94, 101, 141, 152, 169, 174, 189, 190, 195, 218, 238, 243, 251, 265
 Duck Blood-fluke (*Bilharziella palonica*), 205
 Duck Flea (*Ceratophyllus garei*), 81, 85, 87, 94, 97, 101, **110**, 169
 Duck Leech (*Protoleipsis tessellata*), 208, Fig. p. 210
 Dunlin (*Caladris alpina*), 189
 Eagle, 14, 15, 190
 Earthworm, 53, 176-178, 183, 184
 Earwig, 245
 Eastern Crow (*Corvus brachyrhynchus*), 193

- Echidnophaga gallinacea*, see Hen Stick-tight Flea
Echidnophaga myrmecobii, see Marsupial Stick-tight Flea
Echinorhynchus pachyacanthus (Spiny-headed Worm), 190
Echinostomatoidea (Flukes), 205
Eider Duck (*Somateria mollissima*), 195, 197, 225
Eiders (*Somateria*), 30
Eidmanniella (Feather Lice), 153
Eimeria (Protozoa), 160, 163
Eimeria avium (Protozoan), 163, Fig. 2a p. 162
Eimeridae (Protozoa), **161-164**
Elephant, 41, 50, 78, 208
Empusa (Fungi), 243
Enicmus minutus (Beetle), 250
Enoplida (Worms), 186
Entamoeba (Protozoa), 174
 Fig. 2i p. 162
Entamoeba lagopodis (Protozoan), 174
Entoconcha mirabilis (Mollusc), 47
Entomophthoraceae (Fungi), 243
Epidermoptes bilobatus (Mite), 226
Esquimo Curlew (*Numenius borealis*), 194
Eudynamis (Cuckoos), 261
Eulaelaps novus (Mite), 227
Eulaemobothrion (Feather Lice), 155
Eureum (Feather Lice), 150
Eutrichomastix gallinarum (Protozoan), Fig. 2f p. 162
Falcolipeurus (Feather Lice), 140
Falconiformes (Birds of Prey), 140, 151, 163-164
Falcons (*Falco*), 15, 173, 222
Falculifer rostratus (Mite), 226
Fannia (Flies), 251
Farren's House-Martin Flea (*Ceratophyllus farreni*), 85, **108-109**
Feather Lice (Mallophaga), 3, 7, 9, 28, 41, 43, 44, 45, 46, 52, **56-60**, 69, 70, 71, 72, 75, 84, **118-157**, 193, Pls. I, XXI, XXII, XXIII, XXIV (6, 130, 131, 146, 147)
Feather Mites (Analgesidae), 28, 42, 225, 226, Pl. XXXI (226)
Fieldfare (*Turdus pilaris*), 15
Field-mouse Flea (*Ctenophthalmus agyrtes*), 76
Filaria (Roundworms), 43, 98, 125, 172, 217, 219
Filicollis (Spiny-headed Worms), 190
Filicollis anatis (Spiny-headed Worm), 190
Fimbriaria fasciolaris (Tapeworm), 195
Finch Louse-fly (*Ornithomyia fringillina*), 213-214
Finches (Fringillidae), 80, 85, 165, 222, 225, 226, 240
Fish, 23, 32, 47, 78, 161, 178, 183, 187, 189, 194, 206, 208, 217, 233, 239, 254
Fish Crow (*Corvus ossifraga*), 193-194
Fish lice, see Copepoda
Flamingoes, see Phoenicopteridae
Fleas, (Aphaniptera), 3, 41, 45, 51, 52, **56-117**, 171, 177, 217, 227, 228, 245, 248, 249, 251, 252, Pls. V, X, XI, XII, XIII-XVI, XVII, XVIII, XIX, XXXIII (22, 35, 50, 51, 66-67, 82-83, 98, 99, 114, 242)
Flesh-flies (*Sarcophaga*), 221
Flies (Diptera), 1, 3, 7, 16, 41, 45, 49, 51, 52, 163, 197, **211-223**, 228, 245, 248, 251, 252, Pls. IX, XII, XXIX, XXX, (34, 51, 210, 211)
Floor Maggots (*Aucheromyia* sp.), 44
Flukes (Trematoda), 35, 39, 42, 45, 48, 145, **176-178**, **192-208**
Fly Larvae, 9, 28, 48, 49, 50, 51, 247, 251
Flycatchers (Muscicapidae), 25, 247, 248, 250
Fonsecaonyssus sylvorum (Mite), 225
Formica rufa, see Wood Ant
Fowl or Chicken (*Gallus domesticus*), 111, 121, 126-127, 137, 156, 163, 168, 172, 173, 174, 179, 181, 183, 184, 186, 187, 195, 204, 218, 219, 220, 224, 226, 227, 231, 237, 238, 239, 241, 247, 263, 267
Fowl cholera, 238
Fowl Leukaemia Virus, 241
Fowl Paralysis Virus, 241
Fowl Pest Virus, 241
Fowl relapsing fever, 232
Fowl Tick (*Argas persicus*) 232
Fowl-pox Virus, 31, 241
Fox, 15, 94
Franklin's Gull (*Larus pipixcan*), 15
Fresh-water Shrimp (*Gammarus pulex*), 184, 189, 195
Frigate Birds (Fregatidae), 254
Frog, 25, 42, 185, 189, 207, 208, 209, 216
Frontopsylla (Fleas), 95
Frontopsylla frontalis (Chough Flea), 100
Frontopsylla laetus (Chough Flea), 100
Fulicoffula (Feather Lice), 155
Fulmar Petrel (*Fulmarus glacialis*), 17, 149, 153, 197, 231, 240
Fungus, 28, 128, 197, 217, 222, 251, **242-244**
Gadwall (*Anas strepera*), 189
Galliformes (Game-birds) 129, 130, 156, 163, 183, 184, 197, 227
Game-birds, see Galliformes
Gammarus (Fresh-water Shrimps), 184, 186, 195, 204
Gammarus pulex, see Fresh-water Shrimp
Gannet (*Sula bassana*), 189, 226, 231, 254, 255
Gape-worm, see *Syngamus trachea*
Garganey (*Anas querquedula*), 184, 195, 205
Gentoo Penguins (*Pygosceles taeniata*), 13, 197
Giardia (Protozoa), 159, 173
Geese, 12, 85, 101, 163, 174, 183, 195, 205, 220
Gigantobilharzia (Flukes), 205
Giraffe, 22
Glaucous Gull (*Larus hyperboreus*), 197, 233

- Glossina morsitans*, see Tsetse Fly
 Glossiphonidae (Leeches), 208
Gnathoncus (Beetles), 249
Gnathoncus buyssoni (Beetle), 250
Gnathoncus nidicola (Beetle), 250
Gnathoncus punctulatus (Beetle), 249, Fig. p. 117
 Gnats (Culicidae), see also Mosquito, 7, 185, 214-218, 220
 Goat, 212
 Goby (*Gobius minutus*), 32, 52, 201, 202, Pls. VII, XXVIII (30, 179)
 Godwit (*Limosa lapponica*), 204
 Golden Eagle (*Aquila chrysaëtus*), 7, 152
 Goldcrest (*Regulus regulus*), 18, 113
 Golden-eye (*Bucephala clangula*), 195, 206
 Goldfinch (*Carduelis carduelis*), 82, 237
 Golden Oriole (*Oriolus oriolus*), 156
Goniocotes (Feather Lice), 128
Goniodes (Feather Lice), 128, 156
 Goosander (*Mergus merganser*), 184
 Grasshopper, 184, 185
 Great-crested Grebe (*Podiceps cristatus*), 197
 Great Northern Diver (*Colymbus immer*), 189
 Great Shearwater (*Puffinus gravis*), 13, 17
 Great Skua (*Stercorarius skua*), 254
 Great Spotted Cuckoo (*Clamator glandarius*), 258, 264
 Great Spotted Woodpecker (*Dryobates major*), 189, Pl. II (7)
 Great Tit (*Parus major*), 18, 25, 165, 247, 249, 250, Pl. III (14)
 Greater Black-backed Gull (*Larus marinus*), 206, 254
 Greater Yellowshank (*Tringa melanoleucos*), 194
 Grebes, see Podicipitiformes
 Green-bottle Fly (*Lucilia*), 181, 221
 Greenfinch (*Chloris chloris*), 224
 Greenland Falcon (*Falco rusticola*), 231
 Green Sandpiper (*Tringa ochropus*), 225
 Green Woodpecker (*Picus viridis*), 151, 224
 Gregarines (Protozoa), 103
 Grey Phalarope (*Phalaropus fulicarius*), 23
 Grey Seal (*Halichoerus gryphas*), 189
 Grouse (*Lagopus scoticus*), 3, 38, 163, 169, 174, 181, 230, 241
 Grouse Louse-fly (*Ornithomyia lagopodis*), 213
 Grouse Roundworm (*Trichostrongylus pergracilis*), 38, 181
 Gruiformes (Coots and Moorhens), 163
 Gudgeon (*Gobio fluviatilis*), 195
 Guillemot (*Uria aalge*), 183, 195, 205, 225, 231, 255
 Guillemot Tick (*Ixodes uriae*), 231, 232
 Guinea-pig, 75
 Gulls (Laridae, *Larus* sp. or suborder Lari), see also Sea-gull, 15, 17, 32, 45, 130, 143, 173, 190, 194, 195, 197, 199, 204, 205, 206, 224, 225, 240, 253, 254, 266
Gyrocelia (Tapeworms), 193
Haemaphysalis cinnabarina (Tick), 231
Haemaphysalis leporis-palustris (Tick), 231
Haematobia (Flies), 136
 Haemogregarines (Protozoa), 170
Haemophilus gallinarum (Bacterium), 239
 Haemoproteidae (Protozoa), 170
Haemoproteus (Protozoa), 167, 169, 170, 172, 214, Fig. 2c p. 162
 Haemosporidia (Protozoa), 164
 Hair-follicle Mites (Demodicidae), 227
Halipeurus (Feather Lice), 153
Halteridium, see *Haemoproteus*
 Hang-nests (Icteridae), 265
 Hare, 98
Harpyrynchus (Mites), 227
 Harvest Mites (Trombididae), 227
 Hawks (Accipitridae), 6, 129, 135, 137, 148, 149, 151, 205, 222, 250
Hectopsylla psittaci, see Parrot Stick-tight Flea
 Hedge-Sparrow (*Prunella modularis*), 221, 222, 225, 250, 252, 258, 263
 Hedgehog, 69, 230
 Helmet Fleas (Stephanoceridae), 100
 Helomyzidae (Flies), 251
 Hemiptera, see Bugs
 Hen Flea (*Ceratophyllus gallinae*), 46, 68, 69, 70, 72, 73, 81, 84, 86, 91, 93, 94, 97, 101, III, 249, Pls. X, XI (35, 50)
 Hen Stick-tight Flea (*Echidnophaga gallinaceus*), 58, 62, 63, 68, 70, 74, 79, 84, 99
 Heron (*Ardea cinerea*), 44
 Heron Louse-Fly (*Lynchia albipennis*), 214
 Herons (Ardeidae), 159, 173, 184, 225, 233, 249
 Herring-gull (*Larus argentatus*), 17, 87, 197, 202, 206, 241
 Herring-gull Fluke (*Cryptocotyle lingua*), 31, 32, 39, 206, Fig. 5 p. 203, Pls. XXVII, XXVIII (178, 179).
Heterakis (Roundworms), 172
Heterakis gallinae (Roundworm), 183
 Heterophyids (Flukes), 205
Hexamita (Protozoa), 173
 Hippoboscidae, see Louse flies
 Hippopotamus, 2
Hirudo medicinalis, see Medicinal Leech
Hister merdarius (Beetle), 100, 250
 Histeridae (Beetles), 249
Histomonas meleagridis (Protozoa), 172, 183
Histrichopsylla talpae, see Mole Flea
 Hobby (*Falco subbuteo*), 15

- Hofmannophila pseudospretella* (Moth), 251
 Hog Slater (*Asellus aquaticus*), 190
Hohorstiella (Feather Lice), 154
Holomenopon (Feather Lice), 152
 Honey Buzzard (*Pernis apivorus*), 233
 Honey-guides (Indicatoridae), 10, 268
 Hooded Crow (*Corvus cornix*), 113
 Hoopoe (*Upupa epops*), 150
Hoplopyllus (Fleas), 93
Hoplopyllus glacialis lynx (Flea), 92
 Hornbills (Bucerotidae), 226
 Hornets, 27
 Horse, 7, 16, 76, 172, 208, 212
 House-flies (Muscidae), 11, 55, 211-212, 220-223, 243
 House-fly (*Musca domestica*), 181
 House-gnat (*Culex pipiens*), 165, 172, 211, 215, 216, 241, 243, Pl. XXX (211)
 House-martin (*Martula urbana*), 43, 61, 79, 85, 92, 171, 247, 248, 251, Pl. XXXIX (268)
 House-martin Flea, *see* Common House-martin Flea
 House-sparrow Flea (*Ceratophyllus fringillae*), 62, 94, 115
Houttuynia struthiocameli (Tapeworm), 145, 194
 Human Flea (*Pulex irritans*), 44, 70, 72, 73, 92, 94, 107
 Human Louse (*Pediculus humanus*), 139
 Humming-birds (Trochilidae), 28
Hyalomma marginatum (Tick), 231
 Hydracnid Mites, 217
 Hydrobia, *see* Spire Shell
Hydrotaea (Flies), 251
 Hymenolepidae (Tapeworms), 195
Hymenolepis (Tapeworms), 194, 195
Hymenolepis anatina (Tapeworm), 195
Hymenolepis himantopodis (Tapeworm), 194
Hymenolepis macracarthus (Tapeworm), Fig. 4 p. 196
 Hymenoptera (Bees, Ants and Wasps), 26, 27, 55, 232, 245, 251
 Hyphomycetales (Fungi) 243
Hypoderma bovis (Warble Fly), 215
Incidifrons (Feather Lice), 155
 Indian Hawk Cuckoo (*Hierococyx varius*), 263
 Influenza Virus, 44
 Insects, 18, 21, 27, 28, 34, 42, 43, 64, 72, 195, 207, 240, 245, 246, 248, 249, 255
 Ischnocera (Feather Lice), 132, 139, 143, 148-156 Pl. XXII (131)
 Isospora (Protozoa), 163, 164
 Itch Mites (Sarcoptidae), 226
 Ivory Gull (*Pagophila eburnea*), 13, 233
Ixodes (Ticks), 231
Ixodes brunneus (Tick), 231
Ixodes canisuga (Sand-martin Tick), 231, 250
Ixodes caledonicus (Tick), 231
Ixodes passericola (Tick), 231
Ixodes ricinus, *see* Sheep Tick
Ixodes unicavatus, *see* Shag Tick
Ixodes uriae, *see* Guillemot Tick
 Ixodidae (Ticks), 39, 229, 230
 Ixodoidea, *see* Ticks
 Jackal (*Canis aureus*), 190
 Jackdaw (*Corvus monedula*), 17, 23, 27, 89, 115, 146, 171, 181, 189, 231, 245, 247, 250
 Jack Snipe (*Lymnocyrtus minimus*), 195
 Jay (*Garrulus glandarius*), 169, 171, 181, 226
 Jelly-fish, 42, 53
 Jigger (*Tunga penetrans*), 44, 93
Joubertia microphyllus (Mite), 226, Pl. XXXI (226)
 Jungle Fowl (*Gallus gallus*), 69, 156
 Kea, (*Nestor notabilis*) 18, 23
 Kentish Plover (*Leucopoliis alexandrinus*), 189
 Kestrel (*Falco tinnunculus*), 14, 181, 184
 Kingfisher (*Alcedo atthis*), 14, 150, 190
 Kingfishers (Alcedinidae), *see also* Coraciiformes, 190
 Kites (*Milvus*), 14
 Kittiwake (*Rissa tridactyla*), 97, 115, 206, 255
 Kittiwake Flea (*Mioctenopylla arctica*), 97
 Koala Bear, 43
 Kudu Antelope, 22
Kurodaia (Feather Lice), 151
 Laelaptidae (Mites), 227
 Laemobothriidae (Feather Lice), 148
Laemobothrion (Feather Lice), 135, 148, 151
Lagopoecus (Feather Lice), 156
Laminosioptes cysticola (Mite), 226
 Lampern (*Petromyzon fluviatilis*), 195
 Lapwing (*Vanellus vanellus*), 25, 230
 Lark (*Calandrella dukhunensis*), 164
 Larks (*Alauda*), 165, 229, 230
 Lathridiidae (Beetles), 250
 Leeches (Hirudinea), 3, 7, 31, 41, 42, 46, 49, 50, 171, 176-178, 206, 207, 208-210
 Legionary Ants (Dorylinae), 25, 51
 Leopard, 233
 Leprosy (Bacillus), 98
Leucocytozoon (Protozoa), 167, 169, 172, 217, Fig. 2b p. 162
Libellula quadrimaculata, *see* Dragonfly
Ligula intestinalis (Tapeworm), 177, 195
Limnaea (Pond Snails), 205, 206
 Linnet (*Carduelis cannabina*), 171, 221, 252, 257
Lipeurus (Feather Lice), 156
 Little Auk (*Alle alle*), 225
 Little Owl (*Athene noctua*), 172, 181, 189, 238

- Little Tern (*Sterna albifrons*), 15, 155
Littorina littorea, see Common Periwinkle
 Lizard, 185
 Long-eared Owl (*Asio otus*), 230
 Long-tailed Duck (*Clangula hyemalis*), 195, 208
 Long-tailed Skua (*Stercorarius longicaudatus*), 254
 Long-tailed Tit (*Aegithalos caudatus*), 14, 15
 Louse, 7, 120
 Louse-flies (Hippoboscidae), 52, 128, 136, 170, **211-214**, 252, Fig. p 157, Pl. IX, 34
Lucilia, see Green-bottle Fly
Luniceps (Feather Lice), 154
 Lung Mites (Cytolichidae), 226
Lycitoris campestris, see Antho-corid Bug
Lynchia albipennis see Heron Louse-fly
 Lynx (*Felis lynx*), 190
 Macronyssidae (Mites), 225
 Maggots, 9
 Magpie (*Pica pica*), 23, 24, 181, 220, 221, 264, 265
 Malaria, see Avian malaria
 Mallard (*Anas platyrhyncha*), 132, 173, 190, 195, 205, 206
 Mammals, 42, 48, 50, 59, 76, 93, 186, 189, 194, 207, 208, 209, 212, 216, 217, 218, 219, 220, 227, 229, 230, 232, 236, 239, 242, 243, 249, 255
 Man (*Homo sapiens*), 3, 16, 17, 20, 21, 33, 36, 44, 49, 54, 94, 98, 164, 170, 173, 174, 177, 180, 184, 186, 194, 205, 206, 207, 208, 215, 216, 226, 233, 236, 237, 240, 241, 242, 247, 248
 anx Shearwater (*Puffinus puffinus*), 143, 153, 197, 241, 243
 Marabou Stork (*Leptoptilos crumeniferus*), 39
Maritrema oocysta (Fluke), 204
 Marsh-Sandpiper (*Tringa stagnatilis*), 194
 Marsupial Stick-tight Flea (*Echidnophaga myrmecobii*), 69
 Marsupials, 100
 Marten, 95
 Martins (*Martula*), 16, 17, 66, 67, 95, 101, 245, 250
 Mastigophora (Flagellata), 160, **170-173**
 Meadow-Pipit (*Anthus pratensis*), 221, 258, 289, 260
 Medicinal Leech (*Hirudo medicinalis*), 209
Megninia strigis-otis (Mite), 225
Melophagus ovinus, see Sheep Ked
Menacanthus (Feather Lice), 142, 149, 150, 156
Menacanthus stramineus (Chicken Louse), 121
Menopon (Feather Lice), 156
 Menoponidae (Feather Lice), 148
Meoneura (Nest Flies), 251
Meoneura lamellata (Nest Fly), 222
Meoneura neottiophila (Nest Fly), 222
 Merganser (*Mergus serrator*), 195, 202, 206
 Merlin (*Falco columbarius*), 15
Meropoeus (Feather Lice), 150
 Mice, 1, 2, 30, 36, 80, 91, 208, 253
Michaelichus bassani (Mite), 226
 Microfilariae (Larval Roundworms), 185
Microglotta gentilis (Rove Beetle), 249
Microglotta nidicola (Rove Beetle), 249
Microglotta picipennis (Rove Beetle), 249
Microglotta pulla (Rove Beetle), 249
Microlichus avus (Mite), 226
 Micro-parasites, **235-244**
 Microphallidae (Flukes), 204
 Midges (Ceratopogonidae), 3, 7, **220**, 243, Pl. XXIX (210)
 Miller's Thumb (*Cottus gobio*), 195
Mioctenopsylla (Fleas), 95
Mioctenopsylla arctica, see Kittiwake Flea
 Mites (Acarina), 3, 9, 18, 28, 36, 42, 45, 48, 50, 51, 52, 104, 128, 155, 195, 197, 217, 222, **224-234**, 243, 245, 246, 248, 250, 252, Pls. V, XXXI (22, 226).
 Mole, 12, 184
 Mole Flea (*Histrichopsylla talpae*), 61
 Mollusc, 30, 45, 52, 195, 205, 207
Moniezia (Tapeworms), 197
Monilia (Fungi), 243
 Monkeys, 26
Monopis ferruginella (Moth), 251
Monopis rusticella (Moth), 251
Monopsyllus anisus (Flea), 94
Monopsyllus sciurorum, see Squirrel Flea
 Moorhen (*Gallinula chloropus*), 156, 168, 190
 Moorhen Flea (*Dasyopsyllus gallinulae*), 84, 85, 86, 91, 92, **113**
 Mosquitoes (Culicidae), see also Gnats, 3, 42, 46, 48, 49, 77, 136, 165, 167, 185, 208, **211-212**, **214-218**, 219, 241, 243
 Moth Larvae, 251
 Moths (Lepidoptera), 217, 220, 228, 245, 251
 Motmots (Momotidae), 144
 Mourning Dove (*Zenaidura carolinensis*), 169-170
Mucor (Fungi) 243
Mulcticola (Feather Lice), 150
 Mussel, see *Mytilus*, *Unio*, *Anodonta*
Musca domestica, see House-fly
 Muscidae, see House-flies
 Mute Swan (*Cygnus olor*), 189, 194
 Mycobacteriaceae (Bacteria), 236
Mycobacterium (Bacteria), 236
Myialgopsis trinotoni (Mite), 153
 Mynahs, 24, 25
Myrsidea (Feather Lice), 149
Mytilus edulis (Marine Mussel), 30, 205, Fig. p. 37.
Naubates (Feather Lice), Pl. XXIII (146)
 Nematoda, see Roundworms

- Nematoparataenia* (Tapeworms), 194
Neophilopterus (Feather Lice), 152
Neottiophilum (Flies), 251
Neottiophilum praeustum (Nest Fly), 221
Nest Flies (Carnidae), 211-212, 220-223
Newts (*Triton*), 209, 217
Nightjar (*Caprimulgus europaeus*), 150, 165, 225, 256
Nightingales (*Luscinia*), 189, 195, 221
Nosopsyllus fasciatus, see Common Rat Flea
Notocotylids (Flukes), 205
Nutcracker (*Nucifraga caryocatactes*), 184
- Oeciacus hirundinis*, see Swallow Bug
Oestrus ovis, see Sheep Botfly
Oidium (Fungi), 243
Onchocerca (Roundworms), 185, 219
Opisthorchioidea (Flukes), 202, 207
Opossum, 26
Oribata geniculatus (Mite), 246
Orneacus (Fleas), 95
Orneacus rothschildi, see Scottish House-Martin Flea
Ornithobius (Feather Lice), 152, 153
Ornithomyia avicularia, see Common Louse-fly
Ornithomyia fringillina, see Finch Louse-fly
Ornithomyia lagopodis, see Grouse Louse-fly
Ornithopsylla laetitiae, see Shearwater Flea
Osprey (*Pandion haliaetus*), 14, 15, 207
Ostracods, 195
Ostrich (*Struthio camelus*), 142, 145, 194
Ostriches, see Struthioniformes
Oustaletia pegasus (Mite), 226
Oven-bird (*Furnarius rufus*), 247-248
Oviduct Fluke (*Prosthogonimus ovatus*), 204
Owls (Strigidae), 31, 94, 128, 157, 152, 169, 231, 239, 241, 246, 249, 250, 256
- Ox-peckers (*Buphagus*), 21-22, 23, 24
Oxylipeurus (Feather Lice), 156
Oxyspirura mansonii (Roundworm), 184
Oxyspirura sygmoidea (Roundworm), 184
Oyster-catcher (*Haematopus ostralegus*), 129, 189, 204
- Paralges pachycnemis* (Mite), 145
Parrakeet (*Eupsittula canicularis*), 251
Parrakeet (*Platyercus unicolor*), 91
Parrakeet (*Psephotus chrysoterygius*), 251
Parrot Stick-tight Flea (*Hectopsylla psittaci*), 62, 63, 93
Parrots (Psittacidae), 14, 93, 128, 1240
Partridge (*Perdix perdix*), 85, 94, 102, 129, 181, 226, 241
Passer domesticus indicus (Sparrow), 194
Passeriformes (Passerines), 144, 149, 150, 165, 188, 189, 214, 224, 227, 257, 261, 263
Pasteurella aviseptica (Bacterium), 239
Pasteurella pestis (Bacterium), 238
Peacock (*Pavo cristatus*), 186
Pecten, see Scallop
Pectinopygus (Feather Lice), 153, Pl. XXII (131)
Pediculus humanus, see Human Louse
Pelecaniformes (Pelicans and Cormorants), 133, 153, 163
Pelicans (Pelicanidae), 3, 133, 147, 208, 215
Penenirmus (Feather Lice), 149, 150
Penguins (Spheniscidae), 91, 100
Penicillium (Fungi), 243, 244
Penicillium notatum (Fungus), 244
Pentastomida, see Tongue-worms
- Perch (*Perca fluviatilis*), 195
Peregrine Falcon (*Falco peregrinus*), 184
Perineus (Feather Lice), 153
Petrels (Oceanites), 13, 143
Phalacrocorax nigrogularis (Cormorant), 125
Phaonia (Flies), 251
Pheasant (*Phasianus colchicus*), 156, 226, 237, 240, 241
Philonthus (Rove Beetles), 249
Philonthus fuscus (Rove Beetle), 249
Philopterus (Feather Lice), 133, 144, 149
Phoenicopteridae (Flamingoes), 59, 133, 141, 142, 146, 194
Phoridae (Flies), 251
Physa (Bladder Snails), 18
Piagetiella (Pouch-Lice), 121
Piciformes, see also Woodpeckers, 150, 163
Pied Flycatcher (*Muscicapa hypoleuca*), 258
Pied Wagtail (*Motacilla alba*), 258 Pl. XXXVIII (265)
Fig, 16, 44, 185
Pigeon (Domestic), 169, 173, 186, 197, 222, 224, 225, 227, 229, 231, 237, 240, 241, 248
Pigeon Bug (*Cimex columbarius*), 247
Pigeon Louse-fly (*Pseudolynchia maura*), 214
Pigeon-pox (Virus disease), 36, 241
Pigeon Tick (*Argas reflexus*), 231, 232
Pike (Esocidae), 195
Pink-footed Goose (*Anser brachyrhynchus*), 202
Pintail (*Anas acuta*), 110, 173
Pipits (*Anthus*), 207, 259
Piroplasma (Protozoa), 170
Plagiorchioidea (Flukes), 189, 204
Plagiorhynchus crassicolis (Spiny-headed Worm), 189
Plague bacillus (*Pasteurella pestis*), 1, 103, 238
Planorbis (Molluscs), 205
Plantain-eaters (Musophagidae), 142
Plasmodidae (Malaria parasites), 164

- Plasmodium* (Malaria parasites)—see also Avian malaria), 2, 7, 34, **164-170**, 172, 241
- Plasmodium falciparum* (Malaria parasite) Fig. 3, p. 166
- Plasmodium gallinaceum* (Malaria Parasite), 168
- Plasmodium relictum* (= *P. praecox*), **165**, 170, 217
- Platyssyllus castoris* (Beetle), 62
- Pleochaetis* (Fleas), 91
- Plovers, 18, 204, 205, 225, 228, 263
- Pochard (*Aethya ferina*), 184, 195
- Podicipitiformes (Grebes), 153, 183, 193, 195, 206
- Polyctenidae (Bugs), 188
- Polymorphidae, 310
- Polymorphus boschadis* (Spiny-headed worms), 189, 190
- Pomatorhine Skua (*Stercorarius pomarinus*), 254
- Porpoise, 13
- Porrocaecum* (Roundworms), 183
- Porrocaecum depressum* (Roundworm), 184
- Powan (*Coregonus lavaretus*), 195
- Prairie Falcon (*Falco mexicanus*), 14
- Procellariiformes (Petrels), 130
- Proctophyllodes glandarius* (Mite), 226
- Prognathobius*, see Purple Martin
- Progynotaenia* (Tapeworms), 193
- Prosthogonimus ovatus*, see Oviduct Fluke
- Prosthorrhynchus transversus* (Spiny-headed Worm), 189
- Protalgus attenuatus* (Mite), 225
- Protocalliphora azurea* (Bird-bottle Fly), 7, 221, Fig. p. 5
- Protocalliphora* (Flies), 221, 251
- Protoleptis tessellata*, see Duck Leech
- Protomonadida (Protozoa), **171-173**
- Protophyllodes glandarius* (Mite), 226
- Protozoa, 3, 7, 9, 29, 36, 39, 41, 42, 52, **159-175**, 197, 217, 222
- Psephotus chrysopterygius*, see Parrakeet
- Pseudolynchia canariensis*, see Pigeon Louse-fly
- Pseudomenopon* (Feather Lice)
- Pseudophyllidea* (Tapeworms), 194, 195
- Pseudo-scorpions, 18, 248, 245
- Psittacosis virus, 240
- Ptarmigan (*Lagopus*), 15, 87
- Pterolichus ardea* (Mite), 225
- Pterolichus bicaudatus* (Mite), 145
- Pterolichus cuculi* (Mite), 225
- Pterolichus obtusus* (Mite), 226
- Ptilonyssus nudus* (Mite), 227
- Puffin (*Fratercula arctica*), 90, 92, 94, 116, 231, 255
- Pulex irritans*, see Human Flea
- Pulicidae (Fleas), 92, 95, 107
- Purple (Mollusc), 205
- Purple Grackle (*Quiscalus quiscula*), 127
- Purple Martin (*Progne subis*), 247
- Purple Sandpiper (*Caladris maritima*), 181, 190, 225
- Pygiopsyllidae (Fleas), 91
- Pythons, 232
- Quadriceps* (Feather Lice), 154, Pl. XXIII (146)
- Quail (*Coturnix coturnix*), 237, 241
- Quill Louse, see Curlew
- Quill Louse
- Rabbit, 54, 92, 98, 230
- Rabbit Flea (*Spilopsyllus cuniculi*), 63, 90, 92, 93, 94, 95 Pls. X, XI (35, 50)
- Railletina anatina* (Tapeworm), 197
- Rainbow Trout (*Salmo irideus*), 206
- Rallicola (Feather Lice), 155
- Ralliformes (Rails), 155-156
- Rat Flea, see Common Rat Flea
- Rats, 6, 45, 75, 79, 91, 94, 171, 179
- Raven (*Corvus corax*), 231
- Razorbill (*Alca torda*), 195
- Red-backed Shrike (*Lanius collurio*), 258, 259
- Red-breasted Goose (*Branta ruficollis*), 14
- Red-breasted Merganser (*Mergus serrator*), 110
- Red deer, 230
- Red Mite of Poultry, 172, 224, 238
- Red-necked Phalarope (*Phalaropus lobatus*), 15
- Redpoll (*Carduelis flammea*), 12
- Redshank (*Tringa totanus*), 199, 202
- Redshank Fluke (*Cryptocotyle jejuna*), 199, 201, 202
- Redstart (*Phoenicurus phoenicurus*), 221, 258, 259, 260
- Red-throated Diver (*Colymbus stellatus*), 197
- Reduviidae, see Assassin Bugs
- Redwing (*Turdus musicus*), 230
- Red-winged Crested Cuckoo (*Clamator coromandus*), 263
- Reed-warbler (*Acrocephalus scirpaceus*), 37, 258
- Reighardia sterna* (Tongue-worm), 233, Fig. 4, 196
- Remora, see Sucking-fish
- Reptiles, 161, 194, 232
- Rhabditida (Worms), 180
- Rhea (*Rhea americana*), 142
- Rhea (*Pterocnemia pennata*), 139, 194
- Rhinoceros, 21
- Rhinyssus neglectus* (Mite), 225
- Rhodnius prolixus*, see Assassin Bug
- Rhynonirmus* (Feather Lice), 154
- Rhizopoda (Protozoa), 160, **173-174**
- Ricinidae (Feather Lice), 148
- Ricinus* (Feather Lice), 148, 149, Pl. XXIII (146)
- Ricinus rubeculae* (Feather Louse), 126
- Ringed Plover (*Charadrius hiaticula*), 189
- Roach (*Leuciscus rutilus*), 195
- Robin (*Erithacus rubecula*), 6, 12, 17, 73, 126, 148, 149, 189, 258, 259, Pl. IV (15)

- Rock-dove (*Columba livia*), 154, 231
 Rock-dove Flea (*Ceratophyllus columbae*), 62, 84, 100, 110
 Rockling (*Onos* spp.), 202
 Rock-thrush (*Monticola saxatilis*), 190
 Roe deer, 49
 Roe-deer Flea (*Dorcadia dorcadia*), 49
 Roller (*Coracias garrulus*), 150
 Rook (*Corvus frugilegus*), 17, 23, 26, 31, 85, 147, 149, 171, 181, 194, 230, 236, 252
 Rose-coloured Pastor (*Pastor roseus*), 231
 Roundworms (*Nematoda*), 3, 40, 41, 43, 54, 99, 125, 176-187, 188, 189, 243, 245
 Rous sarcoma virus, 241
 Rove Beetles (*Staphylinidae*), 5, 28, 50, 51, 101, 249
 Ruby-throated Hummingbird (*Archilochus colubris*), 28
 Ruffed Grouse (*Bonasa umbellus*), 229, 231

Sacculina (Crustacean), 47, 53, 130
Saemundssonina (Feather Lice), 153, 154, Pl. XXI (130)
 Salmon (*Salmo salar*), 195
Salmonella (Bacteria), 98, 237
Salmonella pullorum (Bacterium), 237
 Sanderling (*Crocethia alba*), 189, 225
 Sandhopper (Amphipod), 204
 Sand-martin (*Riparia riparia*), 45, 72, 80, 86, 227, 231, 249, 250, 251, Pls. XXVI, XXXV (163, 258)
 Sand-martin Flea (*Ceratophyllus styx*), 62, 78, 80, 86, 97, 101, 113
 Sand-martin Tick, *see* *Ixodes canisuga*
 Sandwich Tern (*Sterna sandvicensis*), 155
Sarcocystis (Fungi), 243
Sarcophaga, *see* Flesh-flies
 Sarcophagidae, *see* Itch Mites
Sarcosporidia (Fungi), 243
 Scallop (Molluscs), 290
 Scarce House-martin Flea (*Ceratophyllus rusticus*), 94
 Scaup (*Aythya marila*), 173, 189, 190, 206
Scenopinus fenestralis, *see* Window Fly
Schistocephalus (Tapeworms), 195
Schistosomatidae (Flukes), 206
 Schistosomes (Flukes), 205
Schistotaenia (Tapeworms), 193
 Scoters (*Melanitta*), 30, 195, 206
 Scottish House-martin Flea (*Orneacus rothschildi*), 92, 104, 108-110
 Screaming Cow-bird (*Molothrus rufo-axillaris*), 265
 Sea Cucumbers (Holothuria), 47
 Sea-gulls, *see* Gulls
 Seals, 19, 188, 194
 Sedge-warbler (*Acrocephalus schoenobaenus*), 258
 Shag (*Phalacrocorax aristotelis*), 57, 189, 195, 231
 Shag Tick (*Ixodes unicavatus*), 231
 Sharks (Carchariidae), 11, 51
 Shearwater Flea (*Ornithopsylla laetitiae*), 63, 92, 93, 96, 97, 107, 115, Pls. XI, XXXIII (50, 242)
 Shearwaters (*Puffinus*), 90, 92, 94, 153, 241, Pl. XXXIV (243)
 Sheath-bill (*Chionis alba*), 197
 Sheath-bills (Chioidae), 13
 Sheep, 16, 21, 23, 54, 78, 171, 212, 232
 Sheep bot-fly (*Oestrus ovis*), 212
 Sheep Ked (*Melophagus ovinus*), 21, 43, 171, 213, Pl. IX (34)
 Sheep Tick (*Ixodes ricinus*), 230, Pl. XXXII (227)
 Sheld-duck (*Tadorna tadorna*), 90, 183, 189, 202
 Shore Crab (*Carcinus maenas*), 204, Fig. p. 187
 Short-eared Owl (*Asio flammeus*), 19, 184, 225
 Shoveler (*Spatula clypeata*), 173
 Shrew, 184
 Shrikes (Laniidae), 160
 Shrikes (*Lanius*), 165, 173, 184
 Simuliidae, *see* Black-flies
Simulium aureum (Black-fly), 219
Simulium latipes (Black-fly), 219
Simulium venustum (Black-fly), 218, 219
 Siskin (*Carduelis spinus*), 237
 Skuas (*Stercorarius*), 10, 143, 183, 205, 253-255
 Sky-lark (*Alauda arvensis*), 221
 Slender-billed Weaver (*Tetraplois pelzelni*), 14
 Small Fruit Fly (*Drosophila*), 52
 Small Golden Cuckoo (*Lampromorpha caprius*), 257
 Smew (*Mergus albellus*), 206
 Snails (*see also* Mollusc), 18, 19, 35, 178, 197, 202, 204, 205, 206
 Snake, 53, 216, 232
 Snipe (*Capella gallinago*), 129, 197, 238
 Snow-shoe Hare, 229, 231
 Song-thrush (*Turdus ericetorum*), 85, 165, 189, 227
 South American Duck (*Heteronetta atricapilla*), 266
 Sparrow (*Passer domesticus*), 17, 27, 39, 85, 93, 137, 170, 205, 221, 225, 226, 231, 235, 237, 238, 241, 244, 248, 249, 250, 265
 Sparrow-hawk (*Accipiter nisus*), 15, 85, 237, 256
 Spider, 49, 245
Spilopsyllus cuniculi, *see* Rabbit Flea
 Spiny-headed Worms (Acanthocephala), 186, 178, 188-191, 233
 Spire Shell (*Hydrobia ulvae*), 199, 200, 202, 204, 205
 Spirillum (Bacteria), 235
 Spirochaetes (Bacteria), 31, 36, 238
 Spiruroids (Worms), 185
 Spoonbill (*Platalea leucorodia*), 152
 Sporozoa (Protozoa), 160-170
 Springtails, 181, 245
 Squirrels, 14, 91, 94, 170, 230

- Squirrel Flea (*Monopsyllus sciurorum*), 91, 94, Pl. XIII (66)
- Stable-fly (*Stomoxys calcitrans*), 221
- Staphylinidae, *see* Rove Beetles
- Staphylococcus* (Bacteria), 239, 244
- Starfish, 11, 12, 47, 52
- Starling (*Sturnus vulgaris*), 24, 25, 28, 85, 127, 136, 169, 181, 189, 197, 222, 237, 247, 251, 261, 265, Pl. VIII (31)
- Starlings (Sturnidae), 21, 22, 23, 133, 235
- Stenopteryx hirundinis*, *see* Swallow Louse-fly
- Sternostomum caledonicum* (Mite), 225
- Sternostomum waterstoni* (Mite), 225
- Stickleback, 3 spined (*Gasterosteus aculeatus*), 195
- Stoat, 6, 94, 95, 230
- Stock-dove (*Columba oenas*), 17, 154, 246, 247, 265
- Stomoxys calcitrans*, *see* Stable-fly
- Stone Curlew (*Burhinus oedipnemus*), 231
- Storm-petrel (*Hydrobates pelagicus*), 153
- Streptococcus (Bacteria), 239
- Streptomyces griseus* (Fungus), 244
- Strigeoidea (Flukes), 206
- Strigiformes (Owls), 151, 163
- Strigiphilus* (Feather Lice), 151
- Strongylina (Worms), 180
- Strongyloides avium* (Roundworm), 182
- Struthiolipeurus* (Feather Lice), 142, 145
- Struthioniformes (Ostriches), 13, 139, 142, 145, 149, 194
- Sturnidoecus* (Feather Lice), 149
- Sucking-fish (Remoras), 11, 18
- Sucking Louse (Anoplura), 121, 125, 138, 139
- Sun-fish 12
- Swallow (*Hirundo rustica*), 12, 27, 43, 171
- Swallow Bug (*Oeciacus hirundinis*), 2, 247
- Swallow Louse-fly (*Stenopteryx hirundinis*), 213, Pl. IX (34)
- Swallow Red Mite (*Dermanyssus hirundinis*), 224
- Swallows (*Hirundo*), 16, 17, 49, 85, 165, 169, 193, 207, 213, 217, 222, 225, 248, 251
- Swallows and Martins (Hirundinidae), 79, 184, 215, 221, 247, 248, 251, 252, 265
- Swans (*Cygnus*), 153, 195, 249, Pl. XX (115)
- Swift (*Apus apus*), 94, 213
- Swift Louse-fly (*Crataerina pallida*), 213
- Swifts (*Apus* sp., *see also* Apodiformes), 16, 217
- Swifts (Apodidae, *see also* Apodiformes), 194
- Sword-fish, 12
- Syngamus merulae* (Gape-worm), 181
- Syngamus trachea* (Gape-worm), 39, 180, Pl. XXVII (178)
- Syringobia* (Mites), 225
- Syringophylus* (Mites), 227
- Tabanidae (Flies), 11, 16
- Tapeworms (*Cestoda*), 2, 7, 31, 39, 40, 43, 45, 47, 52, 58, 98, 125, 176-178, 179, 188, 191-197, 222
- Tatria* (Tapeworms), 183, 184, 189, 193
- Teal (*Anas crecca*), 195, 205, 208, 237
- Termites, 13, 26
- Terns (*Sterna*), 15, 194, 195, 197, 255, 263
- Tetrabothrius* (Tapeworms), 197
- Tetrabothrius cylindraceus* (Tapeworm), 197
- Tetrabothrius erostris* (Tapeworm), 197
- Tetrabothrius macrocephalus* (Tapeworm), 197
- Tetrameres* (Roundworms), 179, 184
- Tetrameres fissipinus* (Roundworm), 184
- Thecarthra* (Mites), 225
- Theobaldia annulata* (Mosquito), 165
- Thrushes (Turdidae), 28, 80, 165, 169, 171, 172, 181, 185, 190, 197, 221, 226, 227, 241, 250, 254
- Tick Birds (*see also* Ani), 24, 25, 266
- Ticks (Ixodoidea), 3, 7, 22, 32, 38, 40, 41, 42, 45, 46, 48, 208, 228, 229-232, 238, 245, Pls. XII, XXXII (51, 227)
- Tinamiformes (*Tinamous*), 142, 147
- Tinea lapella* (Clothes Moth), 250, Fig. p. 19
- Tinea pellionella* (Clothes Moth), 250
- Tits (Paridae), 18, 25, 195, 221, 222, 226, 249
- Tongue-worms (*Pentastomida*), 3, 232-234
- Top-shell (Mollusc), 205
- Tortoise, 171
- Toxoplasma* (Protozoa), 170
- Trabeculus* (Feather Lice), 153
- Tree-creepers (*Certhia*), 195, 221
- Trematoda, *see* Flukes
- Treponema* (Spirochaetes), 238
- Treponema anserinum* (Spirochaete), 238
- Trichinelle (Worms),
- Trichinella spiralis* (Tapeworm), 186
- Trichobilharzia* (Flukes), 205
- Trichomonadidae (Protozoa), 172
- Trichomonas* (Protozoa), 173
- Trichomonas columbae* (Protozoa), 173
- Trichomonas eberthi* (Protozoa), Fig. 2d p. 162
- Trichomonas fetus* (Protozoa), 173
- Trichomonas gallinae* (Protozoa), 173
- Trichomonas gallinarum* (Protozoa), 173
- Trichosomoides* (Roundworms), 179
- Trichostrongylus pergracilis*, *see* Grouse Roundworm
- Trichurata* (Roundworms) 186

- Trinoton* (Feather Lice), 128, 141, 152, 153, Pl. XXII (131)
Triton, see Newts
 Trombididae, see Harvest Mites
 Tropical Rat Flea (*Xenopsylla cheopis*), 70, 72, 74, 74, 98, 107
Trouessartia minutipes (Mite), 226
Trox scaber (Beetle), 246, 250
Trox scabulosa (Beetle), 250
Trypanosoma equiperdum (Protozoa), 172
Trypanosoma fringillarum (Protozoa), 171
Trypanosoma gallinarum (Protozoa), Fig. p. 175
Trypanosoma lewisi (Protozoa), 172
Trypanosoma loxiae (Protozoa), 172
Trypanosoma noctuae (Protozoa), 172
 Trypanosomes (Protozoa), 3, 36, 42, 54, 98, 171-173, 222, Pl. XXV (162)
 Tsetse Fly (*Glossina morsitans*), 172, 212, 220
 Tuberculosis (Disease caused by *Mycobacterium*), 21
 Tufted Duck (*Aythya fuligula*), 15, 205, 253
Tunga penetrans, see Jigger
 Turkey (Domestic), 164, 169, 172, 181, 212, 218, 226
 Turnstone (*Arenaria interpres*), 15, 204
 Turtle-dove (*Streptopelia turtur*), 197
 Tyroglyphidae, see Cheese Mites
Unio (Freshwater Mussel), 30
Upupicola (Feather Lice), 150
Uria (Guillemots), 195
 Vagabond Flea (*Ceratophyllus vagabunda*), 87, 89, 115
Vibrio (Bacteria), 235
Vibrio metchnikovi (Bacterium), 239
 Virus, 36, 240-241
 Vole, 69
 Vulture, 14
 Waders (*Charadrii*) 85, 129, 130, 189, 190, 193, 194, 199, 225, 266
 Wagtails (*Motacilla*), 190, 207, 221, 259
 Warble Flies (*Dermatobia hominis* and *Hypoderma bovis*), 212, 215
 Warblers (Sylviidae), 80, 85, 165, 214, 221, 222, 260
 Wasps, 13, 26, 68, 97, 217, 248
 Wryneck (*Jynx torquilla*), 110
 Water Flea, see *Daphnia pulex*
 Waxwing (*Bombycilla garrula*), 12
 Weasel, 94
 Weavers (Ploceidae), 10, 14, 15, 24, 257, 265, 266, 268
 Weddell Seals, 13
 Weevils (Beetles), 185
 Whale, 11, 13, 23, 51, 188, 197
 Wheatear (*Oenanthe oenanthe*), 258
 Whelk (Mollusc), 47, 205
 Whinchat (*Saxicola rubetra*), 230, 258
 Whiskered Tern (*Chlidonias hybrida*), 15
 White Stork (*Ciconia ciconia*), 152
 White-tailed Eagle (*Haliaeetus albicilla*), 14
 Whitethroat (*Sylvia communis*), 252
 White Wagtail (*Motacilla alba*), 14, 15, 165
 Wigeon (*Anas penelope*), 12, 195, 206, 208, 253
 Willow-tit (*Parus atricapillus*), 113
 Window Fly (*Scenopinus fenestralis*), 250
 Wood Ant (*Formica rufa*), 14
 Woodcock (*Scolopax rusticola*), 126, 195
 Wood Louse (*Armadillium vulgare*), 184, 245
 Woodpeckers (Picidae), 14, 142, 150, 184, 222, 265
 Wood-pigeon (*Columba palumbus*), 15, 17, 154, 169, 235, 236, 243, 245, 246
 Wood-warbler (*Phylloscopus sibilatrix*), 260
 Worms, 3, 7, 9, 11, 21, 30, 34, 35, 42, 48, 52, 176-210, Pls. XXVII, XXVIII (178, 179)
 Wrasse (*Labrus*), 202
 Wren (*Troglodytes troglodytes*), 14, 27
Xenopsylla (Fleas), 90
Xenopsylla astia (Flea), 75
Xenopsylla cheopis, see Tropical Rat Flea
 Yellow Wagtail (*Motacilla flava*), 25
 Yellow-backed Oriole (*Caccus cela*), 26
 Yellow-billed cuckoo (*Coccyzus americanus*) 266
 Yellow-hammer (*Emberiza citrinella*), 171
 Yellowshank (*Tringa flavipes*, see also Greater Yellowshank), 194

GENERAL INDEX

Main Sections are in heavy type

- Abdomen, fleas, 64
 Abortion, 173
 Abscesses, 93
 Abstinence, 73, 75, 97, 209
 Acanthella, 189
 Acid-fast bacteria, 236
 Activity of flea and louse, 58
 Adaptation, 4, 43-46 :
 to brood-parasitism, 260;
 to climatic conditions, 70;
 confused views on, 179; to
 clinging to feathers, 132;
 of cuckoo's egg, 262; to
 ecological niches, 131, 139;
 of ectoparasites, 44; of
 follicle-mites, 227; to hab-
 its of host, 45, 46; of lice,
 126, 129; of mouth parts,
 73, 139; mutual, 35; of
 parasites, 35, 43, 69; to
 pH, 192; of Protozoa,
 159; to sedentary habit,
 93
 Adhesive discs, 11
 Afterbirth, 13
 Air-sacs, 3, 8, 207, 226, 232,
 243
 Alimentary canal, 3, 192
 Ambulatory processes, 53
 Ancestors, fleas', 63, 93, 118
 Ant-birds, 254
 Antennae :
 fleas, 62, 64; lice, 122,
 140; modified, 57, 64
 Ant-hills, 14
 Antibiotics, 243
 Anting :
 active, 127; functions of,
 128; origin of, 127; pas-
 sive, 127; soldiers', 127
 Appetite, 72, 74
 Asexual :
 generations, 54; reproduc-
 tion, 39, 41, 160, 173, 176,
 200
 Association :
 nesting, 16, 23, 26; origin
 of, 26; predator and prey,
 137
 Balance, host and parasite, 35
 Barns, 16, 21
 Bathing, 126
 Beauty, 3, 198
 Behaviour, 18, 28, 36 :
 mosquitoes, 215; sym-
 biotic, 24
 Bible quoted, 1, 11, 15, 19,
 33, 41, 72, 158, 190, 193,
 235, 256
 Bile-duct, 3
 Black Death, 1
 Blackhead, 172, 183
 Blindness, 43 :
 birds', 232; fishes', 207
 Blinking, 33, 37
 Blood, 3 :
 clotting, 42, 74, 182, 209;
 composition, 137; depend-
 ence on, 46, 48; food of
 fleas, 73; food of leeches,
 31, 41, 209; food of lice,
 121; food of mites, ticks,
 225, 230; food of worms,
 182, 198; quantity im-
 bibed, 74; rat flea's, 72;
 stimulus of, 68, 112, 216
 Blood-letting, 210
 Body-fluids, 44, 48
 Bone-marrow, 171
 Book-lice, 138
 Bottles, milk, 18
 Bracts, 217
 Brain, flea's, 64
 Bristles :
 flea's, 78; -formula, 81;
 reduced, 96
 Bronchi, 3
 Brood-parasitism, 9, 36, 38,
 256 268 :
 characteristics of, 267;
 lice in, 137; origin of, 265;
 rare, 265; specialisation
 in, 268
 Bubonic plague, 1, 70, 98,
 238
 Budding of larvae, 39, 176,
 182
 Bush fires, 13, 25
 Butter, 236
 Canal, gynaecophorus, 39
 Cannibalism, 121
 Carriers, *see* Vectors
 Carton nests, 14
 Castration, parasitic, 31, 35,
 103
 Caterpillars as food, 256
 Cathedrals, 84
 Cave-dwelling, 42, 97, 109
 Cercaria, 32, 42, 200-207
 Chance, 38
 Chitin, 62
 Cigar-butts, 127
 Classification, **104-108**: ar-
 bitrary, 10, 105; of
 bacteria, 236; of cestodes,
 194; of fleas, 62, 107; of
 Ischnocera, 139; of lice,
 129, 148; objects, in
 science, 105; of parasites,
 10, 59
 Claws, 41, 78, 121
 Clepto-parasitism, 10, 25,
 253-255 :
 frigate bird's, 253; cock-
 erel's, 253; skua's, 10, 254;
 thrush's, 254; incipient,
 253
 Climbing, fleas', 78; lice,
 122
 Clotting of blood, 42, 74,
 182
 Cocoons, 72
 Colds, 235
 Collection, fleas, 61; lice,
 147
 Colour :
 cuckoos' eggs, 259, 262;
 fleas', 62; fleas' eggs', 70;
 leeches' blood, 209; lice,
 126; worms, 184, 198,
 Combs, 52, 62; lost, 96
 Commensalism, 4, **11-19** :
 ants', 14, 51; arthropods,
 19; bacterial, 239; birds',
 12, 19; dangers of, 49; de-
 fined, 11; fish's, 12; fish-
 ermen and, 16; flies', 11;
 fungal, 242; incipient, 15;
 insects, 19; nidicoles, 245-
 252; psychological ele-
 ment, 16; rove beetles,
 50; termites, 51
 Communities, 109
 Competition, 137 :
 inter-specific, 35, 52, 128,
 intra-specific, 35; spatial,
 48
 Conchiolin, 31
 Convergence, 96
 Coprophagy, 13, 28, 50
 Copulation :

- blackflies, 49, 218; *Coccidia*, 161; cuckoo's, 257; fleas', 64, 65, 68, 80, 184; flukes', 40; horse's, 172; leeches', 209; mites' 225; mosquitoes', 215; tape-worm's, 191; ticks', 230
- Corpses eaten, 50, 51
- Corpuscles, 3
- Correlation, 129
- Coryza, 239
- Courtship, 252
- Cow pox, 241
- Cowsheds, 16, 71
- Crop, 3 :
 contents examined, 22, 25; of louse, 120, 121; nematodes in, 183, 184; protozoa in, 173
- Cuckold, 262
- Cuticle, 179
- Cyst :
 flukes', 39, 204; intestinal, 45; protozoal, 42, 160; tongue-worm', 233
- Cysticercus, 192
- Cystogenous glands, 204
- Cytostome, 160, 171
- Death :
 of host, 31-37, 57, 97, 104, 136, 163, 181, 186, 221, 225, 236; of male flea, 68; of parasite, 38, 104
- De-leeching, 23
- De-lousing :
 of birds, 28, 232; of cattle, 24; of fish, 23; of mammals, 22; of whales, 23
- Dengue, 217
- Dependence :
 dangers of, 46; degrees of, 9; parasites and, 54; symbiotic, 20
- Dermatitis, 228
- Descent, fleas', 63
- Development, direct, 233; mites', 225; parasites' 48
- Dew, 49
- Diet, 6, 193, 256
- Differences, specific, 140
- Digestion, lice, 121
- Digestive organs, flea's, 64
- Diplostomulum, 207
- Disease :
 carried by fleas, 98-99; carried by flies, 211, 214; carried by leeches, 209; carried by lice, 125; carried by mosquitoes, 217; carried by ticks, 232
- Dispersal, 135, 164
- Distribution :
 alpine-boreal, 111; circumpolar, 111; discontinuous, 133, 142, 233; geographical, 147, 214; zonal, 85; of fleas, 81-89; of feather lice, 146; of nidicoles, 247
- Diurnal periodicity, 185
- Diversity of form, lice, 119
- Dove-cotes, 231
- Dreys, 91
- Dung, *see* Faeces
- Dwarf males, 39, 52, fig. p. 234
- Dysentery, 174
- Ectoparasites, 7, 44
- Eel-grass, 12, 202
- Eggs :
 alike, 54; bacteria in, 120, 236, 238; blackflies', 219; bugs', 247; climate and, 69; cuckoo's, 38, 257, 262-264; destroyed, 18, 28; duck's, 237; embryonated, 181, 188; feather lices', 123, fertilisation of, 65; fertility of, 44; fixing of, 69; gnats', 215; hatching, 70, 123; laid in hosts' absence, 112; laying of, 70, 132, 212; laying reduced, 37, 217; mites', 225; number of, 38, 70, 180, 188, 191, 216, 230, 232, 258; parasites', 38; parthenogenetic, 40, 123; poisonous, 232; shape of fleas', 70; skuas', 254
- Encephalitis, 225
- Endoparasites, 7, 42, 44
- Enemies :
 host as, 103, 126, 222; of blackflies, 219; of fleas, 103; of flies, 222; of mosquitoes, 217
- Environment, 7 :
 bird is flea's, 84; constant, 100, 140; encourages adaptation, 182; prey and 7; feather louse, 57, 129; nests ideal, 19; no adaptation to new, 53; response to, 144; social, 49; stable, of lice, 59
- Enzymes, 74, 242
- Epidemics, 36, 53, 169, 237, 240
- Epipharynx, 74
- Ethology, 146
- Evolution : 47-55
 of birds, 99, 129, 140, 193; of bird fleas, 89; convergent, 96, 133, 134, 144, 145; of feather lice, 59, 129, 138, 139, 140; of fleas, 60; of genitalia, 65; of host and parasite, 164; interest in, 4; of nematodes, 182; parallel, 62, 132, 134, 144, 145, 207, 224; of parasitic worm, 176; of parasitism, 47-55, of physiological race, 69; sexual reproduction in, 41; trends in, 94, 116, 138
- Examination of lice, 147
- Excretory organ, flea's, 64, flukes' 198, 200
- Exhaustion, of parasite, 38
- Exoskeleton, 62, 106
- Eyelids, flukes below, 2, 207
- Eyes, 3 :
 feather lice, 122; fleas', 62, 77; inflamed, 240; larval fluke in, 207; lost, 97; nematode in, 184
- Faeces, 13, 48, 50, 71, 161, 172, 176, 177, 189, 191, 197, 243, 251, 252
- Fasting, *see* Abstinence
- Fauna, nidicolous, 19, 245, 252
- Fear of mosquitoes, 215
- Feathers :
 eaten, 3, 50, 57, 118, 119; exudate of, eaten, 222; pith eaten, 225; structure of, 137;
- Feeding :
 feather lice, 120; fleas', 74-76; -spots, 75
- Females, 49 :
 cuckoo, 256; feather lice, 123; flea, 63, 64; f. sex parasitic, 49; genitalia, 65; gnat, 215; hatch first, 78; mites attracted by,

- 104; outliving males, 73, 79; outsize, 182; parasitized by males, 40; polymorphic, 114; protecting offspring, 212; sedentary, 58, 75
- Fertility, 44
- Fever, relapsing, 225, 232
- Fidgeting of host, 33
- Fights of cuckoos, 260
- Filariasis, 217
- Fishermen, 16
- Fission :
- binary, 236; multiple, 161
- Fixing of eggs, 69, 123, 212
- Flagellum, 170, 235
- Flattening of body :
- of bugs, 248; of fleas, 57;
 - of lice, 57, 119; of louse-flies, 212
- Flocks, 21, 25, 202
- Flowers, symbiosis and, 28
- Food, 3, 10, 11, 58, 72, 173, 183, 198, 248
- Form, diversity of, 119
- Formic acid, 127
- Fossils, 54, 141, 215
- Fosterers, 36, 258-262
- Gall, 48 :
- bladder, 3
- Gapes, 41, 181
- Genal comb, 62
- Genera, primitive, 143
- Genitalia :
- of flea, 65 ; of lice, 140
- Gentes, 258
- Geographical :
- distribution, 147, 214;
 - history, 100; races, 85, 87, 113
- Geological record, 48, 141, 215
- Geotropism, 78
- Gills, 11
- Gizzard, 184, 185, 256
- Glacial periods, 87
- Glands :
- cystogenous, 204; penetration, 32; stomach, 184;
 - uropygidial, 209
- Granules in crop, 120
- Grazing :
- symbiosis and, 21, 23;
 - tapeworms and, 197
- Grouse disease, 222
- Gynaecophorus canal, 39, 206
- Habitats of flukes, 199
- Haemorrhage, 31
- Halteres, 211
- Hatching, 70, 123
- Hermaphrodites, 40, 53, 191, 209
- Hibernation, 97, 114, 217, 252
- Hitch-hiking, 18, 98, 222, 228, 248
- Host :
- abnormal, 93, 95; castration of, 31; changing, 92, 93, 116; death of (*see* Death); defence by, 79; distribution of, 84, 146; eating fleas, 103; effects on, 30-37, 186-187; finding of, 38, 42, 213; habits of, 33; haemorrhage in, 31; injuries to, 4, 31, 74, 125; phylogeny of, 141, 142, 164, 193; pigmentation of, 32; -preference, 100, 101, 189, 222; resistance of, 33; sharing parasites, 59; smell of, 76; -specificity, 43, 44, 45, 46, 58, 70, 100, 135, 168, 202; wounding of, 74
- Host-specificity, 43-46 :
- in bird fleas, 100; in feather lice, 135; in mammal fleas, 70; in Protozoa, 168; in Tapeworms, 45, 193; in Flukes, 202
- Hunger of parasites, 38
- Hunting, symbiotic, 25
- Hybrids, 247
- Hyperparasites, 103, 128, 197, 217, 243
- Hyphae, 242
- Hypopus, 104, 227
- Ice ages, 87, 89
- Identification of lice, 147
- Ignorance, 145, 156, 246
- Immunity, 34, 99 :
- birds', 163; ducks', 111; horses', 76; molluscs', 200; partial, 34; swans' 102
- Infection, virulent, 37
- Infestation, secondary, 143
- Influenza, 36, 44
- Injuries, 4, 31, 74, 125
- Instinct, 212, 252, 266, 267
- Integument, fleas', 56
- Intermediate hosts (*see* also Vectors) :
- amphipods as, 204; amphibians as, 207; ants as, 197; arthropods as, 172; beetles as, 197; birds as, 190; cockroaches as, 184; copepods as, 195; crustacea as, 184, 188, 194, 204, 207; dragonfly as, 204; earthworm as, 184, 186; fish as, 32, 183, 194, 201, 202, 203, 206-207; fleas as, 98, 103, 177; flies as, 197; freshwater shrimps as 185, 186, 195; function of, 178; grasshoppers as, 183; hog-slaters as, 190; *Hydrobia* as, 202; insects as, 188, 195, 207; leeches as, 209; lice as, 125; mammals as,; 184 mites as, 197; molluscs as, 30, 195, 197, 205, 206, 207; multiplicity of, 42; mussels as, 30; ostracods as, 195; periwinkles as, 204; sand-hoppers as, 204; shore crabs as, 204; vertebrates as, 232; water fleas as, 184, 195; weevils as, 185; woodlice as, 184; worms as, 195; of worms, 177
- Iron necessary, 72
- Islands, 45, 46, 52, 90, 138
- Isolation, 45, 85, 90, 133, 138
- Jargon, 106
- Keratin, 120, 250
- Kidneys, 3
- Kissing, 42
- Labium, 74
- Lacinia, 74
- Larvae, 9, 47 :
- acanthella, 189; black-flies', 219; budding of, 39; clothes moths', 250; cysticercus, 192, 195; Diplostomulum, 207; emergence of, 71; food of, 58, 72; free, of flea, 57; houseflies' 221; host specific, 45; infected, 232; louseflies', 213; mites',

- 224; moulting of, 71; mouth-parts of, 71; nests, in, 61, 247; parasitic, 55; parasitised, 251; predacious, 50; proceroid, 194; scavenging, 251; suited by nests, 101; suppression of, 43; Tetracotyle, 206; tongue-worms', 23; worms', 176
- Leap of flea, 77, 78
- Legs :
flea, 58, 77; lice, 58, 122; lost, 41; vestigial 233
- Lemon juice, 127
- Length of tapeworm, 191
- Leprosy, 98
- Leucocytes, 168, 173
- Licking, 42
- Life-cycle :
Ascaris, 180; *Capillaria*, 186; *Cryptocotyle*, 203; fig. 5, p. 203; Echinostomes, 205; ectoparasites, 178; fleas, 68; flukes, 178, 198-208; gnats, 216; *Heterakis*, 183; insects, 68; leeches, 209; lice, 123; midges, 220; *Oxyspirura*, 184; parasites, 47; *Plasmodium*, 165; *Prosthogonimus*, 204; Roundworms, 179-186; Sporozoa, 160; Strigeoidea, 206; Strongylina, 182; *Syngamus*, 181; tongue-worms, 233; tape-worms, 194-197
- Life-cycles :
contrasting, 9; complex, 42; duration of, 73, 112; simple, 43
- Light, reaction to, 164
- Liver, 3, 173
- Locomotion, 121
- Longevity, 73, 112
- Luminous :
bacteria, 239; organs, 239
- Lungs, 3, 180, 226, 243
- Lymph, 3
- Malaria, 164 170, 214, 217
- Males :
asymmetrical, 226; attached to females, 39; dwarf, 39, 53, 230; dying before females 68; flea, 64, 68; genitalia, 140; gnat, 216; parasite of females, 40; surviving, 54
- Mange, 226
- Mantle, 30
- Marrow, 33, 171
- Mating, *see* Copulation
- Measles, 235
- Mesmerism, 260
- Metacercaria, 206
- Metabolism affected, 31
- Metamorphosis, 57, 125, 211
- Microclimes, 84
- Microfilariæ, 185
- Microhabitats, 245
- Microparasites, 36, 235-244
- Migrations, 42, 80, 97, 150, 180, 207
- Milk, 217
- Milk-bottles, 18
- Mimicry, 263
- Miracidium, 200
- Mobbing, 25
- Modification, 4; of antennae, 57; of bristles, 96; of flies, 211; of head, 119; of lice, 129; of mouth-parts, 63, 73, 119; views on, confused, 179
- Mole-hills, 13
- Mortality :
of cuckoos, 264; of host, 31-37, 57, 97, 104, 136, 163, 181, 186, 221, 225, 236; of nestlings, 99; of parasites, 38
- Mother of pearl, 30
- Moult, 57, 71
- Mountain ash, 12
- Mouth, 3, 11, 41, 119, 160, 198, 209, 232
- Mouth-parts :
armature of, 41; bugs', 248; feather lice's, 119; fleas', 62; gnats', 216; hypopus, 228; leeches', 209; mites', 227; ticks', 229, 230
- Movement :
of fleas, 77; of lice, 122, 132; of louse-flies, 212
- Mud-flats, 198
- Muscles, 3, 243
- Mutations, 52
- Mycelium, 242
- Mycosis, 243
- Mysteries, of cuckoo, 259
- Nagana, 172
- Nasal cavities, 3, 225, 232
- Natural selection, 52
- Nectar, 7, 49
- Nerve cord, flea, 64
- Nesting association, 16, 23, 26, 27
- Nesting sites, 10, 102
- Nests :
beetles in, 50, 245-252; bugs in, 247-248; carton, 14; cliff-swallows, 14; crows, 246; Dermestids in, 248; deserted, 97, 260; domed, 14; dry, 94; ducks', 15; emptied, 261, 268; eyes lost in, 97; fleas collected from, 61, 72; -flies, 220; fly larvae in, 251; ground, 91, 101; hibernation in, 252; house martins, 16; ideal environment in, 19; moths in, 250; mud, 102; numbers in, 72, 245, 247; ospreys', 14; owls', 246; parasites in, 7; ptarmigans', 15; rocky, 87; sand martins', 80; scavengers in, 251; sparrows', 85; swallows', 16; swifts', 213; temperature of, 249; verminous, 246; voles', 69; weavers', 14; wet, 87, 101
- Niche, ecological, 131, 133, 139
- Nostril, fleas in, 49
- Numbers :
effects of large, 32; of eggs, 38, 69; of fleas, 58; of fleas per bird, 61, 75; per nest, 61, 72, 245, 247; per rat, 68; sand-martin, 80; of individuals, 54; of feather lice, 58; of mammal fleas, 89; of parasites per host, 3; of Protozoa, 159; of roundworms, 178; of species, 53, 138
- Nymphs, 57, 125, 205
- Oceanic islands, 45, 46, 52, 90, 138
- Ocelli, 77
- Oocyst, 161
- Operculum, 123
- Orders, 106
- Organs :
of attachment, 41; of locomotion, lost, 41

- Origin of bird fleas, 89 :
feather-lice, 129, 131;
parasitism, 49; pigeon,
110
- Overparasitisation, 37
- Paludrine, 164
- Parasites:
accidental, 9; asexual re-
production of, 39; bud-
ding in, 39; chances of,
38; copulation of, 39;
death of, 38; defined, 6;
dwarf males of, 39; effect
of, on hosts, 30-37; eggs
of, 38; encystment of,
39; evolution of, 47-55,
144; exchange of, 110;
facultative, 9, 10, 221,
251; fleas', 103; herma-
phroditism of, 40; host-
specific, 43; hunger in,
38; intermediate hosts of,
41-43; life a gamble for,
38; life cycles of, 42; loss
of legs of, 41; mating of,
39; micro-, 36; modifica-
tions of, 47, 51; mouths of,
41; numbers of, 3, 38, 54;
obligate, 7, 45; organs of
attachment, 41; parthen-
ogenesis in, 40; periodical,
8; permanent, 7; phylo-
geny of, 141; placental,
55; polyembryony in, 40;
predator and, 6; repro-
duction of, 39, 53; res-
triction of, 43, 44, 46, 58;
sense organs of, 42; sexual
reproduction in, 39; spec-
ialisation of, 43; strobilis-
ation in, 39; temporary, 8,
208; transference of, 42;
tropisms of, 42; variation
in, 36, 51; vectors of, 42
- Parasitism : 6-10
adjustments in, 35; ad-
ventitious, 266; brood-
9, 36, 38, 256-268; clep-
to-, 10, 253-255; conse-
quences of, 6, 55; de-
pendence and, 54; devel-
opment of, 4, 48; effects
of, on host, 30-37; effects
of, on parasite, 38-46;
evolution of, 47-55; muta-
tions and, 52; natural
selection and, 52; oppor-
tunity for, 49; origin of,
224, 266; pre-adaptation
to, 50, 52; super-, 35
- Parapodia, 234
- Parthenogenesis, 40, 123,
182, 206, 225
- Pastures, symbiosis in, 24
- Pearls, 30
- Penetration glands, 32
- Penicillin, 244
- Penis, flea's, 65
of cattle, 175
- Petroleum, 48
- pH, 192
- Phagocytes, 33
- Phoresy, 4, 18, 98, 136, 157,
228 (see also hitch-hiking),
Fig. p. 157
- Phototropism, 77, 122
- Phylogeny, 141
- Physogastry, 222
- Pigeon lofts, 231
- Pigment, 32
- Pig-sty, 16
- Piracy, 254
- Pith, eaten, 225
- Placental parasite, 55
- Plague, 1, 99, 103
- Plough and commensals, 17
- Pneumonia, 240
- Polyandry, 267
- Polyembryony, 40, 182
- Polygamy, 267
- Polymorphism, 114, 171
- Population, limitation of,
125, 128
- Pork, measly, 186
- Pox, avian, 241
- Pre-adaptation, 52-53 :
of bugs, 248; of birds'
fleas, 103; of elephant's
trunk, 51; of leech's
sucker, 51; of louse flies,
52; of mites, 224; of Nema-
todes, 179; to nidicolous
life, 103; to parasitism, 52,
of squirrels' fleas, 91
- Predators, 6, 50
- Preening, 33, 103, 126
- Primitive characters, 132
- Proboscis, 190, 214
- Progenesis, 177
- Promiscuity, 264, 267
- Pronotal comb, 62, 96
- Protein, 183
- Proventriculus, 183
- Pseudopodium, 174
- Psittacosis, 240
- Psychological relations, 12,
17
- Pullorum disease, 237
- Pupae :
of blackflies, 219; of
fleas, 57, 72, 73; in nests,
61
- Pygidium, 77
- Quarries, 114
- Quotations :
Addison 129, Andersson
in Bannerman 21, 22,
Aristotle 72, Bacon, Fran-
cis 105, Bible see Bible,
Browning, Robert 30, Buf-
fon 176, Cervantes 118,
Chandler, A. C., 164
Chisholm, A. H. 127,
Coleridge, S. T. 253,
Condry 127, Davies, W.
H. 17, de Morgan, Augus-
tus (modern version) 103,
Denny, Henry 118, Elton,
C. S. 18, Franklin, Ben-
jamin 125, Gaius 38,
Gray, Thomas 16, Herod-
otus 20, Hill 108, Hirst,
L. F. 106, Hooke, Dr.
61, Huxley, J. S. 54.
Johnson, Dr. 56, Jonson,
Ben 6, Lucretius 44, Mitz-
main M.B., 104, Mouffet,
Thomas 210, 211, 213,
214, 218, 224, 226, 229,
Pennant, Thomas 21, Pliny
23, 30, 68, 127, 208, 259,
262, Shakespeare, William
16, 220, 245, Shipley, A.E.
3, 220, Snodgrass, R. E.
60, 65, Somerville, Wil-
liam 2, Spenser, Edmund
47, Waterston, J. 79, 245
- Races, geographical, 85, 87,
113
- Raft, gnats' egg-, 215
- Range, extension of, 87, 109
- Reactions of host, 4, 33, 125,
128
- Receptaculum seminis, 66,
109, 113
- Record, fossil, 48, 54, 141
- Redia, 200
- Relapsing fever, 225, 238
- Relations, psychological, 12,
17

- Releaser, 259
 Reproduction :
 asexual, 39, 161; fungal, 242; hermaphrodite, 40; parthenogenetic, 40, 123, 182, 206, 225; sexual, 39
 Resistance of host, 32-34
 Respiration :
 anaerobic, 192; cutaneous, 232; tracheal, 63
 Restriction of parasite :
 to head, 58; to one host, 58; to one order, 130
 Ringworm, 242
 Rostrum of tick, 229

 Saliva, 31, 74, 219, 232
 Saltings, 199
 Sand, 114
 Saprophytes, 236, 242, 251
 Sarcoma, 241
 Scabies, 226
 Scaly-leg, 226
 Scattering of eggs, 70
 Scavengers, 51, 121, 251
 Scent of host, 76
 Schizogony, 161, 163; exoerythrocytic, 165
 Scolex, 191
 Seasons and fleas, 68
 Sedentary habit, 116
 Seed-ticks, 230
 Sense-organs :
 lice, 121; lost, 42
 Senses, fleas', 75
 Sentinels, 15, 21
 Sexes, proportion of, 79; dimorphism of, 167, 179
 Sexual reproduction, 39
 Sites of infection, 3, 8, Fig. 1 p. 8
 Size: fleas', 62; lice's 119; parasites' 50
 Skin, 3
 Sleeping sickness, 98, 172
 Smallpox, 241
 Soup, flea in, 112
 Specialisation, 46, 212
 Speciation, 45, 85, 133, 137
 Species, 107, 108
 Specificity :
 ethological, 45, 146; host, 43 46; phylogenetic, 44, 45
 Spermathecae, 65
 Spermatozoa, 65
 Spines, 41, 74, 78, 122, 190-191
 Spiracles, 63
 Spleen, 33
 Spores, 42, 103, 236, 242, 243
 Sporocyst, 204, 206
 Stables, 16
 Starvation, 75
 Strength, flea's, 78
 Strobila, 192
 Strobilisation, 39, 182
 Sub-species, 85, 90, 116
 Success: of fleas and lice, 59; of cuckoos, 2
 Suckers, 41, 52, 104, 159, 191, 194, 198, 208, 228, 229
 Super-families, 106
 Superparasitism, 35
 Survival, 97
 Susceptibility :
 of *Culex*, 217; of old birds, 237; of Passerines, 165
 Swarms, flea, 80
 Swimmers' itch, 206
 Symbiosis, 4, 20-29 :
 in ants' nests, 51; bacteria and, 121, 239; defined, 20; delousing and, 22; in flocks, 21; flowers and, 28; fungi and, 242; in grazing, 21, 23; in hunting, 25; mites and, 227; moths and, 251; nidicoles and, 249; wasps and, 26
 Symphiles, 51, 238
 Synsacrum, 261
 Synthesis by bacteria, 239
 Syphilis, 238
 Systematics, 106, 147
 Temperature, attractive, 76; birds' nests', 80; effects of, 137; fleas' eggs and, 70; life cycle and, 70, 124
 Termitaries, 13, 51
 Territory, birds', 257
 Throat-pouches, 3, 121
 Tolerance, 29
 Toxins, 31, 32, 231
 Tracheae, fleas', 63
 Transference, 116, 135, 160
 Transport hosts, 43, 135, 163, 181, 183, 189, 228
 Tropisms, 42, 77, 78
 Tuberculosis, 31, 236-237
 Typhus, 98

 Umbilical cord, 13
 Uropygidial glands, 209

 Vaccination, 241
 Vagina, 40, 173
 Varieties, 81, 85
 Vectors (*see also* intermediate hosts) : arthropods as, 172; blackflies as, 219; fleas as, 98, 172; flies as, 172; insects as, 240; leeches as, 31, 209; louse flies as, 172; mosquitoes as, 165, 217, 241; multiple, 178; red mites as, 172, 238; ticks as, 232; viruses and, 240
 Vermicules, 165
 Vibrio infection, 239
 Vinegar, 48, 127
 Virulence of infection, 36
 Viruses, 240-241
 Vitamins, 183, 193, 239
 Viviparity, 212

 Walnut, 127
 Warmth, attractive, 75
 Weather, 34
 Wing buds, 73
 Wings :
 cast off, 41, 213, 222; lost, 213, 248; molluscs under, 18; reduced, 52, 213
 Wounds :
 caused by leeches, 209; of birds, 187; of hosts, 74, 99; parasitism and, 23; symbiosis and, 22

 Yaws, 238
 Yellow fever. 217

 Zones of distribution, 85, 101, 217

SCIENTIFIC NAMES OF BIRDS MENTIONED IN THE TEXT

- Accipiter nisus*, see Sparrow-Hawk
Acrocephalus schoenobaenus, see Sedge-Warbler
Acrocephalus scirpaceus, see Reed-Warbler
Actitis hypoleucos, see Common Sandpiper
Aegithalos caudatus, see Long-tailed Tit
Alauda arvensis, see Sky-Lark
Alca torda, see Razorbill
Alcedo atthis, see Kingfisher
Alle alle, see Little Auk
Anas acuta, see Pintail
Anas americana, see American Wigeon
Anas crecca, see Teal
Anas penelope, see Wigeon
Anas platyrhynchos, see Mallard
Anas querquedula, see Garganey
Anas strepera, see Gadwall
Anser brachyrhynchus, see Pink-footed Goose
Anthus pratensis, see Meadow-Pipit
Apus apus, see Swift
Aquila chrysaetos, see Golden Eagle
Archilochus colubris, see Ruby-throated Humming-bird
Ardea cinerea, see Heron
Ardea purpurea, see Purple Heron
Ardeola ibis, see Buff-backed Heron
Arenaria interpres, see Turnstone
Asio flammeus, see Short-eared Owl
Asio otus, see Long-eared Owl
Athene noctua, see Little Owl
Aythya ferina, see Pochard
Aythya fuligula, see Tufted Duck
Aythya marila, see Scaup
Bombycilla garrula, see Waxwing
Bonasa umbellus, see Ruffed Grouse
Botaurus stellaris, see Bittern
Branta bernicla, see Brent Goose
Branta leucopsis, see Barnacle Goose
Branta ruficollis, see Red-breasted Goose
Bucephala clangula, see Golden-eye
Burhinus oedicnemus, see Stone-curlew
Cacicus cela, see Yellow-backed Oriole
Calidris alpina, see Dunlin
Calidris maritima, see Purple Sandpiper
Calandrella dukhunensis, see Lark
Capella gallinago, see Snipe
Caprimulgus europaeus, see Nightjar
Carduelis cannabina, see Linnet
Carduelis carduelis, see Goldfinch
Carduelis flammea, see Redpoll
Carduelis spinus, see Siskin
Charadrius hiaticula, see Ringed Plover
Chenopsis atrata, see Australian Black Swan
Chionis alba, see Sheath-bill
Chlidonias hybrida, see Whiskered Tern
Chloris chloris, see Greenfinch
Ciconia ciconia, see White Stork
Cinclus cinclus, see Dipper
Clamator coromandus, see Red-winged Crested Cuckoo
Clamator glandarius, see Great Spotted Cuckoo
Clangula hyemalis, see Long-tailed Duck
Coccyzus americanus, see Yellow-billed Cuckoo
Columba livia, see Rock-Dove
Columba oenas, see Stock-Dove
Columba palumbus, see Wood-Pigeon
Colymbus arcticus, see Black-throated Diver
Colymbus immer, see Great Northern Diver
Colymbus stellatus, see Red-throated Diver
Coracias garrulus, see Roller
Corvus brachyrhynchus, see Fish-Crow
Corvus corax, see Raven
Corvus cornix, see Hooded Crow
Corvus corone, see Carrion-Crow
Corvus frugilegus, see Rook
Corvus monedula, see Jackdaw
Corvus ossifraga, see Eastern Crow
Coturnix coturnix, see Quail
Crex crex, see Corn-Crake
Crocethia alba, see Sanderling
Cuculus canorus, see Cuckoo
Cygnus olor, see Mute Swan

Dryobates major, see Great Spotted Woodpecker

Emberiza citrinella, see Yellow Hammer
Erithacus rubecula, see Robin
Eupsittula canicularis, see Parakeet

Falco columbarius, see Merlin
Falco mexicanus, see Prairie Falcon
Falco peregrinus, see Peregrine Falcon
Falco rusticola, see Greenland Falcon
Falco subbuteo, see Hobby
Falco tinnunculus, see Kestrel
Fratercula arctica, see Puffin
Fringilla coelebs, see Chaffinch
Fringilla montifringilla, see Brambling
Fulica atra, see Coot
Fulmarus glacialis, see Fulmar
Furnarius rufus, see Oven-Bird

Gallinula chloropus, see Moorhen
Gallus domesticus, see Fowl
Gallus gallus, see Jungle-Fowl
Garrulus glandarius, see Jay

- Haematopus ostralegus*, see Oyster-Catcher
Haliaeetus albicilla, see White-tailed Eagle
Haliaeetus leucocephalus, see Bald Eagle
Heteronetta atricapilla, see South American Duck
Hierococcyx varius, see Indian Hawk-Cuckoo
Himantopus himantopus, see Black-winged Stilt
Himantopus mexicanus, see Black-necked Stilt
Hirundo rustica, see Swallow
Hirundo rustica erythrogaster, see Barn-Swallow
Hydrobates pelagicus, see Storm-Petrel

Jynx torquilla, see Wryneck

Lagopus mutus, see Ptarmigan
Lagopus scoticus, see Grouse
Lamprolaima caprius, see Small Golden Cuckoo
Lanius collurio, see Red-backed Shrike
Larus argentatus, see Herring-Gull
Larus canus, see Common Gull
Larus dominicanus, see Dominican Gull
Larus hyperboreus, see Glaucous Gull
Larus marinus, see Greater Black-backed Gull
Larus pipixcan, see Franklin's Gull
Larus ridibundus, see Black-headed Gull
Leptoptilos crumeniferus, see Marabou Stork
Leucopoliis alexandrinus, see Kentish Plover
Limosa lapponica, see Godwit
Loxia curvirostra, see Crossbill
Lymnocyptes minimus, see Jack Snipe

Martula urbica, see House-Martin
Mergus albellus, see Smew
Mergus merganser, see Goosander
Mergus serrator, see Merganser and Red-breasted Merganser

Merops nubicus, see Carmine Bee-eater
Molothrus badius, see Bay-winged Cow-bird
Molothrus rufo-axillaris, see Screaming Cow-bird
Monticola saxatilis, see Rock-Thrush
Motacilla alba, see Pied Wagtail and White Wagtail
Motacilla flava, see Yellow Wagtail
Muscicapa hypoleuca, see Pied Flycatcher

Nestor notabilis, see Kea
Nucifraga caryocatactes, see Nutcracker
Numenius arquata, see Curlew
Numenius borealis, see Esquimo Curlew
Numida meleagris, see Guinea Fowl

Oenanthe oenanthe, see Wheatear
Oriolus oriolus, see Golden Oriole

Pagophila eburnea, see Ivory Gull
Pandion haliaeetus, see Osprey
Panurus biarmicus, see Bearded Tit
Parus atricapillus, see Willow-Tit
Parus caeruleus, see Blue Tit
Parus cristatus, see Crested Tit
Parus major, see Great Tit
Passer domesticus, see Sparrow
Pastor roseus, see Rose-coloured Pastor
Pavo cristatus, see Peacock
Pelecánoides urinatrix, see Diving Petrel
Perdix perdix, see Partridge
Pernis apivorus, see Honey-Buzzard
Petrochelidon albifrons, see Cliff-Swallow
Phalacrocorax aristotelis, see Shag
Phalacrocorax carbo, see Cormorant
Phalaropus fulicarius, see Grey Phalarope

Phalaropus lobatus, see Red-necked Phalarope
Phasianus colchicus, see Pheasant
Phoenicurus ochrurus, see Black Redstart
Phoenicurus phoenicurus, see Redstart
Phylloscopus collybita, see Chiff-chaff
Phylloscopus sibilatrix, see Wood-Warbler
Pica pica, see Magpie
Picus viridis, see Green Woodpecker
Platalea leucorodia, see Spoon-bill
Platycercus unicolor, see Parakeet
Pluvanius aegyptius, see Crocodile-Bird
Podiceps cristatus, see Great Crested Grebe
Podiceps nigricollis, see Black-necked Grebe
Progne subis, see Purple Martin
Prunella modularis, see Hedge-Sparrow
Psephotus chrysopterygius, see Parrakeet
Pterocnemia pennata, see Rhea
Pterotochus rubecula, see Cheucan
Ptychorhamphus aleuticus, see Auklet
Puffinus gravis, see Great Shearwater
Puffinus puffinus, see Manx Shearwater
Pygoscelis taeniata, see Gentoo Penguin
Pyrrhocolax graculus, see Alpine Chough
Pyrrhocolax pyrrhocolax, see Chough
Pyrrhula pyrrhula, see Bullfinch

Quiscalus quiscula, see Purple Grackle

Recurvirostra avosetta, see Avocet
Regulus regulus, see Goldcrest
Rhea americana, see Rhea
Riparia riparia, see Sand Martin

- Rissa tridactyla*, see Kittiwake
Saxicola rubetra, see Whinchat
Scolopax rusticola, see Woodcock
Sitta europaea, see Nuthatch
Somateria mollissima, see Common Eider and Eider-Duck
Spatula clypeata, see Shoveler
Stercorarius longicaudatus, see Long-tailed Skua
Stercorarius parasiticus, see Arctic Skua
Stercorarius pomarinus, see Pomatorhine Skua
Stercorarius skua, see Great Skua
Sterna albifrons, see Little Tern
Sterna hirundo, see Common Tern
Sterna macrura, see Arctic Tern
Sterna sandvicensis, see Sandwich Tern
Streptopelia turtur, see Turtle-Dove
Strix aluco, see Tawny Owl
Struthio camelus, see Ostrich
Sturnus vulgaris, see Starling
Sula bassana, see Gannet
Sylvia communis, see White-throat
Tadorna tadorna, see Sheld-Duck
Teteropsis pelzelni, see Slender-billed Weaver
Tetrao urogallus, see Capercaillie
Tringa flavipes, see Yellowshank
Tringa melanoleuca, see Greater Yellowshank
Tringa ochropus, see Green Sandpiper
Tringa stagnalilis, see Marsh Sandpiper
Tringa lotanus, see Redshank
Troglodytes troglodytes, see Wren
Turdus ericetorum, see Song-Thrush
Turdus merula, see Blackbird
Turdus musicus, see Redwing
Turdus pilaris, see Fieldfare
Tyto alba, see Barn-Owl
Upupa epops, see Hoopoe
Uria aalge, see Guillemot
Vanellus vanellus, see Lapwing
Zenaidura carolinensis, see Mourning Dove



