# Royal Entomological Society



# HANDBOOKS FOR THE IDENTIFICATION OF BRITISH INSECTS

To purchase current handbooks and to download out-of-print parts visit:

http://www.royensoc.co.uk/publications/index.htm



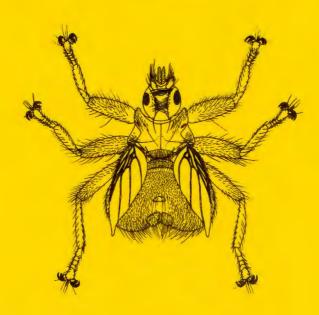
This work is licensed under a <u>Creative Commons</u> <u>Attribution-NonCommercial-ShareAlike 2.0 UK:</u> <u>England & Wales License.</u>

Copyright © Royal Entomological Society 2015

# KEDS, FLAT-FLIES AND BAT-FLIES

# DIPTERA, HIPPOBOSCIDAE AND NYCTERIBIIDAE

A.M. Hutson



# KEDS, FLAT-FLIES AND BAT-FLIES

Editor: M. G. Fitton

# KEDS, FLAT-FLIES AND BAT-FLIES

# DIPTERA, HIPPOBOSCIDAE AND NYCTERIBIIDAE

By A. M. Hutson

Department of Entomology British Museum (Natural History) London SW7 5BD

1984 ROYAL ENTOMOLOGICAL SOCIETY OF LONDON The aim of the *Handbooks* is to provide illustrated identification keys to the insects of Britain, together with concise morphological, biological and distributional information. The series also includes a *Check List of British Insects*.

Each handbook should serve both as an introduction to a particular group of insects and as an identification manual.

Details of handbooks currently available, and an order form, can be obtained from the Royal Entomological Society, 41 Queen's Gate, London SW7 5HU.

World List abbreviation: Handbk Ident. Br. Insects

© Royal Entomological Society of London, 1984

First published 1984 by the Royal Entomological Society of London, 41 Queen's Gate, London SW7 5HU.

Printed by Dramrite Printers Limited, Southwark, London SE1.

#### **Contents**

								P	age
Introduction .									3
General biology.									4
Collecting, prepa		ınd st	orage						5
Acknowledgeme									7
Family HIPPOB	OSCIDA	AE.							7
Life-history .									8
Host relationship	os .								9
Sex ratio, season	ality and	d infe	statio	n rate	es .				10
Predators, parasi	ites, path	ogen	s and	phore	esy.				12
Check list of Hipp	poboscio	lae rec	corded	l fron	n Brita	ain.			13
Glossary									13
Key to genera .									14
Genus Ornithoic	а.								15
Genus Ornithopl	hila .								15
Genus Ornithom	ya .								15
Genus Crataerina	a.								16
Genus Ornithoct	ona .								17
Genus Icosta .									17
Genus Pseudolyr	ıchia.								17
Genus Olfersia .									18
Genus Hippobos	ca .								18
Genus Lipoptena									19
Genus Melophag									19
Field key to the re		Britisl	a speci	es.					19
Family NYCTER									20
Life-history .									20
Host relationship	os .								21
Parasites and par									23
Check list of Nyc		ae rec	orded	from	Brita	in.			23
Glossary									24
Key to genera .									24
Genus Nycteribia									25
Genus Phthiridiu									26
Genus Basilia .									26
Other species tha	it may b	e fou	nd in	Britai	in .		i		27
Field key to the re									27
References					·				28
Figures								•	31
Index	•	•	-	-	-	-	•	•	30

#### Introduction

The Hippoboscidae, Nycteribiidae and Streblidae are families of Diptera that have been combined under the name Pupipara. They are permanent, obligate, blood-feeding ectoparasites of birds or mammals and, in common with tsetse-flies (Glossinidae), the females do not lay eggs but nurture larvae internally, singly. When fully developed each larva is released and pupates immediately. The Nycteribiidae and Streblidae are

exclusively parasitic on bats, while the Hippoboscidae parasitise birds and Artiodactyl mammals (with a few species on other mammals). The Hippoboscidae and Nycteribiidae occur throughout the world with the richest fauna in the Old World tropics. The Streblidae are mainly tropical with a few species occurring in the lower temperate latitudes, but not as far as Britain. In the Neotropical Region, Streblidae are particularly diverse, both in number of species and their range of form.

While the term Pupipara is still in common use, opinions vary as to the true relationships of the families included. It is generally accepted that the Hippoboscidae are closely related to the Glossinidae, but there is little concensus on all other relationships. Most authors (e.g. Hennig, 1973; McAlpine et al., 1981) keep the families Hippoboscidae, Nycteribiidae and Streblidae together, either in the belief that they are a monophyletic unit, or for convenience. Griffiths (1972) goes so far as to put them in a single family (Hippoboscidae), partly on the basis that at least the two groups of bat-flies must share family status in view of the (assumed) relatively recent origin of their hosts. Other authors regard the bat-flies as having a quite different origin from hippoboscids (e.g. Schlein, 1970; Maa, 1963; Oldroyd, 1964). Rohdendorf (1964) considers the two groups of batflies to have very independent origins. Even accepting their monophyly, opinions vary as to the relationships with other Diptera. The Hippoboscidae (with or without the batflies) are variously put in a superfamily of their own (McAlpine et al., 1981), with Glossinidae as Glossinoidea (Hennig, 1973), included with the Glossinidae in the Muscoidea (Griffiths, 1972), or even with the Glossinidae in the Gasterophiloidea (Pollock, 1971). In view of the uncertainty about both the internal and external relationships of this group, it is dangerous to make generalisations and assumptions based on their gross similarities of life-style. For this reason, as well as the lack of overlap in their taxonomic characters and hosts, the families included here have been discussed quite separately and in some ways treated differently.

Many of the volumes in the *Handbooks* series have included only scant accounts of biology. The opportunity is taken here to give a much more detailed account of the biology because of the interest shown in these flies by the many workers studying their hosts. The small number of species involved enables direct comparisons of their behaviour and to show where knowledge is uncertain or lacking, in the hope of encouraging further research. Such research contributes not only towards understanding the relationships between the parasites and their hosts, but can help resolve problems of systematic relationships within and between the families. This account is restricted largely to work done in Britain, but the references will allow access to other literature. The author's unpublished observations have been included, but some are limited and require further data for confirmation.

# General biology

All species are permanent, obligate ectoparasites of birds and mammals. Both sexes feed exclusively on the blood of their hosts, probably taking frequent small meals equivalent to about their own weight of blood every five days. Some Hippoboscidae look like fairly typical flies, but others are strongly adapted for their parasitic mode of life and the Nycteribiidae are so highly modified that their general appearance bears no resemblance to true flies. They all have a curious, to some alarming, ability to move very rapidly in any direction through the fur or feathers of their host.

Mating occurs on the host and may be prolonged — at least males may cling to the females for more than one day. In some cases, e.g. the sheep ked (*Melophagus ovinus*), sperm can be stored by the female and remain viable for a series of pregnancies; others require more frequent mating. All species are larviparous, rearing one larva at a time,

internally, until it is fully developed at three to eight days. At first the larval tracheal system is linked to that of the mother's uterine wall, later the larva respires through its own posterior spiracles, which open to the exterior through the maternal vulva. The head of the larva is enclosed in the anterior part of the uterus and receives nourishment from a "milk gland". By maturity the larva occupies most of the considerably swollen abdomen. The larva is then released as a prepupa which immediately starts to pupate. The actual release of the larva may take as little as two or three minutes and transformation to a pupa as little as one hour. Metamorphosis to the adult may take about 20-30 days (in some species as much as 50 days) or the pupa may overwinter. In emergence an anterior dorsal operculum is forced off by the front legs and head of the fly. The adults of wingless and brachypterous species (and certain other species in some circumstances) emerge sufficiently close to their hosts to have little difficulty in finding them. Others must fly in search of suitable hosts and little is known of this activity.

As with most ectoparasites, there are varying levels of host specificity, ranging from species restricted to a single host species (monoxenous), through species found on a limited number of closely related species (stenoxenous), or species found on a limited number of not especially related species but perhaps restricted by ecological factors (oligoxenous), to species apparently able to live on a wide variety of hosts (polyxenous).

General accounts of the British species can be found in Colyer & Hammond (1964), Edwards, Oldroyd & Smart (1939), which includes some fine coloured illustrations, and Hutson (1978). On a wider scale, Oldroyd (1964) gives an account of the biology of flies of the world; Marshall (1981) gives a thorough comparative review of the ecology of ectoparasitic insects; Waage (1979) discusses the evolution of ectoparasitic relationships; and Askew (1971) reviews all parasitic insects.

# Collecting, preparation and storage

Collecting from live animals often requires specialised techniques of both host trapping, handling and parasite removal and should not be attempted without guidance. Remember that legislation, particularly the Wildlife and Countryside Act, 1981, restricts the catching and handling of most birds, all bats and many other mammals and there are similar laws in other countries. Before embarking on any study ensure that you are acting within the law — if in any doubt consult the Nature Conservancy Council or the British Trust for Ornithology. It is important to minimise disturbance to the hosts, especially, for example, to bats in their breeding colonies or in hibernation.

These flies are relatively large ectoparasites and can often be seen by blowing through the fur or feathers. Once seen the flies can be picked off with forceps or fingers; if felt necessary, they can be immobilised first with a dab of chloroform or ether. On birds the flies tend to concentrate around the neck, under the wing bases and around the base of the tail; on mammals in the anal, genital and axillary regions and sometimes on the neck. Working through the fur of appropriate mammals by hand or with a comb will expose the flies to be picked off. This is not so easy with the woolly fur of sheep. Similarly blowing through the feathers of most small birds is sufficient to expose the flies, although winged species may take active measures to escape during the early part of trapping and handling. An extra person can often help to minimise the losses by catching such escapees. These escapees often make for the hair or beard of the handler. Larger birds and densely feathered birds are not easily searched quantitatively in this way and other techniques may be necessary. Two methods are available.

Special insecticidal powders can be puffed into the feathers and the bird kept bagged for about 5 minutes. This is quite an efficient method of incapacitating many of the smaller parasites, e.g. lice, but is not particularly effective with hippoboscids. The quick

knock-down effect of chloroform makes the Fair Isle Apparatus more effective with flies. I use a collapsible version which consists of strong cardboard rolled into a cylinder and fastened with paper fasteners standing on a white tile or equivalent. A standard cylinder would be about 20cm tall and 10-15cm in diameter — more appropriate sizes can be made for particular species studies. The bird's head is passed through a slit in some material that is supple, strong and air-proof. Oiled silk is the traditional material, but is now difficult to obtain; thin rubber sheeting is a good substitute (available from dental suppliers as "Dental Dam"). Two or three sheets should be available with various sized slits to cater for various size categories of bird. The bird is then supported by a finger each side of its head from behind, with its body suspended in the chamber produced by the tile, cylinder and rubber sheet. An inlet tube near the base if the cylinder allows the operator to blow chloroform fumes into the chamber. Anaesthetised flies should drop off very quickly. While the body of the bird is inside the chamber the operator should keep a constant check that chloroform vapour is not escaping to affect the bird; this can be done by smell and by watching for rapid eye flutter or other signs of distress. Used properly this is a perfectly safe procedure for the collecting of ectoparasites from birds, but should not be attempted with mammals (and will obviously be impractical for the mammal hosts considered here). Using such apparatus as a widemouthed jar with a wad of chloroform-soaked cotton wool inside may be simpler and in some ways more efficient, but could result in birds becoming partially anaesthetised should they drop in and it is more difficult to check that all, especially small, ectoparasites have been removed before the next bird is processed. Fowler & Cohen (1983) offer a method of delousing many birds simultaneously.

Particularly large birds or birds that do not readily fit this kind of apparatus can only be treated by enclosure in a cloth bag inside a polythene bag, keeping the head out of both bags. Again chloroform is introduced within the bags and flies should drop off, but results obtained this way may not be suitable for fly population studies.

Dead birds or mammals can be hand-searched or enclosed in a polythene bag and chloroform or ether introduced. After a few minutes ectoparasites can be brushed out of the animal onto a white surface.

All ectoparasites are best preserved in alcohol (70-80%). For storage in alcohol, tubes can be filled completely, a plug of cotton wool placed in the open end and the tube inverted in a large wide-mouthed jar of alcohol. This allows easy topping-up of alcohol levels and the jars can be used to group species.

Hippoboscids can be pinned, but the abdomen shrinks and many characters become obscured. Nycteribiidae should not be pinned, but some may need to be mounted on slides with the male genitalia extracted. Slides of Nycteribiidae may have to be quite thick and they must be thoroughly dried if they are to be stored vertically. Smit (1957) gives a method of mounting fleas that is suitable for nycteribiids.

Many hosts, e.g. bats, have a wide variety of ectoparasites and it is worth collecting all; many mites are particularly poorly known and more data are welcome on most insect parasites.

Data should include locality (with grid reference), date, collector and host identity, age and sex where possible. If the host is being marked, the mark (e.g. ring number) should be recorded. When population studies are undertaken a complete record of all hosts examined and their individual infestation should be established. Other details often taken as standard during host handling, such as reproductive state, size, weight, moult, etc may be useful in understanding the biology of the flies.

#### Acknowledgements

I am grateful for comments on early drafts of this work by Dr. R.A. Cheke, W.P. Saunders and Dr. D.S. Hill on the Hippoboscid section and Dr. R.E. Stebbings and R. Gardner on the nycteribiid part. Thanks are also due to Professor O. Theodor and Cambridge University Presss for permission to reproduce figures 33, 35, 37, 40-44 from Theodor, O. & Moscona, A. 1954, On bat parasites in Palestine. 1. Nycteribiidae, Streblidae, Hemiptera, Siphonaptera. *Parasitology, Cambridge*, 44: 15-245, and to the Trustees of the British Museum (Natural History), for permission to reproduce figure 27 from Theodor, O. 1967. *An illustrated catalogue of the Rothschild collection of Nycteribiidae (Diptera) in the British Museum (Natural History)*.

#### Family HIPPOBOSCIDAE

The family Hippoboscidae contains about 200 species. Most species occur in the Old World tropics, but about 35 are established in the Western Palaearctic. Thirteen species are recorded from Britain, including five which cannot be regarded as resident. Some of these are unlikely to re-occur, e.g. Olfersia spinifera, recorded from a Frigate Bird (Fregata magnificens). On the other hand some species which have not yet been recorded in Britain might be expected to occur, e.g. O. fumipennis, widespread and common on the Osprey (Pandion haliaetus).

About 75% of species occur on birds. Recorded hosts of Hippoboscidae include 24 of the 27 orders of birds; there are no records from Rheiformes (South American rheas), Apterygiformes (New Zealand kiwis) and Sphenisciformes (southern ocean penguins), although some other groups of birds may not have specific hippoboscid parasites.

Of the mammal hosts, most (80%) are Artiodactyls, the rest are Equidae (horses), Carnivora (carnivores), Lemuridae (lemurs), Indreidae (lemurs) and Macropodidae (kangaroos and wallabies).

The species occurring on birds are commonly known as "flat-flies" or "louse-flies", while those on mammals are often called "keds" (or misnamed "ticks"). They are tough and leathery, flattened dorso-ventrally, generally bristly (but without the true combs which are so much a feature of many groups of ectoparasites). The state of the wings varies from permanently fully winged through reduced or caducous wings (i.e. wings that are shed subsequent to emergence of the adult fly), to wings absent. The claws are strikingly curved and strong. Most species are pale brown to black, but some of the bird flies become bright bottle green. In a few species the thorax is metallic and in some species occurring on larger mammals the thorax is distinctively patterned.

Although flightlessness is a common feature of ectoparasites, its distribution within this family is not easily explained. All the hippoboscid parasites of swifts (Apodidae) are flightless by virtue of reduced wings. These include the whole genus *Myophthiria* and most species of *Crataerina*. Swifts return regularly to the same colonial nest site and hence the flies do not need wings for host finding. The other species of *Crataerina* are similarly flightless and occur on hirundines, which also return to regular colonial nest sites, but there are many fully-winged *Ornithomya* species occurring on other colonial hirundines. *Crataerina* is probably only an extreme form of *Ornithomya*, with reduction of eyes and increased hairiness as well as reduced wings; one as yet undescribed species falls between the two genera. Of the mammal parasites, four genera exhibit flightlessness: three have wings which are shed on reaching a host and one has wings reduced to an inconspicuous veinless knob. Again the distribution of these flightless forms is difficult to explain. One of the genera with caducous wings occurs on Lemuridae while the related Indreidae are parasitised by a permanently fully-winged genus. The

caducous-winged species of *Lipoptena* and *Neolipoptena* occur mainly on Cervidae (deer) and Bovidae (cattle, antelopes, etc), but their hosts in the Bovidae include close relatives of the hosts of both permanently fully-winged species of *Hippobosca* and of the almost wingless *Melophagus*.

Most genera that live on birds are much more closely related to each other than to those that occur on mammals — and vice versa. However, there are some exceptions: the genera from Madagascan lemurs and Australian wallabies are more closely related to the bird parasite part of the family, while the genus from Ostrich is much more closely related to mammal parasites.

The most important general taxonomic works are by Maa (1963, 1969); other important works are by Theodor & Oldroyd (1964) for the Palaearctic and the very detailed work on the American fauna by Bequaert (1953-57). For studies of the structure, physiology and natural history see Bequaert (1953-57). G.B. Thompson published many papers concerning the distribution, hosts, etc., of British species (see George, 1981). Detailed studies of the life-history and ecology of the British species have been made on *Ornithomya* (Hill, 1962b, 1963; Corbet, 1956), *Crataerina* (Summers, 1975; Hutson, 1981a), *Hippobosca* (Roberts, 1925), *Lipoptena* (pers. obs.) and *Melophagus* (Macleod, 1948; Evans, 1950; Tetley, 1958). The information that follows is based largely on these works.

#### Life-history

In the wingless *Melophagus ovinus* the larva sticks to the fur of the host. In the flightless *Crataerina* species and sometimes where the hosts of *Ornithomya* species are hole-nesting or build very bulky nests, the larvae are deposited in or around the nest. In other cases the larvae are deposited away from the host or its nest, but it is unlikely that they are dropped at random as resultant losses could be too high. In the case of the wingless adult deer keds, *Lipoptena*, larvae are certainly deposited while the flies are still on the host and they may stay trapped in the fur for a short time. Possibly most larvae are deposited while the host is resting; in most recorded instances it occured in the late morning to early afternoon. In fully-winged *Hippobosca* and Ornithomyiinae many flies leave the host to find a suitable sheltered site to deposit the larvae.

The pupae are a shiny dark brown to black, rather round and seed-like (fig. 3). Pupal diapause is recorded for *Ornithomya "biloba"* in South Australia (Kennedy, Smith & Smyth, 1975). W.P. Saunders (pers. comm.) reports an instance of *O. avicularia* from Blackbird (*Turdus merula*) passing through two winters before emergence.

The teneral adult is pale and weak, but soon darkens and strengthens. However, in many species the abdominal shape and sclerotisation of plates may have to await at least the first blood meal and in the females of *Lipoptena*, for example, full maturity of the abdomen probably does not occur until about 14 days after emergence (Hare, 1953). *Lipoptena* also undergoes various major modifications to the musculature, and hence shape, of the thorax and neck in connection with its change from an actively flying fresh adult to a wingless mature adult (Schlein, 1967).

Success in establishment and maturation may depend on how quickly the parasite can find a suitable host; the faster the fly finds a host the higher its chances of survival. After five days of searching, even if a *Lipoptena* does find a host it is weakened and has a low chance of survival. Some of the bird flies may be able to survive a little longer before their first blood meal. After the initial feed on a host, ability to withstand starvation is often markedly reduced. Thus the American *Lipoptena depressa* can tolerate four or five days without food after emergence, but only two days after its establishment on a suitable host. *Ornithomya*, *Hippobosca* and *Melophagus* would

normally die within seven days of their removal from their host (Marshall, 1981), but a good proportion of well-fed *Crataerina pallida* can withstand longer periods of starvation (pers. obs.). High humidity and cool temperature can enable this starvation period to be extended, e.g. to 24 days in *Melophagus* (Graham & Taylor, 1941).

Under normal conditions, most species probably feed at least daily. Data on *Crataerina hirundinis* suggest a major daily feed with some supplementary feeding (see also Popov, 1965). *Melophagus* feeds at approximately 36 hour intervals, *Ornithomya* more frequently, while one American bird-fly is reported to feed only every six days (Tarshis, 1958). A full feed may take 5-30 minutes. The initial meal of *C.hirundinis* may be as much as the weight of the lightweight newly-emerged fly. Mature *Melophagus* can imbibe a blood meal equivalent to over 90% of its weight and *C. pallida* has been recorded taking 160% of its own weight, but such maxima are probably exceptional and most mature flies would take about their own weight every three to six days in small, frequent feeds.

Longevity may vary widely between species for established mature adults, but these are relatively long-lived as active flies. Three months is by no means exceptional and up to at least six months is likely in some species. In many species males do not live as long as females which will continue to produce offspring after the males have disappeared. Fecundity varies: *Melophagus ovinus*, with a long life expectancy but more slowly maturing larvae (6-8 days), produce up to 17 larvae per female, while *Lipoptena* species, with a faster larval maturity (about 3 days), may produce twice as many.

#### Host relationships

In Britain Crataerina species are monoxenous: C. pallida on Swifts (Apus apus) and C. hirundinis on House Martins (Delichon urbica), but there are occasional records of the former from hirundines and the latter on Swifts, Sand Martins (Riparia riparia) and Swallows (Hirundo rustica) (and it is quite common on Swallows in continental Europe). The *Ornithomya* species are restricted more by habitat than by host specificity: O. chloropus occurring on all kinds of birds on open or upland areas; O. avicularia and O. fringillina occurring mainly in lower areas of more enclosed vegetation: O. avicularia on larger birds from Greenfinch (Carduelis chloris) upwards, O. fringillina on small birds from Greenfinch downwards. Ornithomya biloba is known in Britain from three specimens found on Swallows, but is very common on Swallows in continental Europe — even as close as Cap Gris Nez, France (pers. obs.). Melophagus is monoxenous on sheep, Hippobosca equina occurs on horses but can maintain populations on cattle, and *Lipoptena* is specific to deer, particularly Roe (Capreolus capreolus) and Red Deer (Cervus elaphus) — it appears that survival rate is poor on Fallow Deer (Cervus dama). Lipoptena cervi will land on many other animals, including man, and frequently commits itself to the wrong host by shedding its wings. This species has only recently colonised Finland where it is spreading rapidly and becoming a considerable nuisance by emerging in large numbers and biting man (Hackman, 1979).

Crataerina pallida occurs mainly on adult birds and later on feathered young, but C. hirundinis occurs more on young than adult birds. Ornithomya species occur mainly on juvenile (i.e. full-grown flying young) birds. Melophagus moves readily from adult on to young sheep. There is no evidence that Lipoptena selects between young and old deer.

It is not possible to sex live hosts of *Crataerina* species and the same is true for many (particularly juvenile) hosts of *Ornithomya* species and there are no data to suggest whether or not these species demonstrate host sex selection. In the culling of Red and Fallow Deer (the best opportunity to examine for keds), males are culled before the

rut and females afterwards. There are, therefore, insufficient data to compare infestations between the sexes on these hosts. On Roe Deer there appears to be little sexual discrimination, but perhaps some concentration of Keds onto female towards the end of pregnancy. Samples examined are small, and behaviour on Roe Deer may be different on account of the different social organisation of this species from Red and Fallow.

Seasonal differences in the levels of infestation may vary with species, age and sex of host. The differences are due partly to differential survival rates of the flies on the different kinds of hosts as much as to active selection. In the polyxenous species of Lipoptena and Ornithomya the degree of host selection may depend on the presence or absence of preferred species or the combination of available species. For example, it is possible that Lipoptena will avoid Fallow Deer if Roe Deer are present, but not much if Roe Deer are absent and Red Deer present; in other words in decreasing order of preference the hosts would be Roe, Red, Fallow.

Further studies are necessary on the movement of flies (particularly females) from host to host. The only large scale mark/recapture study is that of Corbet (1956) of O. chloropus on birds on Fair Isle, Shetland. 92 flies (15.7%) were retrapped of which 75% were on the same individual bird. Of the flies recovered on a different bird 74% (17 of 23) were on hosts of the species upon which they had been released. However, originally the marked flies were not necessarily released on the species from which they had been collected and only 7 (30%) of those flies that had changed host had reverted to the original host species. Similarly, flies released without a host were rarely recovered from the host from which they had been taken. The data are conflicting: in total 93% were recovered (mean interval before recapture: 5.5 days) on the same host species, but it is not certain what proportion of these were the original host species and flies released without a host seemed very unselective. O. chloropus is the sole species on Fair Isle. it has a broad host tolerance (but limited host diversity available) and may be a special case. Elsewhere, further mark/recapture studies and studies of larviposition behaviour, phoresy of mites and lice, occurrence of trypanosomes, and other factors may suggest strong individual host specificity, particularly for O. avicularia, or even the existence of sibling species complexes.

The wingless *Melophagus* can only transfer during direct contact between sheep, but does so actively, concentrating on pregnant ewes before lambing and later onto well-fleeced lambs (Tetley, 1958). There is inter-nest movement in *C. hirundinis* but its extent and importance need further investigation. No data exist for *C. pallida* or *Lipoptena*. Roberts (1925) suggests that most *Hippobosca* roosted on vegetation at night or during inclement weather and so may change host frequently.

# Sex ratio, seasonality and infestation rates

There are data on sex ratio at emergence for only five species of Hippoboscidae and all are in approximately equal ratio of male to female (Marshall, 1981). However, in some highly seasonal bird-flies, e.g. O. chloropus or C. pallida, males have a tendency to emerge first and have a shorter life than females. Such seasonal changes in sex ratio are not exhibited in multivoltine species occurring on birds with a protracted breeding season, e.g. C. hirundinis (Summers, 1975), or in longer lived species, e.g. Lipoptena. In C. hirundinis a higher proportion of females occur on birds than in the nest.

The incidence and infestation rates may also vary greatly in seasonal species, e.g. in O. fringillina (Hill, 1963), O. chloropus (Corbet, 1956), C. pallida (Hutson, 1981), The Ornithomya species appear at the end of June to take advantage of the juvenile birds, reach a population peak in July and have largely disappeared by the beginning

of October, Occasional specimens are found as late as December or even January, C. pallida starts to emerge at the end of April or early May when Swifts return to breed, reaches a population peak by the time the young are sufficiently well feathered to be adequate hosts and the population dies off before the birds migrate back to Africa after a relatively short stay of 3.5 months. C. hirundinis starts to emerge in May when House Martins are settling in to nests, the greatest population being found in June to August. but some continue into September or later. A few are carried with the birds at least at the start of migration (pers. obs.), but the species is not recorded from Africa (Summers. 1975, 1978). The population pattern of *Melophagus* is severely interrupted by shearing and dipping of their hosts, but populations build up in late winter and early spring and concentrate on the lambing ewes. They then, while populations are still increasing, largely transfer to the lambs. Shearing closely followed by dipping results in exaggerating a natural summer population decline, numbers then building up slowly through the winter (Macleod, 1948; Evans, 1950). Lipoptena begins to emerge towards the end of August, the main emergence is in October and emergence is over by December. Emergence is probably timed to coincide with the production of winter coats. There are not enough data to see seasonal changes in infestation, but it seems likely that survival (and hence infestation) is high through the winter, but subsequent mortality reduces the population to a minimum by the time of the fresh emergence in August. In Britain, Hippobosca is a summer species occurring from May to October, but peaking in August and early September.

Most species are univoltine, but the extended breeding season of House Martins allows *C. hirundinis* a number of overlapping generations; and *Melophagus* breeds throughout the year.

The seasonal population changes, together with variations in host selection, result in differing rates of incidence (% hosts infested) and infestation (number of flies per host). Thus adult Swifts may start their stay in Britain with an incidence rate of less than 10% and an infestation rate of less than 0.3 flies per bird, reach a peak of 70% or 2.6 flies per bird and dwindle to less than 10% or 0.2 flies per bird at the end of the season. During this time individual infestations may vary from zero to more than 30. On the smaller House Martin, over 40 of the smaller C. hirundinis have been found (pers. obs.). There is no direct evidence that such heavy parasite loads debilitate their hosts significantly and it may be that such high infestations are very temporary in a genus of flies which is closely associated with the host's nest. High infestations on Swifts and House Martins are quite commonly reported, but they do not appear to be common in the hosts of Ornithomya species. About 80 O.avicularia have been reported from an emaciated juvenile Buzzard (Buteo buteo (C. Jones, pers. comm.) but this seems to be exceptional. Infestation of more than four flies is rare on small birds (hosts of O. fringillina and chloropus). With O. chloropus and O. avicularia on larger birds there is evidence that the larger the bird the more flies it may carry. It is not clear whether this is active selection for larger birds which would be easier to find and the higher fly populations would give better mating opportunities. The same may be said of *Lipoptena*: up to 224 have been taken from one lateral half of a Red Deer, while Roe Deer carry much smaller populations, although there was no correlation between number of flies and weight within the Roe Deer. The only figures available for Hippobosca are from cattle (rather than its preferred equine host) and seem very low: six cattle had an average of 9.8 (range 4-17). The data for *Melophagus* are rather artificial; Tetley (1958) gives figures of up to more than 300 on one ewe, but most of his figures are involved with artificial introductions of keds onto experimental sheep; Macleod (1948) gives means of up to 220 on adult sheep in May.

#### Predators, parasites, pathogens and phoresy

Undoubtedly the major cause of adult hippoboscid mortality is host predation (Bequaert, 1953; Corbet, 1956; Hill 1963), although hirundines and particularly swifts may not be efficient predators. Little is known of this or other mortality factors.

Bacteria, such as *Bacillus anthracinus*, and Rickettsiae, e.g. *Rickettsioides melophagi*, are known from Hippoboscidae, but most species may have no impact on the fly or its host. Hippoboscids may play a minor role in the spread of *B. anthracinus* (Bequaert, 1953; Steinhaus, 1963).

Baker (1967, 1975) discusses the role of hippoboscids as vectors of protozoa. The trypanosome Trypanosoma melophagium is transmitted by M. ovinus. Sheep are infected by crushing infected keds in the mouth. The trypanosome is not pathogenic to sheep, but may be harmful to the ked. Bird-flies also transmit trypanosomes. O. avicularia is a vector of a Trypanosoma species in corvids in Britain, but relatively little investigation of the hippoboscids as vectors of other trypanosomes has been attempted here. Swifts carry Trypanosoma cypseli in Europe, but examination of blood smears from 70 English swifts and the flies they were carrying proved negative (R.A. Cheke, M.A. Peirce, D.H. Molyneux & A.M. Hutson, pers. obs.). In the Haemasporina, O. avicularia and O. chloropus have been found carrying Haemoproteus species on Woodpigeon (Columba palumbus) and Red Grouse (Lagopus scoticus) respectively. Hippoboscids are probably important vectors of many species of Haemoproteus, a common blood parasite of birds. Peirce's (1981) list of the Haematozoa of birds in Western Europe may suggest other host-parasite relationships worthy of investigation.

The tropical and subtropical *Hippobosca longipennis* Fabricius transmits the dog filarial heartworm *Dipetalonema dracunculoides* in parts of its range (Nelson 1963). Laboulbeniomycete fungi have been recorded from a few tropical hippoboscids (Bequaert, 1953).

Astigmatid mites of the family Epidermoptidae are common on species of Ornithomya. Hill, Wilson & Corbet (1967) reviewed the British epidermoptids occurring on hippoboscids (the genera Myialges and Microlichus and including the Analgid genus Strelkoviacarus). Up to 40% of flies may be infested by these mites which are usually (at least in Myialges) adult females producing egg masses. They are firmly attached to the flies by their mouthparts and front legs. To what extent they feed and are thus parasitic on the flies or are merely phoretic for the production/dispersal of offspring is not clear. Perhaps Myialges is more strictly parasitic than the others. Hutson (1981b) found more mites on female flies than on males in a species from Gibraltar, but no such trend was obvious in the study by Hill et al. (1967). Fain (1965) has reviewed the Epidermoptidae and Gaud & Atyeo (1982) discuss the status of Strelkoviacarus.

The phoresy of feather lice (the "Mallophaga" of the order Phthiraptera) on bird hippoboscids is reviewed by Kierans (1975), who believed that mostly such phoresy was a "last ditch" attempt by the lice to get from a dead or dying host to a more viable one. However, the rate of occurrence of some louse species on flies from healthy birds suggests that this is an active dispersal system, e.g. over 40% of 156 O. chloropus on Starlings (Sturnus vulgaris) on Fair Isle were carrying up to 22 Sturnidoecus sturni (Corbet, 1956) and high numbers of Brueelia marginata (Burmeister) are found on O. avicularia from thrushes (Turdus species) in England. Thrips and pseudoscorpions have also been found attached to hippoboscids.

Bequaert (1953) and Thompson (1953) discuss two species of Pteromalidae, *Nasonia vitripennis* Walker (= *brevicornis* Ashmead) and *Dibrachys cavus* Walker, reared from puparia of *C. pallida* and possibly *C. hirundinis*. These are both widespread parasites of a wide range of insect hosts.

#### Check list of Hippoboscidae recorded from Britain

#### ORNITHOMYINAE

ORNITHOPHILA Rondani, 1879 *metallica* (Schiner, 1864)

ORNITHOMYA Latreille, 1802 avicularia (Linnaeus, 1758) viridis Latreille, 1805 viridula Meigen, 1830 biloba Dufour, 1827 chloropus Bergroth, 1901 lagopodis Sharp, 1907 fringillina Curtis, 1836

CRATAERINA Olfers, 1816 OXYPTERUM Leach, 1817 STENEPTERYX Leach, 1817 hirundinis (Linnaeus, 1758) pallida (Latreille, 1811) kirbyanum (Leach, 1817)

ICOSTA Speiser, 1905

LYNCHIA: auctt., nec Weyenbergh, 1881

S. ORNITHOPONUS Aldrich, 1923 minor (Bigot, 1858) falcinelli: (Corbet, 1956), nec (Rondani, 1879)

S. ARDMOECA Maa, 1969 ardeae (Macquart, 1835)

OLFERSIA Say, 1823 spinifera (Leach, 1817)

HIPPOBOSCINAE HIPPOBOSCA Linnaeus, 1758 equina Linnaeus, 1758

LIPOPTENINAE LIPOPTENA Nitzsch, 1818 HAEMOBORA Curtis, 1824 ORNITHOBIA Meigen, 1830 cervi (Linnaeus, 1758) pallipes (Curtis, 1824) pallida (Meigen, 1830)

MELOPHAGUS Latreille, 1802 ovinus (Linnaeus, 1758)

#### Glossary

Included here are only the few more specialised terms used in the keys, plus the names of a few structures that are so highly modified in this family that they may be difficult to recognise. A full morphological account of the family can be found in Bequaert (1953) with modifications in Maa's later papers. Notation of the venation and cells of the wings is given in figures 10 and 14 (Sc; subcosta; R: radial veins; M: median veins; Cu: cubital veins; A: anal veins; r: radial cells; m: median cells; a: anal cells; bc: basal cells).

Antenna (fig 22, ant). Greatly reduced to short broad structures on either side of front of head.

Axillary cord (fig 22, ac). Sclerotised lateral extension of scutellum leading to wing base. Humeral callus (fig 22, hc). Antero-lateral part of thorax.

Inner orbit (fig 22, io). Area between margin of eye and mediovertex.

Jugular bristles (vibrissae) (fig 23, jb). Row of bristles on each side of antero-ventral surface of head.

Laterocentral bristles (fig 7, lcb). Group of bristles on each side of central part of thorax, excluding the two rows that run down the centre of the thorax (which are the acrostical bristles).

Lunula (fig 22, lun). Crescent-shaped area between antennae and mediovertex.

Mediovertex (fig 22, mv). Central part of dorsal surface of head.

Mesobasisternum (fig 23, mbs). Main ventral plate of thorax.

Mesonotal suture (fig 22, mns). Main transverse line across centre of thorax, not always complete; divides mesonotum into an anterior prescutum and posterior mesoscutum. Mesonotum (fig 22, mn). Main dorsal part of thorax.

Mesoscutum (fig 22, ms). Area of mesonotum posterior to mesonotal suture.

Ocelli (fig 22, oc) up to three simple eyes present on postvertex, often reduced or absent. Palps (fig 22, pa) paired structures at front of head protecting haustellum (the sucking tube of the proboscis).

Postorbit (fig 22, po). Area between posterior margin of eye and posterior margin of head.

Postvertex (fig 22, pv). Central posterior area of dorsal surface of head.

Prescutum (fig 22, ps). Area of mesonotum anterior to mesonotal suture.

Prosternal lobes (fig 23, pl). Paired remnants of prosternum lying between front legs. Scutellum (fig 22, sc). Posterior dorsal part of thorax.

Tergal plates (fig 7, tp). Most of the dorsal (tergal) and ventral (sternal) plates of the abdomen are reduced or absent. The remnants are mainly small median often poorly differentiated sclerites.

Vibrissal area (fig 23, vib). Area from which the jugular setae arise, sometimes produced anteriorly as a lobe or spur.

#### Key to genera

As well as the genera already recorded from Britain the key includes others that may occur here. Exotic genera can be associated with common regular migrants, e.g. the single British record of *Ornithophila metallica* was from a Whitethroat (*Sylvia communis*), or the growing number of vagrant bird species. Those genera that do not occur regularly are placed in square brackets. A complete key to genera is given by Maa (1963; see also Maa, 1969). A simplified field key to the regular British species follows the notes on individual genera. It is considered impractical to give the hosts and distributions of the common species in detail. It is hoped these will be the subject of a separate paper.

a se	parate paper.
1	Wings fully developed and functional (figs 1, 2, 6, 9)
_	Wings reduced or absent (either by reduction or loss) (figs 4, 5, 7, 8)
2	Tarsal claws simple, but with a pale basal lobe (fig. 17); humeral callus weak, not produced
	horn like along side of head (figs 6-9)
-	Tarsal claw bifid and with a pale basal lobe (fig. 16); humeral callus strong and horn-like along
	side of head (figs 1, 4, 5, 22, 23); on birds
3	Wing with one or two cross-veins (figs 6, 9); R4+5 well separated from Costa until apex;
	on mammals4
_	Wings with three cross-veins enclosing cells posterior to the radial veins (cf. fig. 1); apical
	half of vein R4+5 running very close to Costa; on birds[Ornithoica] (p.15)
4	Wing clear and hyaline, with only one cross-vein; head much broader than long (fig. 6); thorax
	markedly flattened; on deer
_	Wing distinctly crenulated and tinted, with two cross-veins; head not much broader than
5	long (fig. 9); thorax not so markedly flattened; on horses Hippobosca (p.18)
3	Wing with three cross-veins posterior to radial veins (figs 1, 2, 10-13); vein Cu + 1A well
	developed, like 2A; scutellum with four or more strong bristles (figs 1, 18, 19, 21) $\dots$ 6 Wing with one or two cross-veins posterior to the radius; vein Cu + 1A poorly developed,
_	hardly visible except at base (figs 14-15); scutellum at most with two strong bristles (fig. 20)
	8
6	Vein R2 + 3 with apical 3/5 fused with Costa; wing membrane entirely bare (fig. 13)
•	
_	Vein R2+3 well separated from Costa except at apex; wing membrane usually with
	microtrichia (figs 1, 2, 10-12)

7	Antennae small and narrow, much longer than broad (figs 1, 22); axillary cord fringed with
	soft pale hairs (figs 18, 19)
_	Antennae large and very broad, at most twice as long as broad; axillary cord fringed with
	strong, black bristles (fig. 21)
8	Wing with only one cross-vein [Pseudolynchia] (p.17)
	Wing with two cross-veins (figs 14, 15)9
9	Scutellum with two strong bristles (fig. 20)
	Scutellum with only soft short hairs (fig. 24) [Olfersia] (p.18)
10	Wings reduced but entire and with well developed venation (figs 4,5); tarsal claws bifid and
	with a pale basal lobe (fig. 16); humeral callus well developed (figs 4, 5); head not broader
	than long; on birds
_	Wings either reduced to a veinless knob or broken off, leaving a broad flat veined stump
	(figs 7, 8); tarsal claws simple with a pale basal lobe (fig. 17); humeral callus weak (figs 7,
	8); head much broader than long; on mammals
11	Wings reduced to a veinless solid knob; haltere absent (fig. 8) Melophagus (p.19)
	Wings broken off leaving a broad flat using distump; bultered present (fig. 7) Lipoptons (n. 10)

#### Genus Ornithoica Rondani

This genus has not yet been recorded in Britain. O. turdi (Latreille) occurs widely in Africa and into North Africa and the Mediterranean on a wide range of hosts. It has also been recorded occasionally in Central Europe and so could occur here. Most species of the genus are very small. Maa (1966) revised the genus, including 22 species.

#### Genus Ornithophila Rondani

A small genus of two species: O. metallica Schiner is a widespread Old World tropical and subtropical species recorded from a very wide range of hosts. It has also been recorded rarely in temperate latitudes. O. gestroi Rondani is a poorly known species recorded from Falconidae around the Mediterranean. Maa (1969) discusses the genus. Apart from the single natural introduction there are two specimens in the British Museum (Natural History) from imported birds: one from Pekin Robin (Leiothrix lutea), Yorkshire, xi. 1965; one from Ring-necked Parakeet (Psittacula krameri), London Airport, x.1975.

Wing length 4-5mm; palpi about 0.6 times length of lunula ...... metallica (Schiner)
 One British record from Sylvia communis, Wales, Bardsey Is., v. 1966. (Thompson, 1968).

## Genus Ornithomya Latreille

A genus of about 25 mostly Old World species, but others await description. Maa (1963) delimits three extant species-groups, Theodor & Oldroyd (1964) revised the Palaearctic species and Hill (1962a) revised the adults and pupae of the regular British species. See also Maa (1964), Hutson (1971, 1981). Apart from the four species discussed here, an additional species was collected from an early swallow but the specimen was lost during transit for confirmation of identification. All records of O. biloba Dufour are from early swallows, which would be well worth examining for further records of this or possibly other species. Note that in the avicularia-group (avicularia, fringillina and chloropus) characters are not always constant and that the outer pair of scutellar bristles may be finer and paler than others. Hill (1962b) discusses the hosts and distribution and (1963) the life-history of the British species of the avicularia-group.

#### Key to species

- Wings with macrotrichia more or less uniform in apical half, cells 3r and 1m without distinct bare stripes (fig. 12); eye smaller (postorbit not shorter than greatest width of inner orbit, eye not longer than greatest interocular distance); ocelli small; scutellar bristles not confined to a single transverse row near hind margin (fig. 22) ...... biloba Dufour Argyll, Hertford, Yorks. v-vi. On swallow (Hirundo rustica). Throughout Palaearctic.
- Wing macrotrichia restricted in apical half of wing, bare strips present in cell 1m and usually 3r (figs. 1, 2, 10, 11); eye larger (postorbit shorter than greatest width of inner orbit, eyes longer than greatest interocular distance); ocelli large and conspicuous (fig. 1); scutellum with only a distinct row of 4-8 (sometimes 10) bristles near hind margin (figs. 1, 18, 19)...........
- 2 Larger species, wing length 5.5-7.0mm; scutellum with a row of 8 (sometimes 9 or 10) bristles; head and thorax pale; wing setulae reduced leaving large clear area in cell 3r (fig. 1) ...

  avicularia (Linnaeus)

Common throughout most of England, Wales and Ireland, but scarce in northern England and southern Scotland. vi-x (with occasional individuals surviving into winter). On larger passerines from size of Turdus, Sturnus, etc. (sometimes smaller passerines, e.g. Carduelis chloris), Ciconiiformes, Anseriformes, Accipitriformes, Falconiformes, Galliformes, Gruiformes, Charadriiformes, Columbiformes, Cuculiformes, Strigiformes, Caprimulgiformes, Piciformes. Throughout Palaearctic, Pakistan, Australia; stray records from Africa.

- Smaller species, wing length less than 5.5mm; scutellum with four or six bristles (figs. 18, 19)
   3

Common in northern England, in Scotland, Ireland, more remote upland areas of Wales and off-shore islands in these areas, scarce in central England, becoming rare in south. Associated with open (particularely upland) country, vi-x. On most species of open habitat, particularly Accipitriformes, Falconiformes, Galliformes, Charadriiformes, Cuculiformes, Passeriformes (Alaudidae, Motacillidae, Turdidae, Sturnidae, Fringillidae, Emberizidae). Mainly northern Palaearctic with ?stray records from southern Palaearctic.

#### Genus Crataerina Olfers

A small genus of seven, mainly Old World, species. The Palaearctic fauna is revised by Theodor & Oldroyd (1964). On birds of the families Apodidae and Hirundinidae. Two species are common in Britain.

#### Key to species

Common throughout England, Wales and at least parts of Scotland and Ireland. v-x. On Delichon urbica; occasionally Riparia, Hirundo and Apus. Passer may become infested temporarily when occupying Delichon nests. Most of Palaearctic region and into north of Oriental region.

#### Genus Ornithoctona Speiser

I consider it unlikely that this genus will be recorded in Britain, but *O. laticornis* Macquart is common and widespread on a wide range of hosts in Africa, including Palaearctic migrants. *O. laticornis* is one of the smallest members of the genus with a wing length of about 7mm and could possibly be mistaken for *Ornithomya avicularia* on an early migrant. The antennae are very different, there are four scutellar bristles and there is a distinct row, almost a comb, of bristles on the axillary cord. Maa (1969) has revised this genus of 12 species distributed throughout most of the world except for the Palaearctic.

#### Genus Icosta Speiser

This is by far the largest genus of the family — and the most difficult to identify. The 56 species, mainly palaeotropical, are divided into five subgenera in the revision by Maa (1969); other species await description. Theodor & Oldroyd (1964) include the species most likely to occur in Britain, two of which have been recorded rarely (Thompson, 1955b, 1974). These two belong to subgenera in which the mesonotum is largely bare, the distance between the two scutellar bristles is more than twice the median length of the scutellum, vibrissal area is not produced into a tooth-like projection.

#### Key to species

Recorded twice from Shetland (Fair Is.), Dorset. iv-v. From Anthus trivialis and Crex crex respectively. Found throughout Africa and the Mediterranean, mainly on passerines.

# Genus Pseudolynchia Bequaert

A small genus of five species. The so-called Pigeon fly, *P. canariensis* Macquart, is now found throughout the tropics and subtropics with frequent occurrence in more temperate regions and as far north as southern Sweden. It is likely, therefore, to be

recorded in Britain eventually. Although occurring mainly on Columbiformes and Falconiformes it has also been recorded from a wide range of other birds. In *P. canariensis* wing macrotrichia do not extend as far as vein 2A, leaving part of cell 2m + 1A and all of cell 2a bare. In this respect it is similar to *P. garzettae* Rondani, a species of the Palaeaotropics that also occurs in the Mediterranean region, principally on Caprimulgiformes (but also Strigiformes and others). In *O. canariensis* the palp is distinctly more than twice as long as broad, the median length of the scutellum is about ¼ distance between bases of scutellar bristles, hind margin of scutellum more or less straight, male mid-tarsus with a group of peg-like spines under segment one at base. Maa (1966) revised the genus, but see also Maa (1969).

#### Genus Olfersia Say

A small genus of seven mainly tropical and subtropical species. The only species recorded from Britain so far is Olfersia spinifera Leach from a Frigate bird (Fregata magnificens), found exhausted on Tiree Island, Inner Hebrides, vii. 1953 (Stephen, 1953). Although the species has also been found in similar circumstances in France, the chances of it re-occurring are remote. As stated in the introduction, another species is more likely to occur in Britain: O. fumipennis Sahlberg, a very widespread and common species on Osprey (Pandion haliaetus). Since the Osprey is once again a well established breeding bird in Britain, it is likely that its fly will also occur here, but whether the fly breeds in the northern parts of its recorded distribution (to 62°50'N in Europe) is unknown. O. fumipennis can be identified by the following combination of characters; 1st basal cell long and narrow with macrotrichia only on vein R4+5; 2nd basal cell reaching at least to apex of Sc; wing microtrichia absent on both surfaces of half of cell 2m + 1a and whole of cell 2a; posterior margin of head more or less straight (upper orbits and postvertex not strongly produced or separated by distinct notches). Bequaert (1957) has revised the genus.

# Genus Hippobosca Linnaeus

A genus of seven described species, all on larger Artiodactyl or Perissodactyl mammals, except for one species on Carnivora. All species occur in Africa and the Middle East with the ranges of three species extending into the Oriental region and southeast Asia. Their natural distributions at the extremes of this range are confused by introductions of their hosts. One species, *H. equina*, also occurs widely in the Palaearctic and Thompson (1955) discusses its status in Britain. Another species worth mentioning is *H. rufipes* Olfers, a mainly southern Afrotropical species of larger antelopes (and cattle) that is spreading into the Mediterranean region. Its particular interest here is its frequent occurrence in tins of corned beef. It has distinctly orange-red legs, prescutum with a median posterior large yellow spot and three pairs of spots around lateral and anterior margin, mesoscutum with a pair of apico lateral spots, scutellum with median half orange-red clearly separated from yellow lateral spots. Bequaert (1939) provides a key to species.

— Scutellum with pale median patch, extending as a line across mesoscutum and onto prescutum; pale humeral borders of prescutum and apico-lateral corners of mesoscutum; mid and hind tibiae with pale median bands (fig. 9) . . . . . . . . . . . . equina Linnaeus Formerly common in Hampshire, Dorset and much of Wales, with scattered records, some of doubtful authenticity, as far north as Edinburgh. Now apparently only common in New Forest, Hampshire, with occasional records in other southern counties, e.g. Devon. All non

New Forest records would be of interest, particularly if local breeding can be assured. It is said that there are now more horses in Britain than there were in the last century, but perhaps changes in their use and husbandry have resulted in a decline. v-x. On horses, occasionally cattle, man, dog, etc.

#### Genus Lipoptena Nitzsch

A relatively large genus of about 30 species, including four species found in the western Palaearctic. One occurs in Britain. A second species, *L. capreoli* Rondani, may occur here on goats, although it is really a species of the dry parts of eastern Europe through the Middle East to adjacent parts of the Oriental region. It has not been recorded from domestic goats here and most of our feral herds are living in cold wet upland areas. The genus is restricted to ruminant Artiodactyl mammals; there are species groups restricted to the Afrotropical region and to the Americas, but most species occur in the Oriental and Palaearctic regions. One species has been described from the Spanish Sparrow (*Passer hispaniolensis*) from Kazakhstan (Grunin & Doszhanov, 1974), but since it clearly belongs to the *capreoli*-group, the type-specimen still has wings and alates often land on the wrong host, it seems likely that this specimen belongs to a species that would normally inhabit an artiodactyl. Maa (1965, 1969) discusses the systematics and its relationship to host and geographical distribution. Thompson (1969) has discussed the distribution of the British species.

Distributed throughout Great Britain, but details patchy, i-xii. (alates: viii-xii). Principally on Roe Deer (Capreolus capreolus) and Red Deer (Cervus elaphus), also Fallow Deer (Cervus dama), Sika Deer (Cervus nippon) and Reindeer (Rangifera taranda). Stray records from e.g. Badger, Human, Dog.

# Genus Melophagus Latreille

A small genus of three Palaearctic species on Bovidae (Maa, 1969), one of which occurs in Britain. Of the other two species, one occurs on Chamois (Rupicapra rupicapra) and Ibex (Capra Ibex) in Europe, the other on Mongolian Gazelle (Procapra gutturosa). The species that occurs in Britain, M. ovinus the sheep ked, has a wide Palaearctic distribution and has been introduced throughout most of the world, with varying degrees of success in establishing itself. Thompson (1955b) gives a bibliography of its occurrence in Britain.

— Palp as long as head; inner orbit with about 20 bristles; female with one medially divided tergal plate; male without median tergal plates (fig. 8) . . . . . . . . ovinus (Linnaeus) Formerly widespread in Britain, but increased use of pesticides has reduced populations and distribution; present status uncertain. i-xii (peak iv-v). On domestic sheep (Ovis "aries").

# Field key to the recorded British species

1	Wings fully developed and functional
	Wings reduced or absent 6
2	Head deeply sunk into thorax (figs 1, 22); wings without longitudinal folds (figs 1, 2, 10-15); on birds
	on birds

_	Head not sunk into thorax (figs 6-9); wings with longitudinal folds (figs 6, 9); on mammals
	5
3	Upper surface of head and thorax dark; parts of underside of head and thorax dark (fig.
	23); six scutellar bristles (fig. 19); on all birds in upland country Ornithomya chloropus
	Upper and undersurface of head and thorax more or less pale (often green); four or at least
	eight scutellar bristles; microtrichia in cell 3r more restricted (figs 1, 11)
4	4 scutellar bristles (fig. 18); small species (wing length less than 5.5mm); on small passerines
	Ornithomya fringillina
_	8-10 scutellar bristles (fig. 1); larger species (wing length 5.5-7mm); on larger passerines and
	non-passerines Ornithomya avicularia
5	Wings milky, with only 3 or 4 longitudinal veins and one cross-vein (fig. 6); eyes very small;
	on deer Lipoptena cervi
_	Wings slightly tinted, with seven longitudinal veins and two cross-veins (fig. 9); eyes large;
	on horses Hippobosca equina
6	Wings reduced but complete (figs 4-5); on birds
_	Wings absent or broken off near base (figs 7, 8); on mammals
7	Wings long and narrow (fig. 4); on House Martin Crataerina hirundinis
_	Wings short and broad (fig. 5); on swifts Crataerina pallida
8	Wings absent (fig. 8); on sheep Melophagus ovinus
_	Wings broken off near base (fig. 7): on deer Linontena cervi

### Family NYCTERIBIIDAE

The family Nycteribiidae contains over 250 species, most of which are found in the Old World (particularly the Oriental and Pacific areas). About 12 species occur in Europe, of which three have been recorded in Britain. Their general appearance (figs 25, 27) is very spider-like by virtue of the considerably modified thorax in which the ventral plates (sterna) are more or less fused into a single broad flat plate, the lateral plates (pleurae) are displaced dorsally and the main dorsal plates (mesonotum) are reduced and membranous. In consequence the long legs and head arise dorsally from the thorax, the head lying backwards with its dorsum on the mesonotum. Wings are absent (although halteres are retained) and many other standard adaptations to an ectoparasitic existence are present, e.g. combs of spines, strong claws, reduced eyes, reduction of free-living immature stages. The resting position of the head makes the insect more streamlined but to feed they usually stand with their body perpendicular to the skin of the host and rotate the head forward to bring the mouthparts in contact with the skin.

The taxonomy of the Palaearctic fauna has been revised by Theodor (1954) and a monograph of the world fauna published by Theodor (1967). Maa (1971) gives an annotated bibliography of the family.

# Life-history

The basic pattern of the life-cycle is given in the general introduction. Males take a few days to mature after emergence and then attempt mating with any female, young or old, gravid or not; even other males, other species, other parasites or inanimate objects may be "courted". They sit on the large abdomen of the female, curling the abdomen down onto that of the female and hold themselves in position with the midlegs, the abdominal comb and with the strong anal claspers which are hooked under the tip of the female abdomen.

At the maturity of each larva the female leaves the host bat and deposits the larva (now strictly a prepupa) near the bat colony. The larva is hemiovoid and sticky secretions

ensure that the flat ventral surface is securely glued to the substrate. A narrow "skirt" round the edge helps to form a better seal. Two behavioural features ensure a secure fixture. When first deposited the larva performs marked peristalsis to get an airtight seal between it and the substrate, while the female backs over it and presses it down with her thorax or abdomen. The freshly deposited larva is soft and white, but quickly hardens to a dark red-brown pupa (fig. 26). In long established large bat colonies areas of the substrate near the bats may be thickly encrusted with the old and current puparia of bat-flies.

Sex ratio at emergence appears to be about equal and samples collected subsequently from the bats themselves show a similar proportion. Of *Nycteribia kolenatii* collected quantitatively by the author during recent years, 50.7% (n = 211) were female with no appreciable seasonal trend. Including earlier collections of the author and other material in the British Museum (Natural History) 52.5% (n = 244) were female and there was still no seasonal variation apparent. Both infestation rates and sex ratios showed no change throughout the year. Many winter flies were fresh fed, suggesting that they had been actively feeding even on torpid bats, and pairs were frequently seen in copulation on torpid bats, but production of young would appear to be arrested. No obviously gravid females were present in winter samples. Funakoshi (1977) was able to study quite large samples of bats carrying *Penicillidia jenynsi* throughout the year in Japan. This is a relatively much larger parasite with a much lower infestation rate than *N. kolenatii*. He found no gravid females or copulation in winter. Studies of particular relevance to temperate species are papers of Schulz (1938), Ryberg (1947) and Hurka (1964).

#### Host relationships

In Britain Nycteribia kolenatii might be regarded as monoxenous on Daubenton's Bat (Myotis daubentoni) — it is extremely common on this species, although there are occasional records from other Myotis species (some at least of which may be host misidentifications). Similarly Basilia nana has only been found on the rare Bechstein's Bat (Myotis bechsteini) except for one suspect record. On the other hand, Phthiridium biarticulatum occurs mainly on Horseshoe bats (Rhinolophus species) but there are also sufficient records of it from Long-eared Bats (Plecotus species) for it to be considered oligoxenous. As the study of bats and their parasites advances it is becoming apparent that few, if any Nycteribiidae are truly polyxenous.

Infestation rates and seasonality. Most of the data from Britain provide little more than locality. Incidence of B. nana on M. bechsteini is high in Britain and also in Czechoslovakia (Hurka, 1964), but samples are small and the species has been recorded from a variety of bats in Europe.

There is little information on *P. biarticulatum* in Britain, which may have declined in recent years. Horseshoe bats, particularly Greater Horsehoe Bat (*R. ferrumequinum*), have declined markedly this century and particularly in the last 20 years (Stebbings & Jefferies, 1982). In particular the size of colonies has dwindled and many of the remaining colonies may now occupy marginal nursery sites, which may have contributed to the demise of the nycteribiid. Austen (1906) mentions finding at least 18 flies on a single Lesser Horseshoe Bat (*R. hipposideros*) in North Devon and Humphries (1959) found 152 flies on 195 *R. hipposideros* and one on 149 *R. ferrumequinum* over a period spanning two winters in Gloucestershire. The *R. hipposideros* had an infestation rate of 0.78 flies per bat (range 0-11) and an incidence rate of 33.8%. In recent years the author has examined 114 *R. ferrumequinum* mainly from Wales, but also from Sussex, Dorset, Wiltshire and Gloucestershire, and 38 *R. hipposideros* from Wales (Dyfed and Gwynedd), Wiltshire, Dorset, Gloucestershire and Devon. None of these bats was parasitised by a nycteribiid. On the continent of Europe *R. ferrumequinum* would

appear to be the most widely recorded host, but R. hipposideros would appear to be the most frequent host in Britain and in certain parts of Europe (Hurka, 1964).

Rather more can be said about N. kolenatii which is still a common parasite of the common Daubenton's Bat (Myotis daubentoni). Again published information consists merely of records of locality, date and host. Of 118 Daubenton's bats examined by the author (mainly in autumn and winter), 72.9% were carrying flies and the overall average infestation was 2.2 flies per bat (range 0-13). The fly was not found on any other species examined, including all the other British Myotis species. Infestation varied from site to site, but no seasonal trend in population change was observable. Funakoshi (1977) found infestation rates in Penicillidia jenynsi in Japan much lower in winter than in summer, but Aellen (1963) found little variation in numbers through the year in Switzerland.

There were, however, strong links between infestation and sex of host in the author's material: females are much more heavily parasitised than males, but no evidence for any preference by age of bat is evident (average infestation rates: adult female (n=27) 3.33, juvenile female (n=20) 3.15, adult male (n=59) 1.49, juvenile male (n=12) 1.58. This sharp distinction is not so obvious in the incidence rate; the rate for juvenile males approaches that of adult females (overall incidence: adult female 81.5%, juvenile female 90.0%, adult male 64.0%, juvenile male 75.0%). These rates of occurrence might be expected in view of the relatively limited contact adult males have with the nursery colonies where most Nycteribiid pupae are deposited, but there may be active selection against males, including juveniles.

Twelve bats (10.17%) had infestation rates of more than five flies and these were seven adult females, four juvenile females and one juvenile male.

Thompson (1972) gives a bibliography and distribution maps of the published records of the British species.

Information on the identification and biology of bats in Britain can be found in Stebbings (1977). Popular reviews of bat biology are given by Yalden & Morris (1975), Hill & Smith (in press) and Schober (in press) with more detailed treatment in Wimsatt (1970-77). The names of bats used here follow Corbet's (1978) review of the Palaearctic mammal fauna.

There follows a list of bat species recorded from Britain, plus a few that might occur here, in parentheses, and a list of the Nycteribiidae recorded from them from throughout Europe. Principal parasites are placed first, occasional parasites included in parentheses, and species recorded from Britain are in italics. The list suggests that several other species of Nycteribiid could occur in Britain, although some of the listed species have a strictly southern distribution

#### RHINOLOPHIDAE

Rhinolophus ferrumequinum Phthiridium biarticulatum (Nycteribia latreilli,

pedicularia, schmidlii, vexata, Basilia nana, Penicillidia

conspicua, dufouri)

R. hipposideros Ph. biarticulatum (N. kolenatii, schmidlii, vexata, Basilia

nattereri, Pen. conspicua, dufouri).

#### **VESPERTILIONIDAE**

M. daubentoni

Myotis bechsteini Basilia nana (N. kolenatii, schmidlii, vexata)
M. brandti no records separated from M. mystacinus

(M. dasycneme) N. kolenatii, B. nana

N. kolenatii, Pen. monoceros (N. schmidlii, vexata, Pen.

dufouri)

M. myotis

M. mystacinus

(Probably includes records

from M. brandti)

M. nattereri

(Vespertilio murinus)

Nyctalus leisleri

N. noctula

(Eptesicus nilssoni)

E. serotinus

(Pipistrellus nathusii)

P. pipistrellus

Barbastella barbastellus Plecotus auritus

(probably includes records from P. austriacus

P. austriacus

N. latreilli, vexata, Pen. dufouri

(N. kolenatii, pedicularia, schmidlii,

Ph. biarticulatum, B. italica, nana, Pen. conspicua)

B. italica (N. kolenatii, ?pedicularia, schmidlii, vexata, B. nana, nattereri, Pen. ?conspicua, ?dufouri)

B. nattereri, nana (N. kolenatii, ?pedicularia

Pen. dufouri, monoceros)

(N. kolenatii, Pen. monoceros)

no records

(N. pedicularia)

no records

(N. kolenatii, latreilli, B. nattereri)

(? N. kolenatii)

(N. kolenatii, schmidlii, Ph. biarticulatum, B. nana)

(N. schmidlii)

(N. kolenatii, pedicularia, schmidlii,

vexata, Ph. biarticulatum, B. nana, nattereri,

Pen. monoceros)

no records separated from P. auritus

## Parasites and pathogens

Laboulbeniomycete fungi of the genus Arthrorhynchus are restricted to Old World Nycteribiidae. Five species are known, one of which (A. eucampsipodae) is recorded from Nycteribia kolenatii in Britain (Blackwell, 1980). A. eucampsipodae and the related A. nycteribiae both occur principally on cave bat nycteribiids, both occur from western Europe and Africa to south-east Asia or even Australia, and there is overlap in host bat-flies and bats. Further collecting is required to understand the ecological differences between these species.

Rickettsiae (*Enterella* species) have been found in *Nycteribia kollari*, *Phthiridium biarticulatum* and *Nycteribia* "blasii", but not yet in Britain (see Steinhaus, 1963).

Flagellate protozoa (Mastigophora) have been found in *Nycteribia schmidlii*, *Penicillidia pachymela* and *Cyclopodia sykesi* (Wallace, 1966). Nycteribiids are frequently suspected as vectors of sporozoa (e.g. of *Polychromophilus* species by Garnham, 1973) but their efficiency in this has yet to be demonstrated. Hutson & Turner (pers. obs. 1980) found *Polychromophilus* in British *Myotis daubentonii* associated with an infestation of *Nycteribia kolenatii*, but the flies have not yet been examined for protozoa.

Dermanyssid mites have been found to be phoretic on Nycteribiidae (e.g. Marshall, 1970), but not yet in Britain.

One Chalcidid (Hymenoptera) has been reared from puparia of Cyclopodia greeffi in Africa (Urich, Scott & Waterston, 1922).

# Check list of Nycteribiidae recorded from Britain

NYCTERIBIA Latreille, 1796

kolenatii Theodor & Moscona, 1954

latreilli: Brit. auctt., nec (Leach 1817)

pedicularia: Brit. auctt., nec Latreille, 1805 blasii: Brit. auctt., nec Kolenati, 1856 PHTHIRIDIUM Hermann, 1804 CELERIPES Montagu, 1808 STYLIDIA Westwood, 1840 biarticulatum Hermann, 1804 vespertilionis (Montagu, 1808) hermanni (Leach, 1816)

BASILIA Miranda Ribeiro, 1903 nana Theodor & Moscona, 1954 nattereri: Brit. auctt., nec (Kolenati, 1857)

#### Glossary

There follows a list of the features mentioned in the keys that may be less familiar to some users or that are particularly strongly modified in this family.

Aedeagus (figs 33, 34, aed). The intromittent organ of the male, composed of two fused plates.

Anal segment (figs 25, 32, as). The elongate terminal segment of the abdomen bearing the anal and genital openings. Bilobed in female, conical in male.

Anterior spiracle (fig. 25, asp). Spiracle outside notopleural suture, lateral or just posterior to the head.

Clasper of male (fig. 33, cl) Pair of strong processes articulating with end of anal segment. Carried under the tip of the abdomen.

Connexivum (fig. 25, co) The elastic membranous part of surface of female abdomen. Genital plate (fig. 31, gp). The genital opening of the female is protected by a dorsal and a ventral genital plate. The ventral plate is not obvious and the dorsal plate may be partly hidden when the abdomen is contracted.

Haltere groove (fig. 25, hg). The haltere lies in a pit by the posterior end of the notopleural suture. In some groups the pit is partially or completely covered by a sclerotised flap.

Mesopleural sutures (fig. 25, msu). Sclerotised ridges running outwards from notopleural suture towards base of mid leg.

Notopleural setae (fig. 25, nse). Row of setae on notopleura.

Notopleural sutures (fig.25, nsu). Pair of longitudinal sclerotised ridges on dorsal surface of thorax, broadening and coalescing posteriorly.

Parameres (fig. 34, pa). Pair of sclerotised plates articulating with the anterior part of the phallobase; probably present to protect the aedeagus in the resting position.

Phallobase (fig. 34, ph). Cone-shaped or triangular sclerite surrounding base of aedeagus.

Sternites of female (fig. 31, s1+2, s3, s4, s5, s6, s7). Ventral plates of abdomen. Sternites of male (fig. 22, s1+2, s3, s4, s5). Ventral plates of abdomen; sternum 5 is usually strongly modified.

Tergites of female (fig.25, t1, t2, t6). Dorsal plates of abdomen, greatly reduced in number, variable in size, shape, bristling, etc.

Tergites of male (fig. 32, t1, t2, t3, t4, t5, t6). Dorsal plates of abdomen, generally without strong modification, but with varying bristle patterns.

# Key to genera

The following key includes the three genera recorded from Britain, plus one genus and one subgenus that could possibly be found here (included in square brackets).

Detailed identification characters are given for the recorded species followed by some notes on others species that might occur. A field key to the recorded species is also given.

1 Eyes present; (tibiae more than four times as long as broad; posterior margin of sternal plate 2 Tibiae short and broad, 2-3.5 times as long as broad; row of setae at posterior margin of sternal plate of thorax either complete or with small gap in middle; 3-4 tergites on female abdomen before anal segment; (Nycteribia) ......3 Tibiae longer and narrower, 4-8 times as long as broad (fig. 29); row of setae on posterior margin of sternal plate of thorax reduced to a small group (or a single seta) on each side; 3 tergites on female abdomen before anal segment; head with a small membranous median 3 Tibiae flattened and almost semicircular (2-2.5 times as long as broad) (fig.28); head partly Tibiae not as flattened and more slender (3.5 times as long as broad); head sclerotised up to the anterior dorsal margin ...... [Nycteribia (Acrocholidia)] (p.27) Haltere groove closed; eyes consisting of a single unpigmented lens; large (3.5-4.5mm), bristly species; head sclerotised to the anterior dorsal margin; female abdomen with 2 or 3 tergites before anal segment ...... [ Penicillidia] (p.27) Haltere groove open; eyes pigmented, with two more or less clearly separated lenses on a common base; smaller (2-3mm), less bristly species; head with or without a small membranous area at the anterior dorsal margin; 2-4 tergites on female abdomen before anal segment ..... Basilia (p.26)

#### Genus Nycteribia Latreille

An Old World genus of about 25 species, 23 of which are in the nominate subgenus, while the other two are in the subgenus *Acrocholidia* Kolenati. The subgenus *Nycteribia* may be divided into three groups: the European fauna consisting of three closely related species of the *pedicularia*-group and one of the *schmidlii*-group. The single British species belongs to the *pedicularia*-group which is distinguished in the female by the presence of three tergites before the conical anal segment and lateral sclerites of sternite 5 widely separated; in the male the claspers are straight or slightly curved (but without a distinct basal angle) and there is a row of spines at the straight or concave posterior margin of sternite 5.

2-2.5mm; 6-9 notopleural setae; tibiae 2.25 times as long as broad and with three rows of setae in the distal half of the ventral edge (fig. 28); male abdomen with surface of tergites 4-6 bare or with very few hairs, long hairs in marginal rows scattered across complete width of tergite 2-6 (fig. 32), sternite 5 with a row of 7-8 spines (occasionally more or less) in the middle of the posterior margin (fig. 33), claspers straight with slightly darkened tips, aedeagus (fig. 34) slender with subapical ventral tooth, phallobase conical without dorsal bulge; female tergite 2 as long or longer than width of tergite 1, strongly convex to pointed posteriorly with a median group of small hairs and 4-6 long marginal bristles; tergite 6 wide, bare on the surface and with 6-8 long marginal setae; sternites 3-7 with marginal rows of long setae (fig. 31), 5 and 6 divided medially, surface of sternites 3 and 4 covered in small hairs, sternites 5-7 only sparsely haired posteriorly, if at all; anal segment short; dorsal genital plate triangular, with 8-10 long setae ...... kolenatii Theodor & Moscona Common on Myotis daubentoni and also recorded from M. nattereri. Widespread. Western Europe to Czechoslovakia and Poland, as far north as Finland and south to the Pyrennees and N. Italy. A parasite of "tree bats", principally M. daubentoni, but also recorded from M. bechsteini, M. dasycneme, M. myotis, M. mystacinus, M. nattereri, Vespertilio murinus, Eptesicus serotinus, Pipistrellus pipistrellus, Plecotus auritus, Rhinolophus hipposideros.

#### Genus Phthiridium Hermann

A genus of over 30 species, divided into the biarticulatum-group from throughout the Old World and the small scissa-group from the Afrotropical region. The single British species is the only one known from the western Palaearctic. The biarticulatum-group is distinguished by having 3-8 setae on each side of the posterior margin of the sternal plate of the thorax and the notopleural setae reaching to half way between the base of the mesopleural suture and the anterior spiracle.

Formerly common on Rhinolophus hipposideros and the rarer R. ferrumequinum. Also recorded from Plecotus auritus and Pipistrellus pipistrellus. Mainly southwestern Britain, coinciding with the distribution of Rhinolophid bats. Central and southern Europe, N. Africa, S.W. Asia to Afghanistan and Kirgizia. On cave bats, principally Rhinolophids (R. ferrumequinum, hipposideros, euryale, mehelyi, blasii), but also recorded from a variety of vespertilionids (Myotis myotis, M. blythi, Miniopterus schreibersi, Pipistrellus pipistrellus, Plecotus auritus).

#### Genus Basilia Miranda Ribeiro

A genus of over 80 species in four subgenera. The single species recorded from Britain belongs to the nominate subgenus, identified by the presence of eyes (usually consisting of two incompletely separated lenses), all tibiae of equal shape and with 3-4 rows of setae in the distal half of the ventral edge, tergite 1 and sternite 1+2 of female less than half the length of the abdomen. The Basilia nattereri-group includes the British species and is distinguished in the females by the presence of three tergal plates before the anal segment, the third being undivided and wider than long.

Found three times on the rare Myotis bechsteini. Gloucestershire, Shropshire, and Wiltshire. (There is also a single specimen stated to be from a Pipistrellus pipistrellus from a cave in Kent, but since P. pipistrellus does not normally occur in caves the record must be questioned). Europe to the Middle East on "tree bats", principally M. bechsteini and M. nattereri; also from M. mystacinus, M. dasycneme, M. blythi, M. myotis, M. emarginatus, Rhinolophus ferrumequinum, Plecotus auritus, Miniopterus schreibersi.

#### Other species that may be found in Britain

Genus NYCTERIBIA Latreille. The N. pedicularia-group consists of pedicularia Latreille, latreilli Leach and kolenatii Theodor & Moscona. Either of the first two could easily be overlooked in Britain and any specimens from species other than M. daubentoni should be especially checked. The very small subgenus Acrocholidia Kolenati includes one European species: N.(A.) vexata Westwood. It is recorded widely in continental Europe, North Africa and the Middle East, mainly on Mouse-eared bats (Myotis myotis and M. blythi), but has also been recorded from other vespertilionids and Rhinolophus species.

Genus PENICILLIDIA Kolenati. P. conspicua Speiser and P. dufouri (Westwood) are both recorded from many parts of continental Europe and North Africa. P. conspicua is found mainly on Miniopterus schreibersi, but has also been recorded from a variety of species of Rhinolophus, Nyctalus, Plecotus and Myotis. P. dufouri is found mainly on Mouse-eared bats (Myotis myotis and blythi) and M. schreibersi, but has also been taken from species of Plecotus, Nyctalus, Myotis and Rhinolophus. P. monoceros Speiser is a poorly known species related very closely to P. dufouri. It is recorded from central and northern Europe and the U.S.S.R. from Myotis daubentoni, M. nattereri, Plecotus auritus, Vespertilio murinus and Eptesicus nilssoni.

## Field key to the recorded British species

As previously stated the descriptive keys given above are designed to ensure that any additional species that may be found in Britain are not overlooked. However, mammalogists, parasitologists or others may feel the need for a short "field" key to the known British species. This is presented below, but workers must not forget the possibility of other species occurring in Britain: 19 species of bat have been recorded in Britain and only three species of nycteribiid, whereas there are 12 species of nycteribiid recorded from the 30 or so European species of bat.

1 A pair of strong claspers at the end of the underside of the abdomen, which ends simply without Abdomen without claspers and ending in a pair of apical lobes (females) .......... 4 2 Tibiae almost semicircular (about 2.5 times as long as broad); claspers straight; group of spines on underside near apex of abdomen consisting of about 6-8 spines; on Myotis 3 Claspers curved; group of 6-8 spines on underside near apex of abdomen; on Myotis bechsteini ..... Basilia nana Claspers straight; group of about 40 spines on underside near apex of abdomen; on Rhinolophus ...... Phthiridium biarticulatum Apical lobes of abdomen about four times as long as broad; on Rhinolophus ...... ..... Phthiridium biarticulatum 

- 5 Tibiae almost semicircular (about 2.5 times as long as broad); middle part of dorsum of abdomen without a tergal plate; on Myotis daubentoni ......... Nycteribia kolenatii
- Tibiae more elongate (about 3.5 times as long as broad); middle of dorsum of abdomen covered with a large tergal plate; on Myotis bechsteini
   Basilia nana

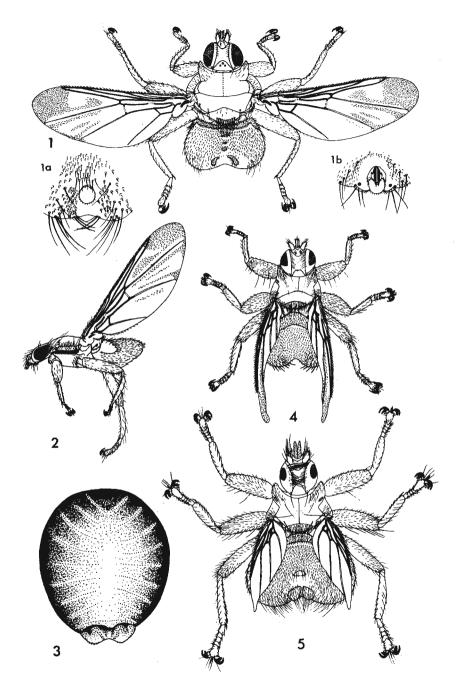
#### References

- AELLEN, V. 1963. Les Nycteribiides de la Suisse, Dipteres parasites de Chauve-souris. Bull. Soc. neuchatel. Sci. nat. 86: 143-154.
- ASKEW, R.R. 1971. Parasitic Insects. Heinemann, London. 316pp.
- AUSTEN, E.E. 1906. Diptera (Flies) in Page, W. (ed.). Victoria History of the County of Devon. Vol. 1. 630pp.
- BAKER, J.R. 1967. A review of the role played by the Hippoboscidae (Diptera) as vectors of endoparasites. *J. Parasit.* 53: 412-418.
- \_\_\_\_\_1975. Epizootiology of some haematozoic protozoa of English birds. *J. nat. Hist.* 9: 601-609.
- BEQUAERT, J.C. 1939. Notes on Hippoboscidae. 13. A second revision of the Hippoboscinae. *Psyche. Camb.* 46: 70-90.
- \_\_\_\_\_1953-57. The Hippoboscidae or Louse-flies (Diptera) of mammals and birds. Part I. Structure, physiology and natural history. Part II. Taxonomy, evolution and revision of American genera and species. *Entomologica am.* 32(1953): 1-209, 33(1953): 211-442, 34(1954): 1-232, 35(1955): 233-416, 36(1957): 417-611.
- BLACKWELL, M. 1980. Incidence, host specificity, distribution, and morphological variation in *Arthrorhynchus nycteribiae* and *A.eucampsipodae* (Laboulbeniomycetes). *Mycologia* 72: 143-158.
- COLYER, C.N. & HAMMOND, C.O. 1964. Flies of the British Isles. Warne, London/New York. 384 pp.
- CORBET G.B. 1956. The life-history and host relations of a hippoboscid fly *Ornithomyia fringillina* Curtis. *J. anim. Ecol.* **25:** 403-420.
- \_\_\_\_\_\_1978. Mammals of the Palaearctic Region: a taxonomic review. British Museum (Natural History), London. 314pp.
- EDWARDS, F.W., OLDROYD, H. & SMART, J. 1939. *British Blood-sucking Flies*. British Museum (Natural History), London. 156pp + 45pl.
- EVANS, G.O. 1950. Studies on the bionomics of the sheep ked, *Melophagus ovinus* L., in West Wales. *Bull.ent. Res.* 40: 459-478.
- FAIN, A. 1965. A review of the family Epidermoptidae Trouessart parasitic on the skin of birds (Acarina: Sarcoptiformes). Verh. K. vlaam. Acad. Wet. Kl. Wet. 27: 1-176 (part 1), 1-144 (part 2.)
- FOWLER, J.A. & COHENS, S. 1983. A method for the quantitative collection of ectoparasites from birds. *Ringing & Migration 4*: 185-189.
- FUNAKOSHI, K. 1977. Ecological studies on the bat fly, *Penicillidia jenynsii* (Diptera: Nycteribiidae), infested on the Japanese Long-fingered Bat, with special reference to the adaptability to their host from the viewpoint of natural history. *Jap.J.Ecol.* 27: 125-140.
- GARNHAM, P.C.C. 1973. Polychromophilus species in insectivorous bats. Trans. R. Soc. trop. Med. Hyg. 67:2-3.
- GAUD, J. & ATYEO, W.T. 1982. The subfamilies of the Analgidae and Psoroptoididae (Acari: Analgoidea). *J. med. Ent.*, *Honolulu* 19: 299-305.
- GEORGE, R.S. 1981. Obituary Gordon Burnett Thompson, 1911-1979. (with bibliography). Entomologist's mon. Mag. 117: 87-96.
- GRAHAM, N.P.H. & TAYLOR, K.L. 1941. Observations on the bionomics of the Sheep Ked (Melophagus ovinus). *Pamph. Counc. scient. ind. Res. Aust.* 108: 5,7,9-26.
- GRIFFITHS, G.C.D.1972. The phylogenetic classification of Diptera Cyclorrhapha, with special reference to the structure of the male postabdomen. *Series Entomolgica*, vol. 8. Junk, Holland. 340pp.
- GRUNIN, K.J. & DOSZHANOV, T.N. 1974. Louse-fly Lipoptena doszhanovi Grunin, sp. n. (Diptera, Hippoboscidae), found on Passer hispaniolensis (Temm.) in Kazakhstan. Ent. Obozr. 53: 925-928.
- HACKMAN, W. 1979. Alglusflugans, Lipoptena cervi, invandringshistoria i Finland. Ent. Tidskr. 100: 208-210.

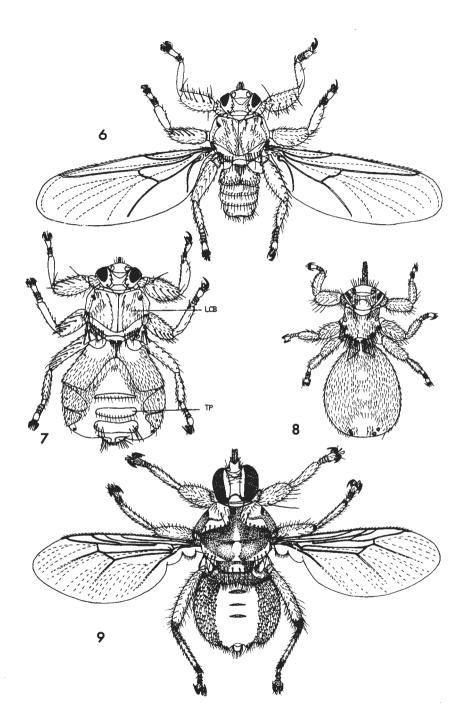
- HARE, J.E. 1953. Bionomics of *Lipoptena depressa* (Say), the common louse fly of deer in western North America (Diptera: Hippoboscidae). *Microentomology* 18: 37-57.
- HENNIG, W. 1973. 31 Ordnung Diptera (Zweiflugler). *Handb. Zool., Berl.* 4(2) 2/31: 1-337. HILL, D.S. 1962a. Revision of the British species of *Ornithomyia* Latreille (Diptera:
- Hippoboscidae). Proc. R. ent. Soc. Lond. (B) 31: 11-18.
- \_\_\_\_\_1962b. A study of the distribution and host preferences of three species of *Ornithomyia* (Diptera: Hippoboscidae) in the British Isles. *Proc. R. ent. Soc. Lond. (A)* 37: 37-48.
- \_\_\_\_\_1963. The life history of the British species of *Ornithomya* (Diptera: Hippoboscidae). Trans. R. ent. Soc. Lond. 115: 391-407.
- \_\_\_\_\_,WILSON, N. & CORBET, G.B. 1967. Mites associated with the British species of Ornithomya (Diptera: Hippoboscidae). J. med. Ent., Honolulu 4: 102-122.
- HILL, J.E. & SMITH, J.D. (in press). *Bats: a natural history*. British Museum (Natural History), London/Texas University press, Texas.
- HUMPHRIES, D.A. 1959. Caves and bats. J. King's Coll. nat. Hist. Soc. Newcastle 1: 18-21. HURKA, K. 1964. Distribution, bionomy and ecology of the European Bat flies with special regard to the Czechoslovak fauna (Dip., Nycteribiidae). Acta Univ. Carol., Biologica 1964: 167-234.
- HUTSON, A.M. 1971. New species of the *Ornithomya biloba*-group and records of other Hippoboscidae (Diptera) from Africa. J. Ent. (B) 40: 139-148.
- \_\_\_\_\_\_1978. Associations with vertebrates, their nests, roosts and burrows. Pp. 143-151 in Stubbs, A.E. & Chandler, P.J. (eds). A Dipterist's Handbook. Amateur Entomologist 15: 1-255. \_\_\_\_\_\_1981a. The population of the louse-fly, Crataerina pallida (Diptera, Hippoboscidae) on the European Swift, Apus apus (Aves, Apodidae). J. Zool., Lond. 194: 305-316.
- \_\_\_\_\_\_1981b. A new species of the *Ornithomya biloba*-group (Dipt., Hippoboscidae) from Crag Martin (*Ptyonoprogne rupestris*) (Aves, Hirundinidae). *Mitt. schweiz. ent. Ges.* 54: 157-162.
- KENNEDY, J.A., SMITH, J.R. & SMYTH, M. 1975. Diapause in *Ornithomya biloba* Dufour (Diptera: Hippoboscidae) parasitic on Fairy Martins in South Australia. *J. parasit.* 61: 369-372.
- KIERANS, J.E. 1975. A review of the phoretic relationship between Mallophaga (Phthiraptera: Insecta) and Hippoboscidae (Diptera: Insecta). *J. med. Ent., Honolulu* 12: 71-76.
- MAA, T.C. 1963. Genera and species of Hippoboscidae (Diptera): types, synonymy, habitats and natural groupings. *Pacif. Insects Monogr.* 6: 1-186.
- \_\_\_\_\_\_1964. On the genus *Ornithomya* Latreille from Africa (Diptera: Hippoboscidae). *J. med.* Ent., Honolulu 1: 197-205.
- \_\_\_\_\_\_1965. A synopsis of the Lipopteninae (Diptera: Hippoboscidae). *J. med. Ent., Honolulu* 2: 233-248.
- \_\_\_\_\_1966. Studies in Hippoboscidae (Diptera). Pacif. Insects Monogr. 10: 1-148.
- 1969. Studies in Hippoboscidae (Diptera). Part 2. Pacif. Insects Monogr. 20: 1-312.
- MACLEOD, J. 1948. The distribution and dynamics of Ked populations *Melophagus ovinus* Linn. *Parasitology, Cambridge* **39:** 61-68.
- MARSHALL, A.G. 1970. The life cycle of *Basilia hispida* Theodor 1967 (Diptera: Nycteribiidae) in Malaysia. *Parasitology, Cambridge* 61: 1-18.
- \_\_\_\_\_\_1981. The ecology of ectoparasitic insects. Academic Press, London/New York. 459pp. MCALPINE, J.F. et al. (eds) 1981. Manual of Nearctic Diptera. vol. 1. Research Branch Agriculture Canada, Monograph 27: 1-674.
- NELSON, G.S. 1963 Dipetalonema dracunculoides (Cobbold, 1870), from the dog in Kenya: with notes on its development in the louse-fly, Hippobosca longipennis. J. Helminth. 37: 235-240.
- OLDROYD, H. 1964. *The natural history of flies*. Weidenfeld & Nicholson, London. 324pp. PEIRCE, M.A. 1981. Distribution and host-parasite check-list of the haematozoa of birds in Western Europe. *J. nat. Hist.* 15: 419-458.
- POLLOCK, J.N. 1971. Origin of the tsetse flies: a new theory. J. Ent. (B) 40: 101-109.
- POPOV, A.V. 1965. The life cycle of the louse flies *Lipoptena cervi* L. and *Stenepteryz hirundinis* L. (Diptera, Hippoboscidae). *Ent. Obozr.* 44: 573-583.
- ROBERTS, J.I. 1925. On the bionomics of *Hippobosca equina*. *Ann. trop. Med. Parasit.* **19:** 81-90. ROHDENDORF, B.B. 1964. Historical development of Diptera. *Trudy paleont*. *Inst.* **100:** 1-311 [in Russian: English translation by Moore & Thiele, published Alberta 1974, 360pp].
- ROTHSCHILD, M. & CLAY, T. 1952. Fleas, Flukes and Cuckoos: a study of bird parasites. Collins, London. 305pp.
- RYBERG, O. 1947. Studies of bats and bat parasites. Stockholm. 319pp.

- SCHLEIN, Y. 1967. Postmetamorphic growth in *Lipoptena capreoli* Rondani (Hippoboscidae) and other insects. *Israel J. Zool.* 16: 69-82.
- 1970. A comparative study of the thoracic skeleton and musculature of the Pupipara and the Glossinidae (Diptera). Parasitology, Cambridge 60: 327-373.
- SCHOBER, W. (in press). The world of bats. Croom Helm, Kent.
- SCHULZ, H. 1938. Über fortpflanzung und vorkommen von fledermausfliegen (fam. Nycteribiidae Diptera Pupipara). Z. Parasitenk. Jena 10: 297-328.
- SMITH, F.G.A.M. 1957. Siphonaptera. Handbk Ident. Br. Insects 1(16): 1-94.
- STEBBINGS, R.E. 1977. Order Chiroptera; Bats. pp. 68-128 in Corbet, G.B. & Southern, H.N. *The Handbook of British Mammals*. Blackwell, Oxford. 520pp.
- <u>& JEFFERIES, C.J. 1982. Focus on Bats.</u> Nature Conservancy Council, London. 16pp. STEINHAUS, E.A. (ed.) 1963. *Insect pathology, an advanced treatise.* 1: London. 661pp.
- STEPHEN, A.C. 1953. Magnificent Frigate-bird in Scotland. Scott. Nat. 65: 193-194. (see also editorial note, p. 156)
- SUMMERS, R.W. 1975. On the ecology of *Crataerina hirundinis* (Diptera: Hippoboscidae) in Scotland. *J. Zool.*, *Lond.* 175: 557-570.
- \_\_\_\_\_ 1978. A record of Crataerina hirundinis (L.) (Dipt., Hippoboscidae) from Morocco. Entomologist's mon. Mag. 114: 174.
- TARSHIS, I.B. 1958. New data on the biology of Stilbometopa impressa (Bigot) and Lynchia hirsuta Ferris (Diptera, Hippoboscidae). Ann. ent. Soc. Am. 51: 95-105.
- TETLEY, J.H. 1958. The Sheep Ked. *Melophagus ovinus* L. I. Dissemination potential *Parasitology, Cambridge* **48:** 353-363. II. Keds acquired by a lamb from its mother. *Ibid.*: 364-374.
- THEODOR, O. 1954. Nycteribiidae. Fliegen palaearkt. Reg. 66a: 1-44
- \_\_\_\_\_\_1967. An illustrated catalogue of the Rothschild Collection of Nycteribiidae (Diptera) in the British Museum (Natural History). British Museum (Natural History), London. 506pp. \_\_\_\_\_\_ 1975. Diptera Pupipara. Fauna Palestina Insecta 1: 1-169.
- & OLDROYD, H. 1964. Hippoboscidae. Fliegen palaearkt. Reg. 65: 1-70.
- THOMPSON, G.B. 1953. Contributions toward a study of the ectoparasites of British birds and mammals. no. 1. Ann. Mag. nat. Hist. (12) 6: 401-425.
- \_\_\_\_\_\_1955a. Contributions toward a study of the ectoparasites of British birds and mammals. \_\_ no. 4. *Ibid.* (12) 8: 25-35.
- \_\_\_\_\_\_1955b. Contributions toward a study of the ectoparasites of British birds and mammals.

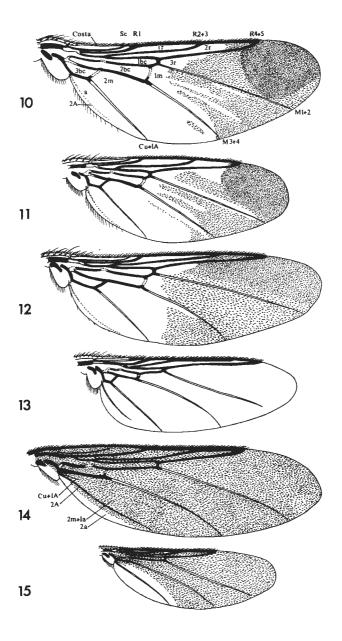
   no. 5. *Ibid.* (12) **8**; 724-730.
- 1968. Ornithophila metallica (Schiner) (Diptera: Hippoboscidae) a species of flatfly new to the British list. Bardsey Observatory Report (for 1967): 46-47.
- \_\_\_\_\_ 1969. Deer Keds: notes and records. Deer 1: 317.
- 1972. An annotated bibliography of the British Nycteribiidae. Angew. Parasit. 13: 106-113.
- \_\_\_\_\_\_1974. The parasites of British birds and mammals. 45. 1. The woodpigeon (Columba palumbus L.) as an important host of Ornithomya avicularia (L.) (Diptera Hippoboscidae). 2. The correct name of the Lynchia (Diptera Hippoboscidae) added to the British list in 1956. Entomologist's mon. Mag. 109: 211-213.
- URICH, F.W., SCOTT, H. & WATERSTON, J. 1922. Note on the Dipterous Bat-parasite *Cyclopodia greeffi* Karsch, and on a new species of Hymenopterous (Chalcid) parasite bred from it. *Proc. zool. Soc. Lond.* 1922: 471-477.
- WAAGE J.K., 1979. The evolution of insect vertebrate associations. *Biol. J. Linn. Soc.* 12: 187-224. WALLACE, F.G. 1966. The Trypanosomatid parasites of insects and arachnids. *Expl. Parasit.* 18: 124-193.
- WIMSATT, W.A. (ed.) 1970-77. Biology of bats. New York & London. vol. 1 (1970), 406pp.; Vol. 2 (1970), 477pp.; Vol. 3 (1977), 651pp.
- YALDEN, D.W. & MORRIS, P.A. 1975. The lives of bats. David & Charles, Devon. 207pp.



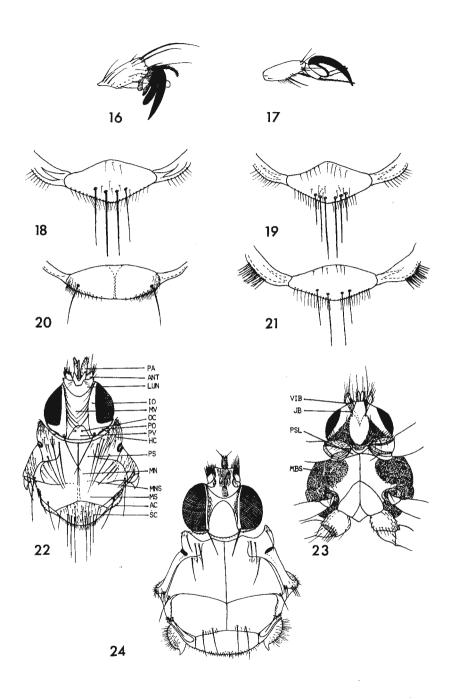
Figs 1-5. 1, Ornithomya avicularia  $\circ$ , dorsal (1a, apico-ventral area of  $\circ$  abdomen; 1b, apico-ventral area of  $\circ$  abdomen). 2, same, lateral. 3, same, pupa. 4, Crataerina hirundinis  $\circ$ . 5, C. pallida  $\circ$ .



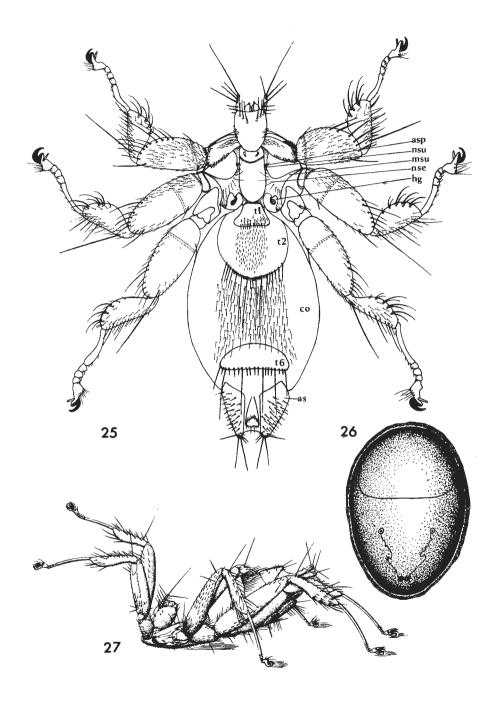
Figs 6-9. 6, Lipoptena cervi  $\, \circ \,$  alate. 7, same, dealate. 8, Melophagus ovinus  $\, \circ \,$  . 9, Hippobosca equina  $\, \circ \,$  .



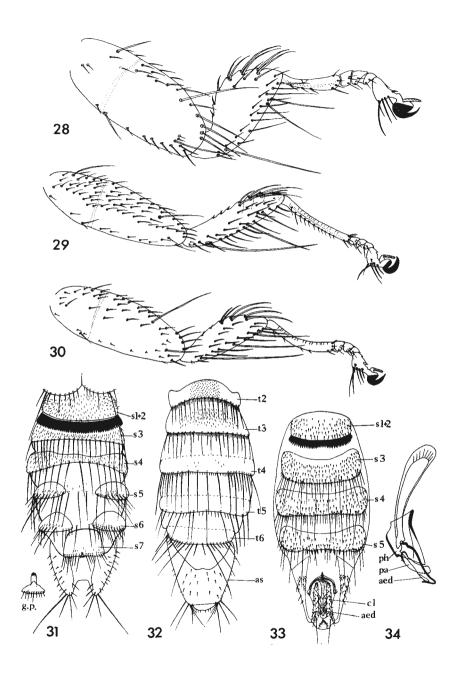
Figs 10-15. Wings. 10, Ornithomya chloropus. 11. O. fringillina. 12. O. biloba. 13, Ornithophila metallica. 14, Icosta ardeae. 15. I. minor.



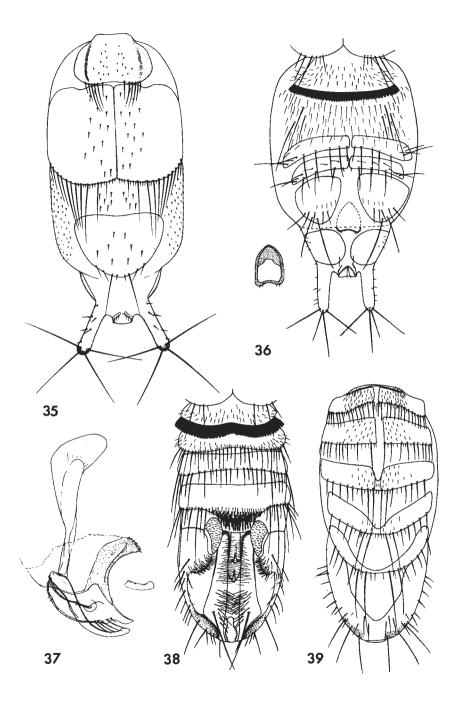
Figs 16-24. 16-17, hind claws. 16, Ornithomya avicularia. 17, Lipoptena cervi. 18-21, scutellum. 18, O. fringillina. 19, O. chloropus. 20, Icosta ardeae. 21, Ornithoctona laticornis. 22-24, head and thorax. 22, O. biloba, dorsal. 23, O. chloropus, ventral. 24, Olfersia fumipennis, dorsal.



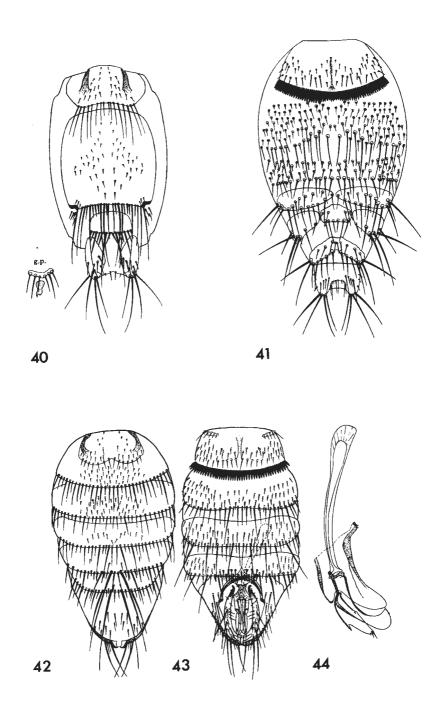
Figs 25-27. 25-26, Nycteribia kolenatii. 25, adult Q, dorsal. 26, puparium. 27, Phthiridium biarticulatum Q, lateral.



Figs 28-34. 28-30, forelegs. 28, Nycteribia kolenatii  $\circ$  . 29, Phthiridium biarticulatum  $\circ$  . 30, Basilia nana  $\circ$  . 31-34, N. kolenatii. 31,  $\circ$  abdomen, ventral. 32,  $\circ$  abdomen, dorsal, 33,  $\circ$  abdomen, ventral. 34,  $\circ$  genitalia.



Figs 35-39. Phthiridium biarticulatum. 35,  $\circ$  abdomen, dorsal. 36,  $\circ$  abdomen, ventral. 37,  $\circ$  genitalia. 38,  $\circ$  abdomen, ventral. 39,  $\circ$  abdomen, dorsal.



Figs 40-44, Basilia nana. 40,  $\circ$  abdomen, dorsal. 41,  $\circ$  abdomen, ventral. 42,  $\circ$  abdomen, dorsal. 43,  $\circ$  abdomen, ventral. 44,  $\circ$  genitalia.

# Index

Principal references are in bold. Synonyms are in italics. Hosts etc. are indexed under both scientific (generic only) and vernacular names.

Accipitriformes 16	deer 8, 9, 19, 20
Acrocholidia 25, 27	Fallow 9, 10, 19
Analgidae 12	Red 9, 10, 11, 19
Anseriformes 16	Roe 9, 10, 11, 19
Anthus 17	Sika 19
Apus 9, 16, 17	Delichon 9, 16
Ardea 17	Dibrachys 12
ardeae (lcosta) 13, 17	Dipetalonema 12
Ardmoeca 13	dog 19
Arthrorhynchus 23	dufouri (Penicillidia) 22, 23, 27
avicularia (Ornithomya) 8-13, 15, 16, 17, 20	dulouii (Felikciiidia) 22, 23, 27
avicularia (Orintholliya) 6-13, 13, 16, 17, 20	Emberizidae 16
Bacteria 12	Epidermoptidae 12
Badger 19	Eptesicus 23, 25, 27
Barbastella 23	equina (Hippobosca) 9, 13, 18, 20
Basilia 21-25, 26, 27-28	equina (Hippodosca) 9, 13, 16, 20
	falainalli (Iaasta) 12
Bat, Bechstein's 21 Daubenton's 21, 22	falcinelli (Icosta) 13
Greater Horseshoe 21	Falconiformes 16, 18
	Fregata 7, 18
Lesser Horseshoe 21	Frigate Bird 7, 18
Long-eared 21	Fringillidae 16
biarticulatum (Phthiridium) 21-24, 26, 27	fringillina (Ornithomya) 9-11, 13, 15, 16, 20
biloba (Ornithomya) 8, 9, 13, 15, 16, 20	fumipennis (Olfersia) 7, 18
blasiii (Nycteribia) 23 Botaurus 17	fungi 12, 23
Brueelia 12	Callifornes 16
Buteo 11	Galliformes 16
Buteo 11	garzettae (Pseudolynchia) 18
congrigação (Degudolymphia) 17, 19	gestroi (Ornithophila) 15
canariensis (Pseudolynchia) 17, 18	Glossinidae 3, 4 Greenfinch 9
Capra 19 capreoli (Lipoptena) 19	Grouse 12
Capreolus 9, 19	Gruiformes 16
	Grantornies 10
Caprimulgiformes 16, 18 Carduelis 9, 16	Harmahana 12
carnivore 7, 18	Haemabora 13
cattle 8, 9, 11, 19	Haemasporina 12,
	Haemoproteus 12
Celeripes 24	hermanni (Phthiridium) 24
cervi (Lipoptena) 9, 13, 19, 20 Cervus 9, 19	Hippobosca 8-14, 18, 20
Chalcididae 23	Hippoboscinae 13
Charadriiformes 16	hirundine 9, 12
	hirundinis (Crataerina) 9-13, 16, 20
chloropus (Ornithomya) 10-13, 15, 16, 20 Ciconiiformes 16	Hirundo 9, 16
Columba 12	horse 7, 9, 11, 19, 20
Columbiformes 16, 18	Loosta 13 15 17
	Icosta 13, 15, 17
conspicua (Penicillidia) 22, 23, 27 corvid 12	italica (Basilia) 23
	Ixobrychus 17
Crataerina 7-13, 15, 16, 20 Crex 17	kirhyanum (Cratagrins) 12
Cuculiformes 16	kirbyanum (Crataerina) 13
	kolenatti (Nycteribia) 21-23, 25, 27-28
Cyclopodia 23	

lagopodis (Ornithomya) 13 Lagopus 12 laticornis (Ornithoctona) 17 latreilli (Nycteribia) 22, 23, 27 Leiothrix 15 lemur 7, 8 lice 6, 10, 12 Lipoptena 8-11, 13-15, 19, 20 Lipopteninae 13 longipennis (Hippobosca) 12 Lynchia 13

man 9, 19
Martin, House 9, 11, 20
Sand 9
Melophagus 4, 8-13, 15, 19, 20
metallica (Ornithophila) 13, 14, 15
Microlichus 12
Minopterus 26, 27
minor (Icosta) 13, 17
mites 6, 10, 12, 23
monoceros (Penicillidia) 22, 23, 27
Motacillidae 16
Muscicapidae 16
Myialges 12
Myophthiria 7
Myotis 21-23, 25-28

nana (Basilia) 21-24, **26**, 27-28 Nasonia 12 nattereri (Basilia) 22-24, 26 Neolipoptena 8 Nyctalus 23, 27 Nycteribia 21-23, **25**, 27-28

Olfersia 7, 13, 15, 18
Ornithobia 13
Ornithoctona 15, 17
Ornithoica 14, 15
Ornithomya 7-13, 15, 17, 20
Ornithomyiinae 8, 13
Ornithophila 13, 14, 15
Ornithoponus 13
Osprey 7, 18
Ostrich 8
ovinus (Melophagus) 4, 8, 9, 12, 13, 19, 20
Oxypterum 13

pallida (Crataerina) 9-13, 17, 20 pallida (Lipoptena) 13 pallipes (Lipoptena) 13 Pandion 7, 18 Passer 16, 19 Passeriformes 16, 17, 20 pedicularia (Nycteribia) 22, 23, 25, 27 Penicillidia 21-23, 25, 27 Phthiridium 21-25, **26**, 27 Piciformes 16 Pipistrellus 23, 25, 26, 27 Plecotus, 21, 23, 25, 26, 27 Polychromophilus 23 Procapra 19 Prunellidae 16 Pseudolynchia 15, 17 Pseudoscorpion 12 Psittacula 15 Pteromalidae 12

Rangifera 19 Rheindeer 19 Rhinolophus 21, 22, 25, 26, 27 Rickettsiae 12, 23 Riparia 9, 16 rufipes (Hippobosca) 18 Rupicapra 19

schmidlii (Nycteribia) 22, 23, 25 scissa (Phthiridium) 26 sheep 5, 9-12, 19, 20 spinifera (Olfersia) 7, 13, 18 Stenepteryx 13 Streblidae 3, 4 Strelkoviacarus 12 Strigiformes 16, 18 Sturnidoecus 12 Sturnus 12, 16 Stylidia 24 Swallow 9, 15, 16 Swift 7, 9, 11, 12, 20 Sylvia 14, 15

thrips 12 trypanosome 10, 12 turdi (Ornithoica) 15 Turdidae 16 Turdus 8, 12, 16

Verspertilio 23, 25, 27 vespertilionis (Phthiridium) 24 vexata (Nycteribia) 22, 23, 27 viridis (Ornithomya) 13 viridula (Ornithomya) 13

wallaby 7, 8 Whitethroat 14 Woodpigeon 12

