A DIPTEROLOGICAL PERSPECTIVE ON THE HOLOCENE HISTORY OF THE NORTH ATLANTIC AREA

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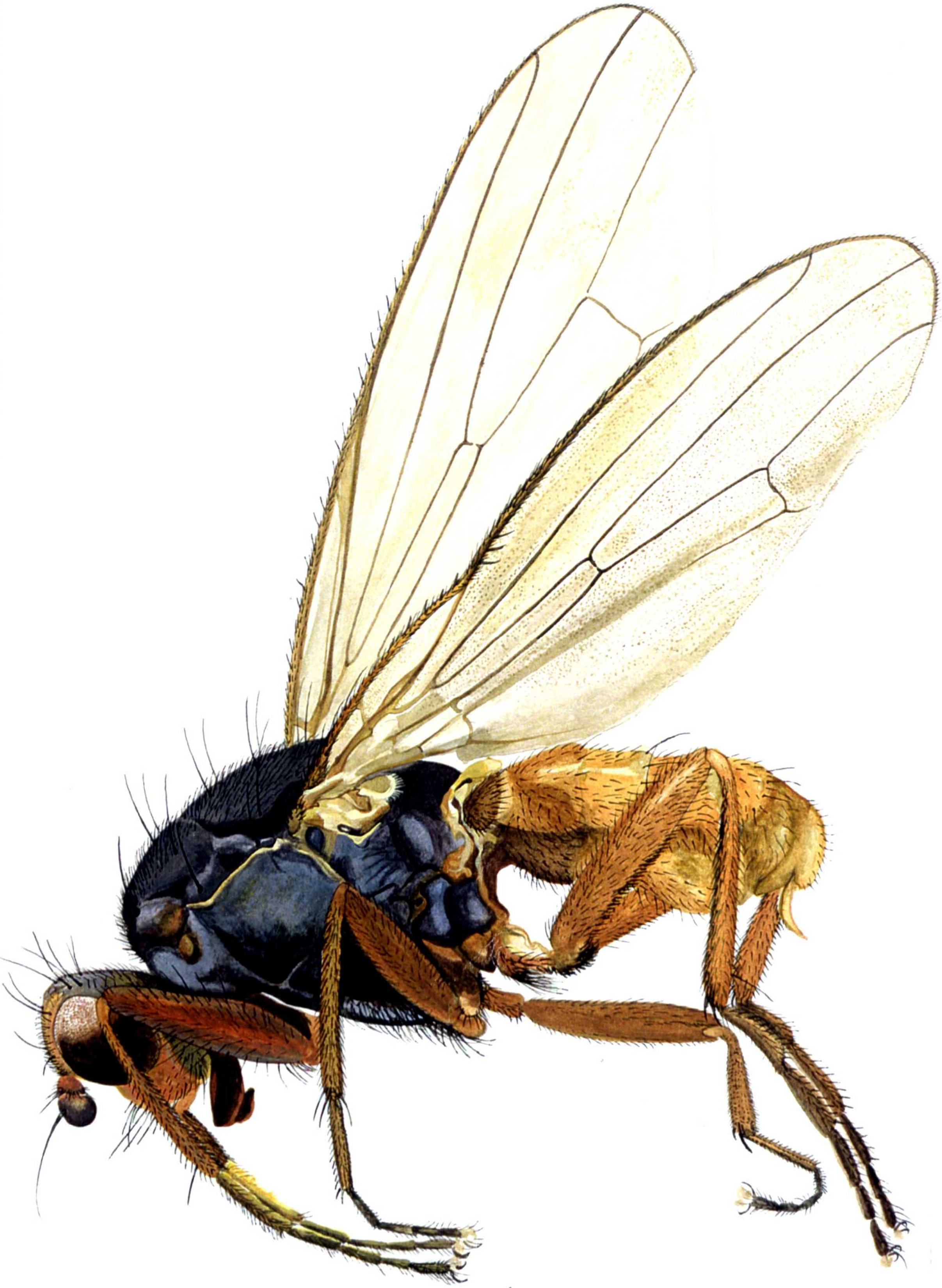

Frontispiece

"The Viking House-fly" Heleomyza serrata (Linnaeus), male.

A DIPTEROLOGICAL PERSPECTIVE ON THE HOLOCENE HISTORY OF THE NORTH ATLANTIC AREA

SUMMARY

Whilst a copious literature testifies to the value of subfossil insect analyses in the interpretation of Holocene deposits (Buckland and Coope, 1991; Elias, 1994), most of this results from studies of Coleopterous material. Although Dipterous fragments are often abundant in the same deposits, they have received little attention. This Thesis is concerned primarily with establishing the great value of Dipterous subfossils and the potential for advances in this field.

Dipterous morphology is considered and features of primary value in the identification of subfossil material are highlighted. Problems with the traditional taxonomic criteria, insofar as identification of such material is concerned, are discussed, and new approaches are recommended. Thus, a brief survey of the morphology of Tipuloid larval head-capsules, and a revisional paper on the puparia of British Sphaeroceridae, are included.

The study includes many case-studies from excavations across the region, spanning the last 5,000 years. Although there is an inevitable bias in favour of archaeological sites, and hence of the more synanthropic elements of the Dipterous fauna, situations unassociated with human settlements are also discussed.

A major objective in this work was to examine the role of Diptera in the insect colonisation of lands left in a state of *tabula rasa* by receding glaciations. The geographical area concerned here comprises the entire North Atlantic continental seaboard and islands from France and Labrador northwards. This area saw the major western expansion of the Celts, Romans and the Vikings, from whose settlements much of the Dipterous material from archaeological deposits was obtained for this Thesis. It also saw the eastern migration of Inuit cultures from the Canadian Arctic into Greenland. Dipterous subfossils tell us much of the living conditions and economies of these peoples.

In zoogeographical terms the Nearctic and Palaearctic meet in the western Atlantic, and a discussion on the Greenlandic Muscid fauna wholly endorses the traditional American view that Greenland's fauna is of Nearctic origin. The area considered here also includes a large proportion of the global Arctic landmass, a study of which must aid in understanding early post-glacial environments.

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ACKNOWLEDGEMENTS

This work would not have been undertaken were it not for the initial involvement with Dr. P. C. Buckland in the study of insect subfossils, and his continued enthusiasm, support and help over many years. It was he who first suggested that I carry out this programme of work and arranged for my registration as a PhD. student with the Department of Archaeology and Prehistory at Sheffield University. It was moreover through him that A. O. C. (Scotland) agreed to support the project financially, and that a steady stream of material from widely scattered excavations came to me. It is to Dr. Buckland and to the Sheffield University authorities that my main thanks are extended. There have however been a considerable number of other people to whom I acknowledge deep gratitude including D. Belshaw, Dr. J. Böcher, A. Brindle, J. Cole, Dr. M. Dinnin, Dr. R. H. L. Disney, Dr. Y. Z. Erzinçlioğlu, Dr. P. Ferrar, A. Godfrey, R. Godfrey, D. Henshaw, C. Johnson, Dr. H. A. Kenward, T. McGovern, I. MacGowan, B. Pitkin, A. C. Pont, Miss T. Roper, Dr. J. P. Sadler, K. G. V. Smith, A. E. Stubbs, Ms. N. Whitehouse and P. Wormell. Also to Mrs. J. Raffles, Librarian of the Royal Entomological Society of London.

1 HISTORICAL BACKGROUND

1a The History of Dipterology

The first scientist to distinguish the true flies from other insects on their possession of a single pair of wings was Aristotle, but it was not until the 17th century that any detailed studies were carried out on them. It was then that Jan Swammerdam (1637- 80), a pioneer microscopist, made a comparative study of the life histories of many insects, including several flies such as mosquitoes, soldier flies and Fanniids. Based on these, he proposed a natural classification of insects in his *Book of Nature*, an English translation of which was published in 1758.

Unquestionably the greatest pre-Linnaean researcher into the biology of Diptera was René Antoine Ferchault de Réaumur (1683-1757). He greatly advanced the researches initiated by Swammerdam, for in his best-known work, *Mémoires pour servir à l'histoire des Insectes* (publ. 1735-41), he describes the larvae and pupae of a large number of Diptera. He was keenly aware of ecology and was the pioneer student of insect faunas of ungulate dung, noting that different species inhabited different dung types. Such was the depth of his studies that almost two centuries passed before some of the species he examined were again noted in the literature (eg. larvae of *Rhingia campestris)*.

Although Linnaeus (1758) added little to the knowledge of biology, he laid the foundation for all future taxonomic work with his binomial system of nomenclature. In his *Systema Naturae*, he described about 200 species of Diptera from the region covered in the present study.

The huge advances made in Dipterology in the succeeding years were superbly reviewed by Westwood (1840). The leading Dipterous taxonomists of this period were Curtis, Dale, Degeer, Fabricius, Fallén, Haliday, Harris, Holmgren, Latreille, Macquart, Meigen, Müller, Panzer, Robineau-Desvoidy, Schrank, Scopoli, Stannius, Stephens and Wiedemann. Moses Harris was the first British author to pay particular attention to Diptera and he distinguished groups on wing-venational details. Latreille was best remembered for his understanding of the higher classification of Diptera, whilst the leading students of dipterous biology during this period were Bouché, Degeer and Dufour.

Although Réaumur and later authors described many Dipterous larvae and were able to publish much on their biology, studies in this order were greatly hampered by identification problems so that great uncertainty surrounds the true identity of the subjects of most early accounts. Already by the late nineteenth century a very large proportion of the currently known Diptera of the North Atlantic area had been described by the earlier taxonomists mentioned above, and later 19th century ones including Becker, Dziedzicki, Egger, Loew, Meade, Osten-Sacken, Pandellé, Rondani, Staeger, Stenhammar, Strobl, Verrall, von Roser, Walker, Winnertz, Zetterstedt and others. But such had been the eagerness in describing new species and difficulties in liaison between their authors, that many taxa were described under different names by different specialists. Synonymies remained undiscovered or unresolved, and these problems fell largely to more recent workers including Collin, Edwards, Frey, Goetghebuer, Hennig, Hendel, Kieffer, Lundbeck, Lundstroem, Mesnil, Michelsen, Pont, Thienemann and many others who studied and compared type material of earlier taxa, produced revisional papers and recognised numerous new species. Thanks to the labours of these workers, and especially in

Britain to C.N.Colyer and C.O.Hammond, who made the study of Diptera readily accessible to the public through the publication of their superb book, *The Flies of the British Isles*, the study of Diptera today is one of the most active areas of entomological research. Not only is this seen in taxonomic aspects of both adult and immature stages, but in the very detailed morphological research which is required in the cladistic studies upon which phylogenetic models depend (eg. Olafsson 1991, Roháček 1982-85, Speight 1969 etc.)

Periodically it is necessary for individuals to compile reviews of the contemporary state of the art similar to that of Westwood (1840). Insofar as the copious literature on the Dipterous immature stages is concerned, Hennig's *Die Larvenformen der Dipteren* (1952) provided a major landmark in assembling all data then available and producing the first keys and detailed account of the larvae of the entire order in a global context. Today we see through Ferrar (1987) and Smith (1989) that the advances made since Hennig's publication are comparable in magnitude to those of the previous 300 years.

As stated above, Linnaeus described about 200 regional species of Diptera. Verrall (1901) recognised 2884 British species, whilst Kloet and Hincks (1947) list 5219. In the second edition of the latter work, published in 1975 the number had risen to 6000, whilst about 250 have been added since in the pages of the journal *Antenna*.

Hand in hand with massive advances of both taxonomic and morphological aspects of Dipterology, there has also been a mushrooming of interest in the biology and ecology of Diptera. It would indeed be true to say that some of our best-understood insects, in all respects of their structure and ecological requirements etc., belong to the

Diptera. Furthermore, through the enthusiasm and dedication of the members of the Dipterist's Group in Britain, notably the pioneers of this movement, P.J.Chandler and A.E.Stubbs, our understanding is set to expand across the entire order as further individuals join the workforce.

1b The past use of subfossil Diptera in site evaluation

For the reasons explained above, the use of Dipterous subfossils in site evaluation has been very limited compared to that of Coleoptera. Only one Dipterous family has been extensively employed, and that mainly during the past 20 years; namely the Chironomidae. The larval head-capsules have been found to be of great value in limnological research since they can indicate changes in water quality in terms of natural or artificial pollutants or hydroseral progression. The utility of this family has been adequately discussed by Walker (1987) and others and is consequently not covered in this Thesis.

Apart from Chironomid studies, Diptera have very seldom appeared in any of the numerous papers on Quaternary palaeoentomological studies referred to by Buckland and Coope (1992) or Elias (1994), despite the occasional recognition of their potential (eg. Böcher and Fredskild 1993 etc.). Belshaw produced an excellent appraisal of Diptera as indicators of cess in archaeological sites (1989) but this paper is not readily accessible. Phipps (1983) gives preliminary notes on the preparation and identification of puparia from archaeological deposits.

1c Advantages and disadvantages of Dipterous evidence

At the outset 4 factors appeared to place Diptera at some disadvantage compared with Coleoptera in studies of subfossils, namely-

a Larger number of species. Over 6200 species of Diptera occur in

Britain compared with about 4000 Coleoptera.

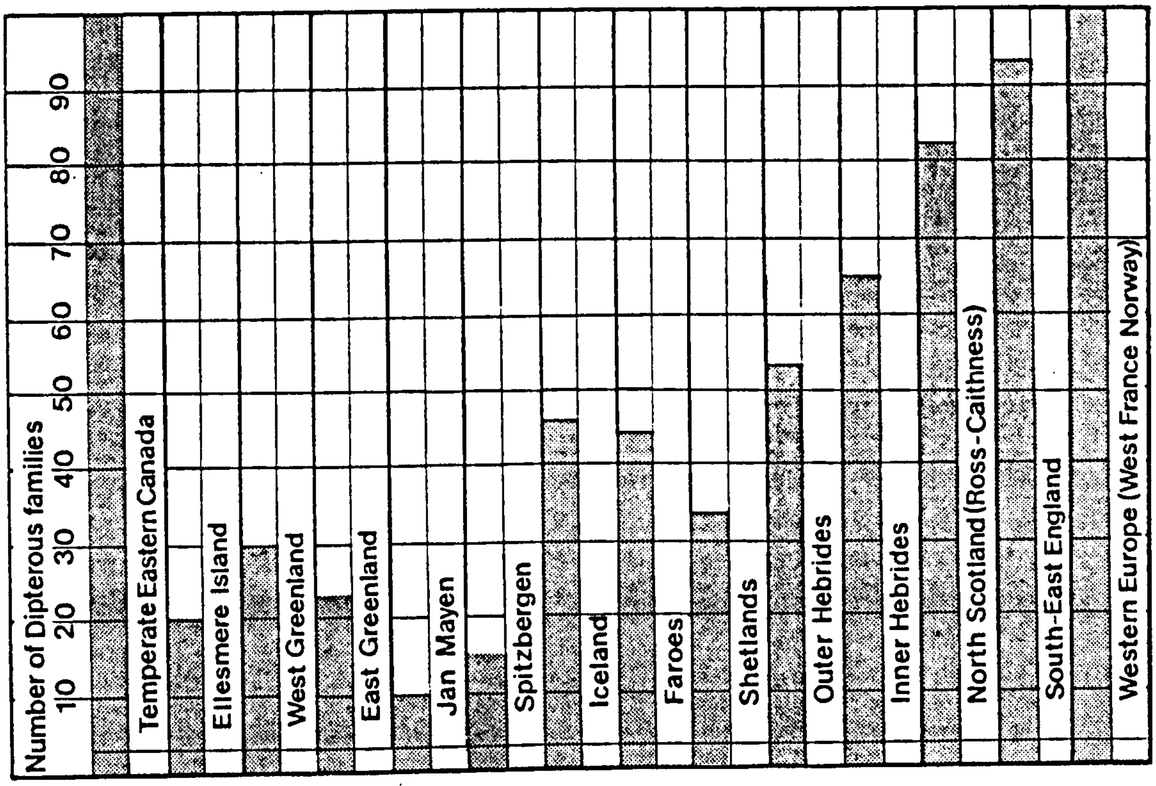
b **Higher dispersal capabilities in Diptera.** They form a major component of high altitude aerial plankton.

c **Poorer degree of sclerotisation in adults.**

d **Poorer state of knowledge of taxonomy, biology and ecology.**

In fact none of these factors posed any particular problems for the following reasons-

a **Numbers of species.** In palaeoecological work one invariably deals with a restricted fauna, whether due to a specialised habitat or to geographical location. Text-figure 1 shows that in the North Atlantic



Text-figure 1 The numbers of Dipterous families represented in various regions of the North Atlantic area, showing decrease with increasing latitude and isolation from continental land-masses.

region, a huge decrease in families occurs with greater isolation from continental land-masses and with increasing latitude. In a large family such as the Muscidae at most only about 10 per cent are likely to occur in association with man, and most of these in small numbers. Eusynanthropes account for less than one per cent of the British fauna.

b, c The question of higher dispersal powers and poorer sclerotisation of adults Diptera is largely irrelevant since the vast bulk of subfossil Dipterous material belongs to larval or pupal stages. In these stages dispersal powers are zero, or nearly so, and sclerotisation commonly equals that of the Coleoptera. In fact whilst the bulk of such Dipterous subfossil material is equally durable to the Coleopterous, it allows greater precision in stratum interpretation since the deposit in which the larval or pupal fragment is found is most likely that in which it developed. Adults may congregate far from their breeding locations (eg. hibernating *Pollenia*).

d **The state of knowledge.** This is a problem of decreasing significance, owing to great and sustained advances in Dipterological research alluded to earlier. Today many of our Dipterous families are better understood than most other insect groups in terms of taxonomy, biology, morphology and ecology.

1d Implications for Dipterology of Research in Subfossil Diptera

Despite the huge advances in Dipterology, the immature stages of many families are at best inadequately known. During this programme of work, it has been necessary to carry out original research into several families which are strongly represented in subfossil assemblages. One of these is the Sphaeroceridae, puparia of which often outnumber all others combined. The available literature proved to be totally inadequate for the identification of this material so after extensive research on modern and subfossil puparia, a revision of the puparia of British Sphaeroceridae was produced (Skidmore 1992). During 1994 a similar study was carried out on the larval head-capsules of the Tipuloidea which often also abound in subfossil assemblages. The literature again proved to be too meagre, so a survey of these structures in a wide range of final instar tipuloid larvae was carried out. A great diversity of form across the Tipuloidea was revealed and the results are incorporated into the section on Dipterous morphology.

A problem with identifying subfossil insect fragments lies in the great inadequacy of most taxonomic literature since this is of course directed towards the identification of complete, modern specimens. In practice, the characters used in such works are seldom present in the subfossil material, which is invariably fragmentary. With this in mind those parts which are most durable have been re-examined and differences have been highlighted which should help subsequent workers to identify their material. It is proposed to publish this section of the Thesis, with this objective in mind, at a later date.

The work undertaken in the present research programme has in fact very clearly demonstrated an unexpected bonus from an entomological point of view, in that work of this type can vastly advance our knowledge of the immature stages of Diptera. This arises from the frequent occurrence of unhatched pupae/puparia in which the adult male genitalia are intact and often remarkably well-preserved (text-figure 10). This facilitates the precise specific identification of species which are unknown, or incorrectly ascribed, in that developmental stage. Thus, the Sphaeroceridae predominating in the samples from Tuquoy were, for example, identified on male genitalic characters and it was possible to demonstrate unequivocally that published descriptions of some of these must have been based upon misidentifications. This discovery led to the revision of Sphaerocerid puparia alluded to above (Appendix 1).

The best work on the immature stages of Cyclorrhaphous Diptera is Ferrar (1987). His global treatment is most valuable, providing data from other continents which can be very useful in giving a clue to the possible biology and morphology of regional species whose immature stages are not known. Smith (1989) covers the entire order but is primarily concerned with the British fauna. Both give long lists of references for particular species or families and it is always wise to check these as they very often provide extremely useful additional morphological details.

In any palaeoecological work it is vital to have information on modern faunas of the area under study. This knowledge helps with identification by narrowing down the options. In a very restricted fauna, where a family may be represented by only a single species, identification to that family is likely to be adequate. Modern check-lists exist for most countries in the North Atlantic area and for Western Europe. It must always be appreciated however that species occurring as subfossils may have become extinct subsequently. In this way palaeoecological studies can assist in an understanding of past climates, and of environments which may have no modern counterpart (Elias 1994).

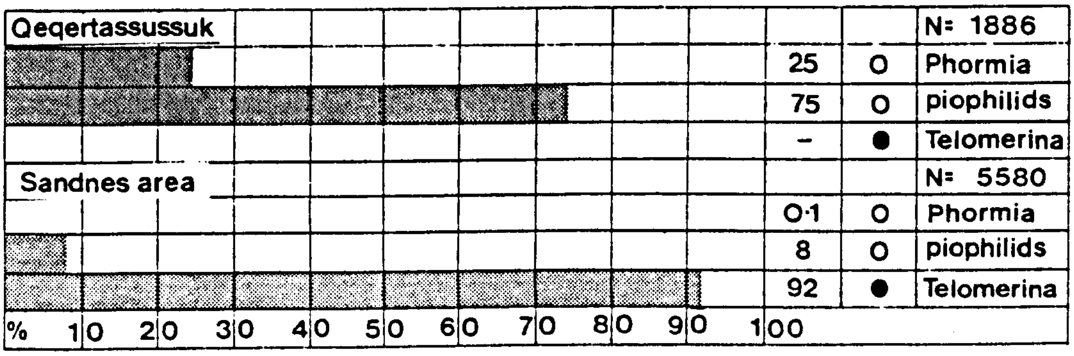
1e Archaeological Implications of Research in Subfossil Diptera

Diptera appear to be particularly useful as indicators of human life-styles. Three examples will suffice to demonstrate this.

The Buiston Crannog study revealed that the House fly (*Musca domestica*) was already abundant and evidently widespread in southern Scotland in early Medieval times. However it seems to have been absent from further north and appears not to have reached Iceland until perhaps the nineteenth century. Analyses of archaeological samples from many sites in England reveal that it was common throughout the country from Roman times. The ecological requirements of this fly, notably its marked thermophily and eusynanthropy, would seem to imply some social cause for its restricted range in Medieval Scotland. At Buiston Crannog it reached massive populations under optimum conditions, revealing much about the human living conditions prevailing there at the time.

An interesting aspect of the Leicester study was the implication of a traditional use of lime for controlling fly plagues emanating from cess pits and sewers. Here, as at Buiston Crannog and Bessastaðir, there was some reason to conjecture significant changes in human population levels and in their economic base over the long periods of time represented by the subfossil samples studied.

A long-standing problem regarding the Norse middens of the Western Settlement in West Greenland was the origin of "twig-layers", which had been interpreted as roof coverings. The abundance of puparia of the troglodytic necrophilous synanthrope *Telomerina flavipes*, combined with an absence of exophilic necrophages, indicated that the "twig-layers" could only be readily interpreted as discarded floor-coverings. The relative abundance of endophilous, and extreme scarcity of exophilous necrophages on these middens (text-figure 2) showed that the Norse settlers removed all meat and marrow from the bone before casting it onto the midden. In stark contrast a Palaeoeskimo midden at Qeqertasussuk in Disko Bay contained a preponderence of exophilic necrophages (text-figure 2). This disparity regarding meat-products between the two cultures is interpreted by Buckland *et al.* (in prep.) as a clear indication of the extreme vulnerability of the Greenlandic Norse culture to climatic instability, and their unwillingness to learn useful survival strategies from the Inuit with whom they certainly came into contact.



Text-figure 2 Occurrence of three species of necrophagous Diptera in two archaeological sites in West Greenland (Qeqertasussuk and Sandnes area). =heliophilous exophiles(ie. *Phormia* and Piophilids) =ombrophilous endophile (*Telomerina flavipes*). The two faunas are complimentary.

2 METHODOLOGY

Soil-samples from horizons exposed during excavation were first subjected to the paraffin-flotation method for isolation of invertebrate remains (Coope & Osborne 1968). The efficiency of this now standard method of extraction was found by Phipps (1986) to be remarkably high. Following removal of the Coleopterous content of this material, the residue, mainly comprising of Dipterous fragments, was passed to the writer. Initial sorting of this residue was carried out at low magnification (up to x 20) and from each sample specimens of all "apparent taxa", and any unidentifiable fragments, were mounted in Euparal on standard glass microslides. A file card was also prepared for each sample. Unmounted specimens were returned to spirit for later re-examination. Following completion of the initial sorting of all of the samples, the main identification work commenced. The "apparent taxa" were referred to the lowest possible taxonomic level (mostly familial or generic name), the unmounted specimens re-examined, identified and counted in terms of minimum number of specimens, and the file cards annotated accordingly. In the case of puparia, particular attention was paid to whether the adults had hatched or not. Such is the fragility of most adult Diptera, that subfossil material largely consists of immature stages. Fly puparia usually predominate in terrestrial deposits, and examples containing remains of unhatched adults provide vital confirmation of identifications based on external puparial features alone. The ratio of hatched to unhatched puparia provide a measure of the health of the fly population in that environment. For statistical purposes, the Minimum Number of

Individuals (MNI) have been estimated. With puparia, this means the number of "end-segments" present; these are easily recognised by their paired posterior spiracular plates. In the case of brachycerous pupae the MNI equals either the number of wing-sheaths, bearing in mind that a left and a right hand one may belong to a single pupa, or abdominal end-segments. In Nematocerous larval head-capsules, the MNI is based on the total number of identical specimens of the predominant size. Most Diptera remain unknown, or are inadequately described, in the immature stages, so identifications of immatures should be verified by adult characters wherever possible, using the most recent literature, and by reference to collections of mounted adults. It is usually possible to identify some taxa by correlating fragments of adults and immatures which would have been unrecognisable alone. Also, by relating overlapping fragments it is often possible to conceptually reconstruct pupae and adults of several taxa. The total mounted and unmounted material in all samples was re-examined several times as further details became apparent, and the file cards were continually updated. Ultimately the final taxonomic list was prepared and the interpretation completed by reference to the most recent available information. It is highly fortuitous that the study of the ecology and biology of the immature stages of Diptera is today one of the major growth areas in entomological research.

3 LIST OF SITES STUDIED

In the list below the sites are numbered and their approximate ages are given, along with numbers of taxa, MNI and totals for puparia. Detailed accounts appear on the pages indicated below, in section 5 (pages 146- 276), and analyses in Appendix 2 (pages 331- 400). The site locations can be found on the maps on pages 147, 207 and 238.

ENGLAND (Map I, p.147)	Taxa	MNI	Puparia	Page	App.2
1 Brigg Raft (Lincolnshire) [Bronze Age]	3	3	2	146	---
2 Catterick Camp (North Yorkshire) [Roman]	1	8	8	149	---
3 Leicester Causeway (Leicestershire) [Roman- Tudor]	25	c.1200	c.1200	149	331
4 Lindow Man II (Cheshire) [Late Iron Age-early Roman]	2	2	1	156	---
5 Lindow Man III (Cheshire) [Late Iron Age- early Roman]	10	193	-	156	345
6 London (Ministry) [?Medieval]	6	1585	1585	159	347
7 Newark Ditch (Nottinghamshire) [17th Century]	14	214	175	161	348
8 Owlesbury (Hampshire) [Roman]	3	33	33	162	---
9 Oxford St.Budoc's (Oxfordshire) [Saxon]	4	41	41	163	---
10 Plymouth Drain (Devon) [Medieval]	3	13	13	164	---
11 Rudston Well (East Yorkshire) [Roman]	18	97	43	165	348
12 Shirley Pool (South Yorkshire) [Post-medieval]	7	34	-	166	349
13 Southampton Pit (Hampshire) [Saxon]	2	19	19	167	---
14 Taunton (Somerset) [Medieval]	28	c.1100	c.1080	168	350
15 Thorne Moor Trackway (South Yorkshire) [Bronze Age]	15	58	12	170	351
16 Worcester Barrel (Worcestershire) [Medieval]	8	40	39	172	352
17 York, a [Roman sewer]	7	c.2150	26	173	---
b [?post-medieval]	3	94	94	173	---

WALES (Map 1, p.147)					
18 Hen Domen (Powys) [Medieval]	17	85	85	175	352
SCOTLAND (Map 1, p.147)	Taxa	MNI	Puparia	Page	App.2
19 Buiston Crannog (Strathclyde) [Dark Ages]	60+	1935	1833	177	352
20 Dun Vulan (South Uist) [Iron Age]	2	2	2	185	---
21 Loch Druidibeg (South Uist) [Post-medieval]	41	215	145	185	367
22 Loch Olabhat (North Uist) [Neolithic]	15	52	45	188	370
23 Papa Stour (Shetland) [Viking]	2	2	1	191	---
24 Pluscarden Priory (?Elgin) [Medieval]	8	436	434	192	370
25 Skara Brae (Orkney) [Late Neolithic]	10	28	17	194	371
26 South Loch Boisdale (South Uist) [Bronze Age]	13	153	13	197	371
27 Tuquoy (Orkney) [Viking]	c.56	11,197	11,050	199	372
ICELAND (Map 2, 207)					
28 Bessastadir [Medieval]	18	934	854	206	376
29 Einhyrningur [Pre-settlement]	1	2	-	214	---
30 Finnbógastadir [Medieval]	10	2136	2136	215	377
31 Gjögur [Medieval]	6	116	116	219	378
32 Holt [Medieval]	1	2	2	220	---
33 Ósabakki [Pre-settlement]	1	2	2	221	---
34 Papey [Medieval]	2	2	2	222	---
35 Reykholt [Post-medieval]	c.21	554	150	222	379
36 Stóraborg [Post-medieval]	35	1875	1770	229	381
GREENLAND (Map 3, p.238)					
37 Qeqertasussuk [Inuit (pre-contact)]	18	2194	2194	237	386

Western Settlement sites [Norse]-

38 Egulagialik (V,45)	5	64	63	241	388
39 Niáqussat (V,48)	27	2661	2645	244	389
40 Nipáatsoq (V 54)	10	1087	1084	250	393
41 Sandnes (Kilaersavik) (V 51)	33	1986	1900	256	394
42 Tumeralik (V 35)	9	1117	1112	275	401
43 Lake site (V 36)	1	1	1	276	401

Total Sites 43 Total MNI 35,722 Total puparia 31,027

4 DIPTEROLOGY

General Classification and Morphology

A detailed account of Dipterous morphology is outside the brief of this Thesis, there being adequate coverage in the Handbooks for the Identification of British Insects produced by the Royal Entomological Society of London. The accent here is on those features which are most relevant to subfossil material.

Diptera, like the other three major orders of Holometabolous insects, namely the Coleoptera, Hymenoptera and Lepidoptera, have a complete metamorphosis- egg, larva, pupa, adult. But adult Diptera, or True flies, differ from these in possessing a single pair of wings, the hind pair being reduced to form the halteres, or balancers. In this order there is an evolutionary decrease in the number of free larval instars. In the advanced Muscoid families Hippoboscidae, Streblidae and Nycteribiidae, all of which were formerly included in a separate suborder, the Pupipara, the entire larval life is spent in the parental oviduct.

In subfossil adult Diptera of course the specimens are hardly ever in a complete state. The most abundant fragments are of heads, thoraces and wings. Nevertheless it is often possible to identify these at least to familial level, as extreme diversity of structure occurs in all of these parts. The general structure of the head, including the shape of the compound eyes and presence or absence of ocelli, and of the sclerites making up the thorax and the sutures between them, exhibit a great range of variation throughout the order. A detailed Atlas figuring the range of forms in these structures across the entire order would be extremely valuable. The chaetotaxy of all external sclerotised areas is of such primary importance that it is often possible to identify a taxon from the bristle arrangement on a small fragment of a sclerite. It has to be appreciated that, whilst bristles and hairs are usually absent in subfossil material, the alveoli from whence these structures arose remain as clear apertures in the sclerite. Text-figure 7 shows parts of the head of a subfossil *Scathophaga* adult in which the alveoli of the bristles in the ocellar and orbital regions are clearly seen. The relative sizes of the setae can be estimated by the diameters of the alveoli. The wing-venation (text-figs. 3- 6) is also of paramount importance, often being characteristic of a particular family, genus or species. In *Lonchoptera* (text-fig. 3 and pl. 15) even the sexes differ. Not only do the arrangement of the wing veins offer valuable identification features, but also the distribution and strength of hairs on the veins and membrane. Often the wing bears a highly distinctive pattern of dark clouding (text-fig. 4; pl. 1, 6, 9 etc.).

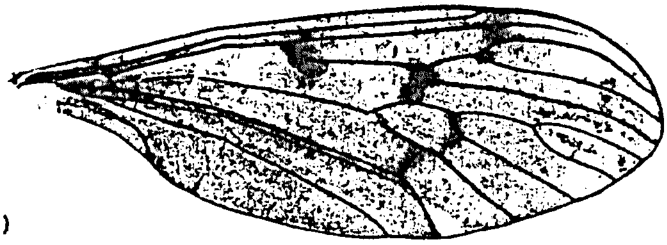
Text-figure 3 Wing of male *Lonchoptera lutea* Panzer (Length 3 mm.)

Of direct relevance to the identification of dipterous subfossils is the traditional division of the Order Diptera into two major groups, namely Nematocera/Brachycera and Cyclorrhapha. In terms of numbers of species, these are of almost equal size (Iceland- 165:207= 372; In UK-3021:2979= 6000).

NEMATOCERA and BRACHYCERA

In these groups one finds the greatest diversity of adult morphology. Whilst the head is usually spherical, in female Bibionidae it is much lengthened behind the eyes (pl. 10). The compound eyes are usually evenly rounded but in the Sciaridae, and many Chironomidae, they are narrowly extended across the frons to form an "eye-bridge" (pl. 9). Often they are anteriorly indented at the level of the antennal insertion as in the Simuliidae (pl. 7). In the males they are commonly holoptic (ie. joined on the frons), whilst in male Bibionidae they also have a conspicuous lateral division between the larger upper facets and smaller lower ones (pl. 10). In some Hybotidae and Dolichopodidae the compound eyes are more closely approximated or coalescent on the face, below the antennal insertions than on the frons (pl. 13). In the Tipuloidea the ocelli are absent.

A great diversity of form is found in the thoraces of Nematocera and Brachycera. In Tipuloidea and Trichoceroidea there is a strong dorsomedial transverse suture (pl.,8), whilst in the Ptychopteridae (pl. 6) there are longitudinal furrows also. In *Dilophus* the front third of the dorsum is armed with two transverse rows of strong spines (pl. 10). In lateral view the relative shapes and sizes of the pleural sclerites shows great diversity, especially in the degree of development of the prothoracic region. In the Ptychopteridae (pl. 6), and many Chironomidae, the pronotum is completely hidden from dorsal view by the anterior margin of the dorsum (ie. mesonotum). In the Simuliidae (pl. 7) the sternopleuron has a deep transverse suture.

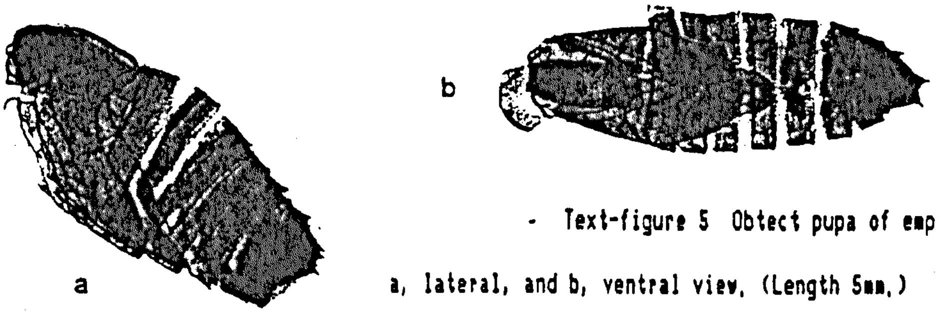


Text-figure 4 Wing of Winter Gnat

Trichocera maculipennis Meigen (Length 10mm.)

The most complex wing-venational patterns in the Diptera are found in the Nematocera (text-fig. 4; pl. 1, 3, 6-9) and many of these are entirely diagnostic. Psychodidae (pl. 6) are characterised by their pointed wings and numerous long parallel veins. In the Bibionidae (pl. 10), Sciaridae (pl. 9) and Scatopsidae the anterior veins (ie. costal, subcostal and radial veins) are usually much more strongly pigmented than the remainder.

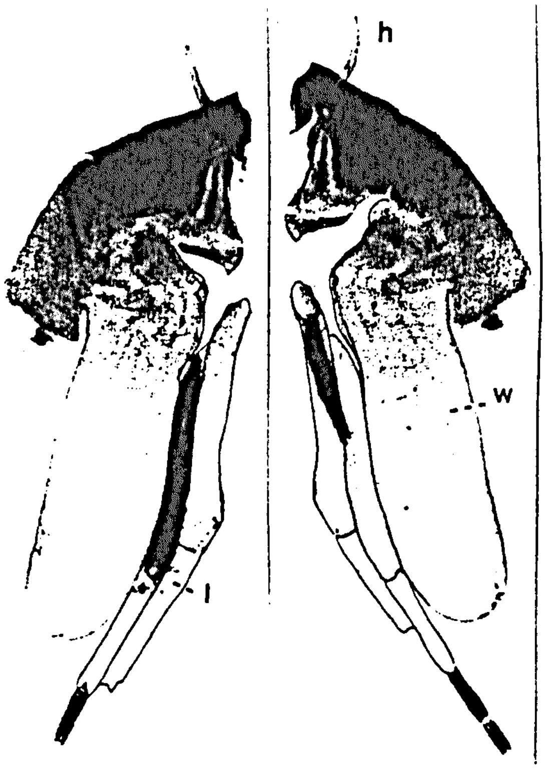
Nematocerous larvae (excluding the Cecidomyiidae) have a distinct head-capsule which is of a highly distinctive form in most families. These may occur in abundance in subfossil assemblages, often in a remarkably good state of preservation. Chironomid larval head-capsules have been widely used in limnological studies as they reflect changes in water quality, and there is consequently a useful literature on this group (Walker 1987). The extensive literature on Tipuloid larvae on the other hand is almost useless for subfossil work since the head-capsules have been largely ignored. As a part of the current research, larval head capsules of several Tipuloid genera have been examined and a remarkable diversity of form has been discovered. In the Tipuloidea the head-capsule lacks a posterior marginal carina, being deeply cleft behind (pl. 1, 2, 4, 5). In Sciarid larvae there are two ventral bridges between the genae (pl.9). Amongst the Brachycera, only the Stratiomyiidae have a fully developed head-capsule, this being of an unmistakably archaic form (pl.12). In other Brachycera there is a progressive reduction of sclerotisation of the head capsule and these forms do not survive subfossilisation processes.



Text-figure 5 Obtect pupa of empid species in a, lateral, and b, ventral view, (Length 5mm.)

In the Nematocera and Brachycera the pupa is almost always obtect or exarate, since during the final ecdysis the entire larval skin and head-capsule are shed to expose the pupa (text-figure 5). Exceptions occur only in the Cecidomyiidae, where certain species produce a "false puparium" (pl.9), and the Stratiomyiidae in which the pupa is enclosed in a true puparium (pl.12). In the subfossil state, pupae of these suborders are usually much-fragmented. Apart from the Tipuloidea and the Chironomidae (Langton 1991), there is an absence of detailed accounts of the comparative morphology of a wide range of these pupae in the literature which makes identification of subfossil specimens difficult below familial level. The pupal case however displays adult features which often afford clues to identity. Of particular importance are the wing-sheaths which, especially when viewed in tangential light, usually show signs of the wing-venation (text-fig.6 and pl.3,6). Other structural details of value in identification occur on the pupae, many of which point to familial identity. Thus, the facial mask in the

Dolichopodidae (pl. 14) is unmistakable. On the distal edge of the facial mask are the palp-sheaths, the shapes of which distinguish Tipulidae from other Tipuloids. The end-segments show major differences between families and have een extensively used in taxonomic work on Tipuloid pupae. Sexual differences also occur in pupal end-segments in

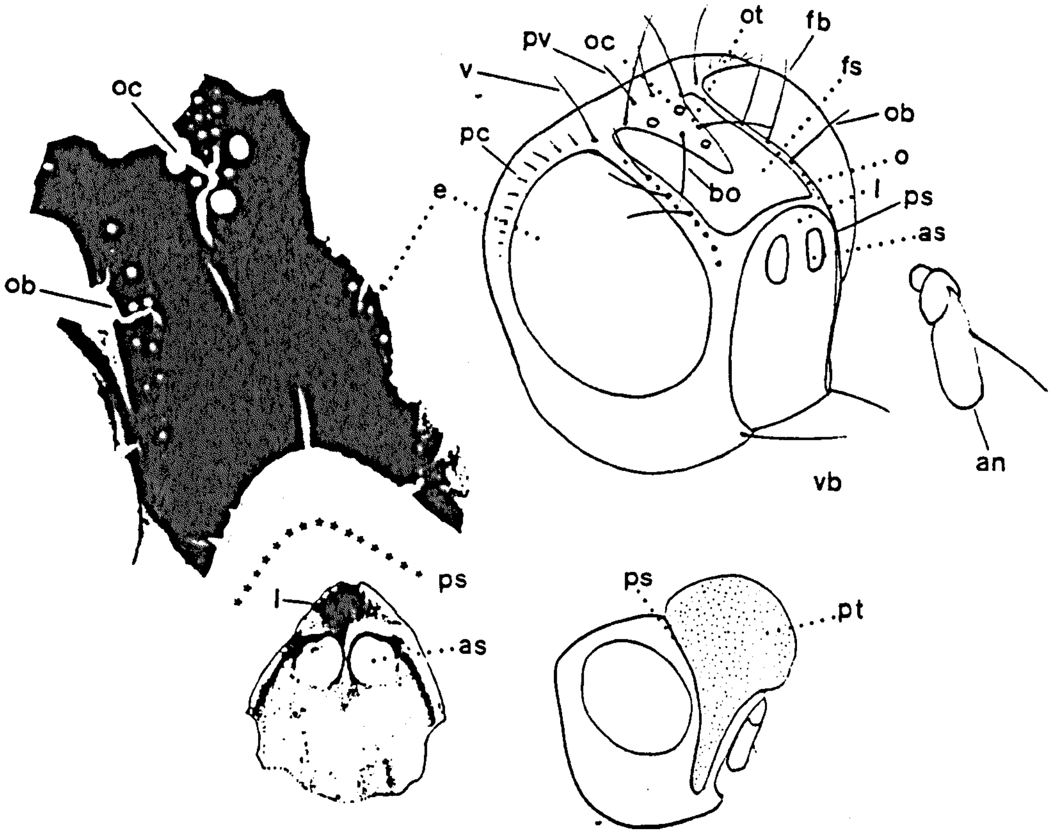


Text-figure 6 Anterior parts of pupa of Crane-fly *Erioptera lutea taenionota*, showing w, wing-sheath, l, leg sheaths(containing fragments of adult) and h, prothoracic spiracular process

those families in which the females possess strongly exerted ovipositors. Brauns (1954) provides a provisional key to pupae of these suborders, but this is of a limited value since most species are undescribed in the pupal state.

CYCLORRHAPHA

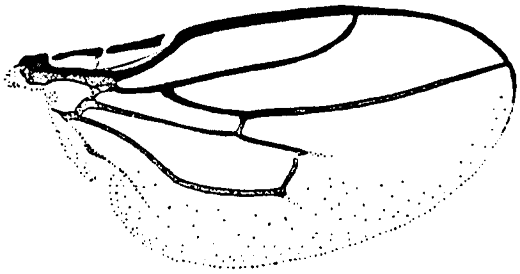
The former subdivision of this suborder into Aschiza and Schizophora is convenient to retain here as it is highly relevant to the structure of the heads of these insects. In the Schizophora a distinct ptilinal suture is present, which, in subfossil specimens is often particularly distinct; indeed the heads often fracture along this suture so that the face becomes separated from the rest of the head (text-fig. 7). The ptilinum is an inflatable sac at the front of the head of adult Schizophora which assists the fly in emergence from the puparium. After emergence the ptilinum is withdrawn into the head leaving the suture to reveal its line of ingress. This suture appears as a conspicuous arched furrow bordering the anterior margins of the compound eyes and meeting over the antennal bases (see pl. 25). In the Aschiza the ptilinum, and hence the suture, is absent.



Text-figure 7 Fragments of head of subfossil *Scathophaga*, showing corresponding features on complete specimen, In the subfossil the face has become detached from the front part of the head along the ptilinal suture, Key to symbols- an, antenna; as, antennal socket; bo, ocellar bristles; e, compound eye; f, face; fb, frontal bristles; fs, frontal stripe; l, lunule; o, orbits; ob, orbital bristles; oc, ocelli; ot, ocellar triangle; pc, postorbital bristles; pt, inflated ptilinum; ps, ptilinal suture; pv, postvertical bristles; v, vertical bristles; vb, vibrissa, Apart from the aberrant parasitic Muscoid families Hippoboscidae (pl.28), Streblidae and Nycteribiidae, the shape of the head and compound eyes shows a remarkable degree of uniformity in this suborder suborder, and especially within the Schizophora. Nevertheless important taxonomic characters are to be found. Especially in the Schizophora, the frons, bounded by the compound eyes, the dorsal line of the ptilinal suture, and the ocelli, is usually clearly divisible into lateral frontal orbits adjoining the dorsal margins of the compound eyes, and a median frontal stripe (text-fig.7; pl.19,25,29). The arrangement of bristles on these regions, around the ocellar triangle, and along the mouth edge, is of great taxonomic importance. In males the compound eyes are usually holoptic in the Syrphoidea and Muscoidea (except the Scathophagidae); but almost never in the remaining superfamilies. The compound eyes are always evenly rounded or oval, never sharply indented as in some Nematocera and Brachycera. In the Syrphoidea there is often a pronounced median facial protuberance.

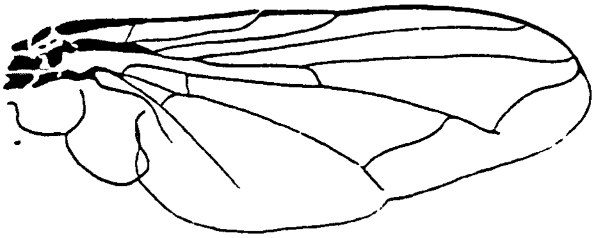
General morphology of heads and thoraces, and especially the chaetotaxy provide valuable characters, and it is often possible to identify a species from the bristle arrangement on a small fragment of sclerite.

In the Aschiza, each family possesses a very characteristic type of wing-venation (pl.15). In the Schizophora, the pattern is very similar throughout (text.figs.9,10; pl.17-20,22,23,25), except that in many Muscoids, especially in Tachinidae and Calliphoridae the discal and cubital veins are strongly convergent or coalescent at, or before, the wing tip (text-fig.10).



Text-figure 8 Wing of Limosinine Sphaerocerid

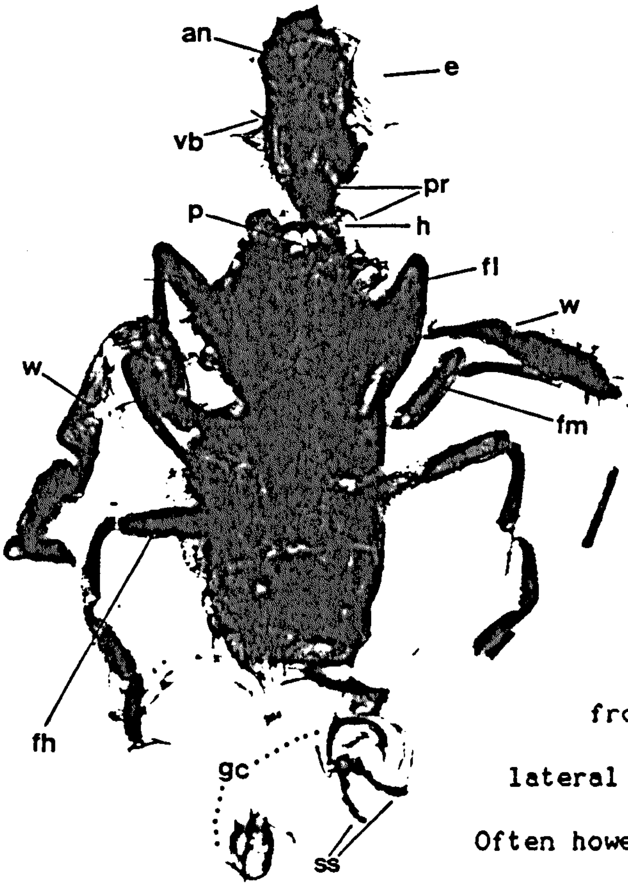
(length 1.5 mm.)



Text-figure 9 Wing of *Calliphora* species

(length 8 mm.)

In the Cyclorrhapha the larval head-capsule is absent, the chitinized parts being reduced to the actual oral mechanism. Just before pupation, the skin of the final instar larva merely contracts and hardens to form a tough puparium which houses the flimsy pupa. Puparia, especially of the Schizophora, are usually very heavily sclerotised and commonly survive undamaged in the subfossil state. In fact, such puparia constitute the vast majority of subfossil Dipterous specimens from terrestrial, and especially from archaeological sites. In entirely natural sites they are far less numerous. In the present study 31,000, or about 87 per cent, of the 35,700 Dipterous specimens examined were puparia, and it is therefore with the puparia of Cyclorrhaphous flies that this research programme has been chiefly concerned.



Text-figure 10 Unhatched male *Heleomyza serrata* (ventral view) dissected from puparium, showing- a, antenna; c, compound eye; vb, vibrissa; pr, proboscis; h, humeral callus; ps, prosternum with prosternal bristles; w, wing; gc, genital capsule showing surstyli(ss).

Following emergence from the pupa, the Schizophoran fly must burst out of its puparium by inflating the ptilinum. This fractures the front end of the puparium along the lateral and transverse lines of weakness. Often however the fly is unable to break out and hence this is a period of peak mortality amongst these flies. For the palaeoentomologist however this is a windfall, since the genitalia of unhatched male flies (text-fig. 10) provide the opportunity for precise specific identification. Wherever possible such confirmation is desirable since published descriptions of puparia are often incorrect. It has been found during this study of some 28,000 subfossil puparia, that populations typically include about 10 per cent of unhatched specimens, of which approximately a half prove to be males.

In assemblages a note should be made of the percentage of unhatched puparia as this gives a measure of the success rate of the population. In unhatched puparia the lateral lines of weakness remain fused. Hatched ones often have dorsal and (or) ventral caps missing. By calculating the ratio of length of the frontal cap to the whole body length on an unhatched specimen, it is possible to estimate the size range of puparia of one taxon within an assemblage, even if most have hatched. This can also be very useful, as in Buiston Crannog, where not only did *Musca domestica* show a success rate of almost 100 per cent in a huge population, but the average size was unusually large, inferring that this population was enjoying optimum conditions.

Owing to the superabundance of Cyclorrhaphous puparia in many subfossil assemblages, they are discussed in more detail here. Their importance in palaeoentomological research derives from the following qualities-

1 Durability; any contents, such as unhatched adult or parasites safely enclosed inside.

2 Sheer abundance of puparia in many deposits

3 Wealth of data they can provide

4 Relative simplicity from statistical standpoint- In Nematocera the head-capsule is shed at each ecdysis so that a stratum will contain head-capsules of different sizes. Whilst in any instar the head does not grow in relation to body size, and hence will not show an even growth rate within a given species, it is often extremely difficult to estimate the number of actual individuals represented, or whether smaller and larger species are intermixed. In the Cyclorrhapha these problems do not arise since almost the entire larval life is spent in the third instar, after which the larval skin hardens, with all of its external features, plus the larval mouthparts, to form the puparium.

5 The study of Diptera is a major growth areas in entomology

PUPARIA (See Plate 16)

Puparial features which are of taxonomic value are detailed below.

a **GENERAL SHAPE** In a restricted fauna species may be identifiable on shape alone. The Cyclorrhaphous families having the most distinctive puparia, and hence larvae, are the Lonchopteridae and Phoridae (pl. 15), and the Fanniidae (pl.27).

b **SIZE** With large numbers of puparia of a given taxon, and providing one or more complete specimens are present, it is possible to calculate the size range within the assemblage by extrapolation from fragments. Some families (eg. Sphaeroceridae) can be ruled out on size alone if the mean length of a taxon exceeds 5mm. There is also a relationship between length of puparium and adult, though this ~~is~~ not constant in all families.

c **PROSPIRACULAR PROCESSES** These exhibit a great diversity of form. In the Sphaeroceridae they may be long and branched to stellate. In many other families they may be multilobed (pl.18,26).

d **POSTERIOR SPIRACLES** Perhaps the most important taxonomic features of the puparium, these are often highly diagnostic of particular taxa. Details of particular significance are-

i general shape and size relative to length of puparium.

ii presence/absence of spiracular processes. In Sepsidae there is a dorsal tooth on the spiracular process (pl.17). Larvae living in liquid media typically possess spiracular processes, whilst those inhabiting drier ones more often lack them. In the Eristaline Syrphids the anal spiracles are located at the ends of an extremely long respiratory siphon (pl.15) which is telescopic in the larval stage.

iii arrangement of respiratory slits (usually 3 on each plate) and the position of internal scar (compare *Ceroxys*, pl. 16, *Orygma*, pl. 17, Muscidae, pl. 28 and *Calliphora*, *pl. 29)*

iv presence of any spines on spiracular plate. These are very distinct in *Loxocera*, *Calobata* (pl. 16) and *Cordilura* (pl. 26).

e **ARRANGEMENT OF PERISPIRACULAR PAPILLAE ON "END-SEGMENT"** The typical Muscoid arrangement is seen in *Scathophaga* (pl. 26), and *Phormia* (pl. 29), where there are 5 to 6 pairs of papillae encircling the spiracles. In many muscoids these may merely appear as cuticular knots or thickenings; in most of the Muscidae and frequently in other related families they are absent. In *Delia fabricii* (plate 27) the inner subspiracular pair are massively enlarged and blackened to form a pair of strong upswept horns. In other Cyclorrhaphous superfamilies the Muscoid arrangement is very rare. Many non-Muscoid families however have highly characteristic papillar arrangements. Thus, the Piophilidae (pl. 21) have a pair of short lobes above the spiracles, and a pair of often longer ones below, the spiracle (see *L. pilosa*, pl. 21).

e **ANAL PLATE AND ADJOINING PAPILLAE** These are seen on the ventral surface of the "end segment" and constitute the true anal segment. These features can be of taxonomic importance. Thus, in certain Muscinae, the anal plate is huge, ascending laterally to the laterodorsal surface. In many Muscoids, but less frequently in other families, the anal papillae may be strongly developed.

f **CUTICULAR FEATURES** In some Muscidae the cuticle, especially on the end-segment, is longitudinally striate. Ephydrid and Drosophilid puparia are usually minutely spiculate over the entire body surface giving them a matt appearance. Similar, though much coarser vestitures also occur in some Anthomyiidae and are very well-developed in *Scathophaga* (pl. 26) which is covered in fine dark hairs. In some Muscoids the entire body is clothed with coarse spicules. More frequently spiculate bands only occur as ventral ambulatory welts on the intersegmental margins, but in many Muscoids these extend over the dorsal surface also (see *Phormia*, pl. 29). The shape of individual spines on these welts can be of value in identification of closely related species (eg. *Calliphora*).

g LARVAL MOUTHPARTS These are found on the internal anteroventral floor of the puparium and consist of three pairs of opposed sclerites- the mouth hooks (oral sclerites), the hypopharyngeal and the pharyngeal sclerites. In most Muscidae (excluding *Musca*, *Stomoxys* and a few related genera) one or more pairs of opposed accessory oral sclerites lie below the mouth hooks (pl. 28) and indicate a predatory mode of life. In *Calliphora* a single accessory oral sclerite lies between the apices of the mouth hooks (pl. 29). Accessory oral sclerites are unknown elsewhere in the Cyclorrhapha. In phytophagous larvae the mouth hooks are often ventrally serrate. A great diversity of form in the larval mouthparts is found in the Muscidae (see Skidmore 1985) and in parasitic groups (eg. some Calliphoridae, Tachinidae, etc.) but otherwise a remarkable uniformity occurs in most of the Schizophoran superfamilies.

h PUPAL RESPIRATORY HORNS In some families, whilst the contracted larval skin is hardening over a period of a few hours, pupal respiratory horns are extruded through the walls of the first abdominal segment of the larval skin. Such processes are common in the Aschiza (see pl. 15), but, apart from the Muscidae, in which they are usually present, and sometimes very conspicuous, they appear to be virtually absent from the Schizophora.

Superfamily TIPULOIDEA Crane-flies (Plates 1- 5)

Adults Ocelli absent (Pl. 3 fig. 1). Anterior thoracic sensory pits on side margins of mesonotum; latter with distinct v-shaped suture (Pl. 1 fig. 4). Wing venation complex (Pl. 1 fig. 5; 3 figs. 3-5).

Larvae Head capsule retractile, the attachment for the pronotal anterior marginal wall often marked by constriction behind eyes (Pl. 1 fig. 6). No hind marginal carina to head-capsule, this usually being tripartite dorsally and bitartite ventrally (Pl. 1 figs. 6, 7).

Family TIPULIDAE Long-palped Craneflies (Plates 1, 2) [87 British]

Adults Rather large to very large, delicate flies of rather uniform appearance in terms of wing venation (Pl. 1 fig. 5) and external features. The head is usually strongly rostrate anteriorly and the pronotum very short (Pl. 1 figs. 1, 2, 3). Taxonomy of regional species well-known, all being readily identifiable on general facies and male genitalia. However, these large fragile insects are only found in a highly fragmented state in subfossil deposits and consequently a more detailed study of their external anatomy is required to recognise species. Tipulid head fragments are not uncommon as subfossils and a preliminary examination of a range of heads of adult Tipulids has revealed characters which appear to be valuable in this regard. Thus, *Prionocera (turcica)* differs from *Tipula* species (ie. examples of most of the regional subgenera), in the possession of conspicuous frontal crescentic structures immediately behind the antennal sockets (Pl. 1 fig. 2). Coupled with the very wide frons, these render *Prionocera* readily separable on cephalic structure alone. The heads of adult *Ctenophora* (s. lat.) and *Nephrotoma* are shiny black and yellow.

Larvae Tipulid larvae are relatively easily distinguished from those of other Tipuloids in the form of the head-capsule and in the papillae of the end segment. The former is a robust, oval structure of rather uniform appearance (Pl. 1 figs. 6, 7; 2 figs. 1-6). One of the most characteristic features of the head-capsule in this family is the clypeo- labrum, with its large and complicated sensory papillae (Pl. 1 fig. 6 inset). Tipulid larval head-capsules occur very commonly in subfossil assemblages, but unfortunately the keys for the identification of Tipulid larvae by Chiswell (1956), Theowald (1957) and Brindle (1960) ignore these structures completely, relying solely on the caudal papillae. Indeed the head-capsules of hardly any regional Tipulids have been described and figured. A preliminary study of the head- capsules of a range of species was carried out for this study and it appears that generic and perhaps subgeneric differences exist in many features (Pl. 1 figs. 5, 6; 2 figs. 1-6). Lignicolous species (eg. *Ctenophora* s. lat.) have much shorter antennae than terrestrial ones (compare Pl. 2 figs. 1, 2 with others here figured). There is also a marked range in the development of the dorsal epicranial furrows. In most these appear as shallow grooves running parallel with the epicranio-frontal margins. Often in dissected head- capsules, tissue

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Plate 1 *Tipulidae* 1 *Tipula confusa*, head of adult (left, laterodorsal view; right, dorsal view); 2 *Prionocera turcica* (left, dorsal view; right, laterodorsal view; x, frontal callosity); 3 thorax of same (lateral view); 4 *T. confusa*, thorax (dorsal view); 5 *P. turcica*, wing; 6 *P. turcica* head-capsule of final instar larva (dorsal view), showing detail of labrum (inset); 7 same (ventral view); 8 pupa of *P. turcica* (ventral view); 9 same (dorsal view); 10 same (lateral view). (Scales- 1- 5 1.0mm; 6,7 0.25mm; 8-10 2.0mm.) (Orig.)

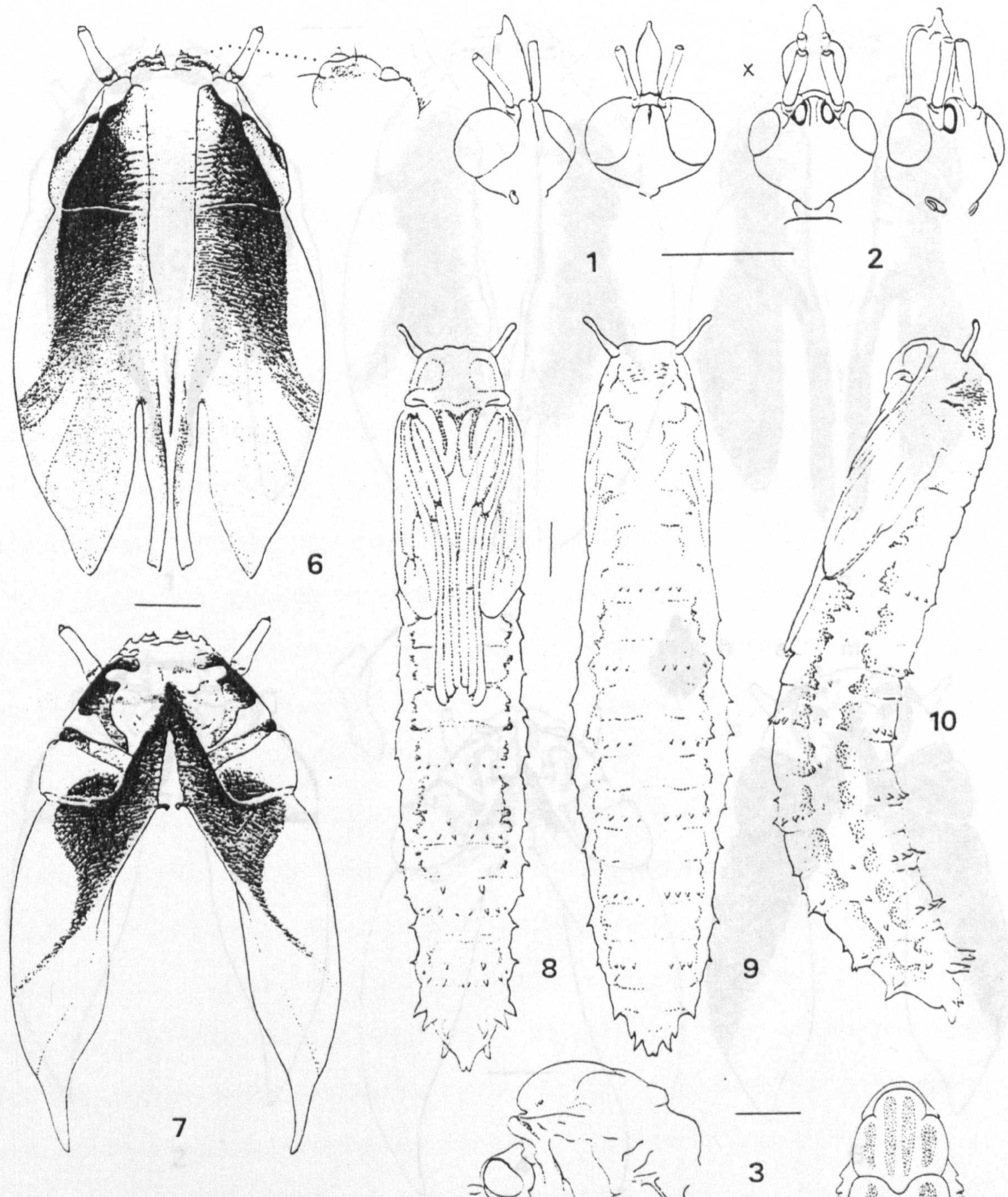


Plate 1

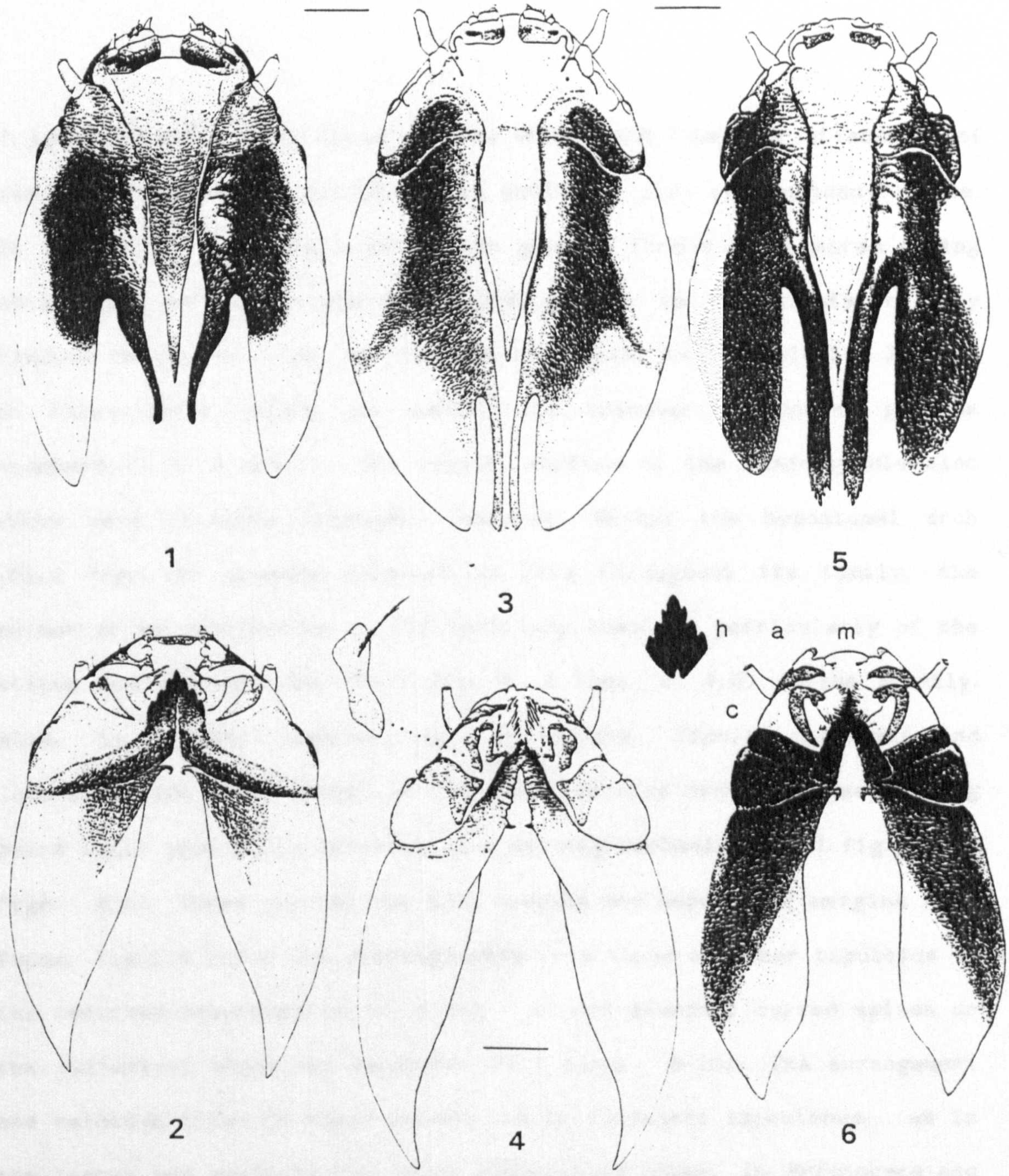


Plate 2

Plate 2 *Tipulidae* Head-capsules of final instar larvae of- 1 *Ctenophora (Dictenidia) bimaculata* (dorsal view); 2 same (ventral view); 3 *Tipula (Savtshenkia) cheethami* (dorsal view); 4 same (ventral view), showing detail of cardo (inset); 5 *Tipula (Yamatotipula) lateralis* (dorsal view); 6 same (ventral view) showing a, antenna; c, cardo; h, hypostomium; m, maxilla, whose dentate margins are hidden by the hairy inner margins of the maxillae. (Scales 1-6 0.25mm.) (Orig.)

fragments remain along these grooves which form lines for attachment of the pronotal envelope enclosing the posterior part of the head-capsule. In *Tipula(s.s.)paludosa* however, the grooves form open fissures ending anteriorly, at the transverse pronotal groove, in high crests, clearly visible in lateral view. Differences also exist in the relative lengths of those parts before and behind the transverse pronotal grooves (compare Pl.2, 3 and 5). The ventral surface of the head-capsule also shows many valuable taxonomic features. Whilst the hypostomal arch (Pl.2 fig. 6h) appears constant in form throughout the family, the extent of sclerotisation of the maxillary complex, particularly of the stipes and the cardines (Pl.1 fig. 7; 2 figs. 2, 4,6) varies greatly. Also, in aquatic species (eg. *Prionocera, Tipula cheethami* and *lateralis*) the inner margin of the galea carries dense brushes of long hairs which presumably function as a seiving mechanism (Pl.1 fig. 7; 2 figs. 4,6). These overlap the oral opening and hypostomal margins .

Pupae. Tipulid pupae are distinguished from those of other tipuloids by the recurved palp-sheaths (Pl.1 fig. 8) and abundant curved spines on the cylidrical abdominal segments (Pl.1 figs. 8-10). The arrangement and relative sizes of these spines are of taxonomic importance, as is the length and shape of the pupal respiratory horns. In *Prionocera* and the woodboring species, pupal horns are very long, in the former straight, in the latter, strongly downcurved. In other species they are shorter (cf.Pl. 1 figs. 8-10), but always tubular. Tipulid pupae are quite common in subfossil deposits, but always in fragmented condition. The parts most commonly found are end-segments of both sexes, abdominal segments, wing-sheaths and facial masks. Theowald (1957) and Brindle (1960) provide keys for the identification of many of the regional

Tipulids.

Biology The most useful published sources are those of Brindle (1960), Chiswell (1956) and Theowald (1957). Stubbs (1992) gives a valuable resumé of the British species, complete with useful ecological and distributional data. Most species of *Tipula* and *Nephrotoma* breed in humus or decaying vegetable matter, some occasionally damaging roots of herbaceous plants. *Prionocera, Dolichopeza* and some *Tipula* species are aquatic, often feeding amongst submerged Bryophytes, frequently in peaty situations. *Ctenophora* s. lat. and some *Tipula* species breed in rotten wood, especially in ancient woodland.

Taxa represented

Prionocera turcica (Fabricius) Larvae develop amongst aquatic mosses. (Larval heads, pupal fragments, adult heads from sites 5; 19; 35)

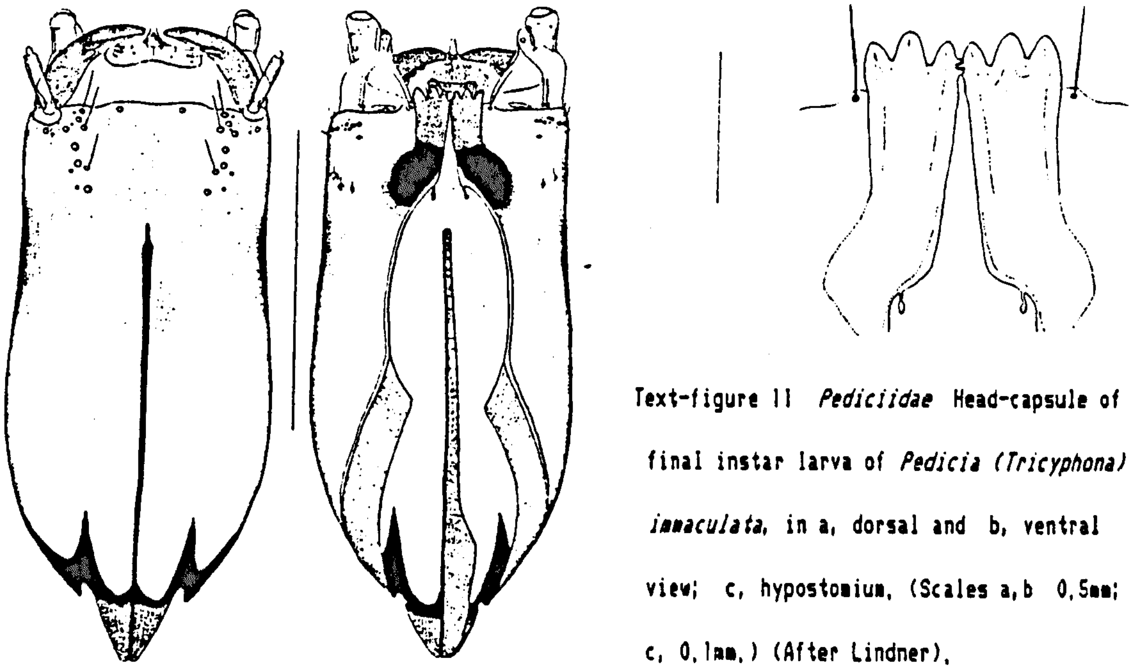
Tipula (Savtschenkia) confusa Wulp, or *rufina* Meigen Larvae in moss and peaty soil. (Larval heads, pupal fragments from sites 29; 35)

T. (Vestiplex) arctica Curtis Descriptions of the larva and pupa of this, the only Greenlandic *Tipula*, appear in Nielsen (1910), who recorded them commonly in North- East Greenland (76° 46'N, 18° 14'W) in circular subterranean cavities 2 to 3cm in diameter, especially under *Cassiope* tufts. Pupae found at the end of June emerged in nature before the 25th and the flight period extended until early August. Böcher & Fredskild (1993) found pupae in the Qeqertasussuk paleaoeskimo deposits. (Pupal fragments from sites 39; 41)

T. ?(Lunatipula) vernalis Meigen Larvae in humus soil. (Pupal fragments from site 19)

T. (s. str.) oleracea Linnaeus or *paludosa* Meigen Larvae attack plant roots in pastures, sometimes invading cow-pats. (Pupal fragments from sites 21 and 27)

T. sp. (Larval heads, pupal and adult fragments from sites 5; 7; 11; 12; 19; 22; 23; 25; 26; 27)



Text-figure 11 *Pediciidae* Head-capsule of final instar larva of *Pedicia (Tricyphona) immaculata*, in a, dorsal and b, ventral view; c, hypostomium, (Scales a,b 0,5mm; c, 0,1mm.) (After Lindner).

Family PEDICIIDAE Hairy-eyed Craneflies (Plate 3, figs. 1, 4, 8-10; 4 figs. 1-7) [21 British]

Adults A small family of small to very large craneflies chiefly characterised by their hairy eyes (Pl. 3 fig. 1). Included here is the largest European cranefly outside the Tipulidae, namely *Pedicia rivosa*. The genus *Ula* is aberrant in many respects, not least in the broad, hairy wings.

Larvae Apart from *Ula*, Pediciid larvae are characterised by the very elongate, heavily sclerotised head-capsule with its powerful curved mandibles (Text-fig. 11). The body form is adapted to an aquatic life, possessing paired abdominal false-legs and long, retractile posterior spiracular processes. *Ula* in contrast conforms closely to the *Limonia* type (p. 35), both in head-capsule structure and in body form.

Biology Apart from *Ula*, which breeds in decaying fungi in woods, all known Pediciid larvae are aquatic carnivores. Most develop in well-aerated, lotic waters, the adults occurring amongst adjacent herbage.

Taxa represented

Pedicia (s. Tricyphona) immaculata (Meigen) Larvae in wet mud by streams or ponds, preying on mites, Oligochaetes etc. (Larval heads, pupal and adult fragments, including wings, from sites 5 and 27)

P. (s. str.) rivosa (Linnaeus) Larvae are aquatic carnivores. (Larval heads from sites 15 and 26)

Family LIMONIIDAE Short-palped Craneflies (Plate 3- 5)

[214 British]

Adults A large and morphologically diverse family of delicate flies distinguished from other Tipuloids by the hairless eyes and distinct tibial spurs. The pronotum is usually relatively long (Pl. 3 fig. 2). There is a great range in wing venation, some genera being unmistakable in this regard; many have spectacular wing-markings. Limoniid wings are not uncommon in some subfossil deposits.

Larvae The main works on Limoniid larvae are those of Lindner (1959) and Brindle (1960), but since only Limoniid head capsules are found subfossil, and Brindle does not deal with these, his work is not applicable here. Lindner on the other hand is of great value since, although he only discusses a very few species, he includes members of the three regional subfamilies and highlights the morphological differences in their head-capsules. A more extensive review of these structures throughout the family is urgently needed.

In groundplan, the Limoniid larval head-capsule (eg. *Limonia* s.lat., Pl.4 figs. 1-2) is short-ovate as in the Tipulidae, but differs most obviously in the clypeo-labrum, on which the dorsal sensory papillae, which are so conspicuous in Tipulids, are at best very poorly developed. In this type the sclerotisation of the dorsal surface is also highly distinctive (Pl.4 figs. ,2). The hypostomal arch is large and conspicuous and bears about 10 teeth, of which the median one is largest (Pl.4 figs. 3-5). In the genus *Helius* the entire head-capsule is almost uniformly sclerotised and the hypostomium is weakly tridentate (Pl.4 figs. 6-7).

In the Hexatominae two very different types of head-capsule are found. In *Austrolimnophila* and *Epiphragma* it is broad ovate with short, thick mandibles (Pl.5 figs. 1-7) as in the Limoniine type, but in Limnophila s.lat. and *Hexatoma* it is elongate with fine, long, curved mandibles and remarkably long maxillar palpi (Pl.5 figs 8-13). *Hexatoma* has a very lightly sclerotised head capsule.

Plate 3 *Pediciidae* 1 *Pedicia (Tricyphona) immaculata,* head of adult (dorsal view); 2 thorax of same (lateral view). *Limoniidae* 3 *Dicranomya mitis,* wing; 4 *Pseudolimnophila lucorum,* apical half of wing; 5 *Erioptera lutea taenionota,* wing; 6 *Limnophila* sp.(sensu lat.), pupa (ventral view); 7 same(dorsal view); 8 same(lateral view); 9 same, facial mask, showing a, antennal, and p, palp sheaths; 10 same, showing arrangement of spines on abdominal tergite; 11 same, showing end-segments of female pupa (a, dorsal b, lateral view) and male (c, dorsal, d, lateral view). (Scales 1, 3-9 1mm; 2, 15 0.6mm; 10,11 0.25mm.) (Orig.)

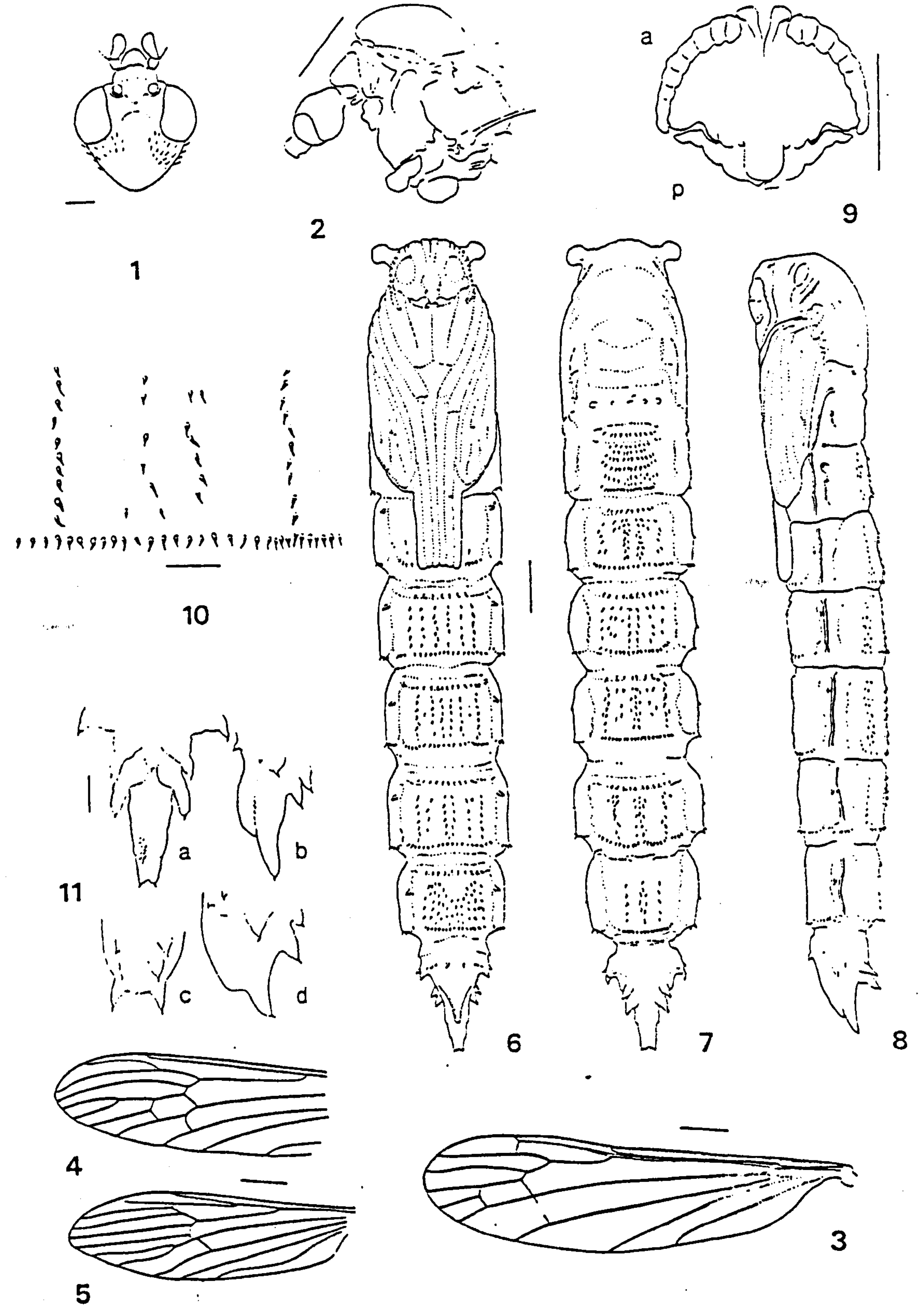


Plate 3

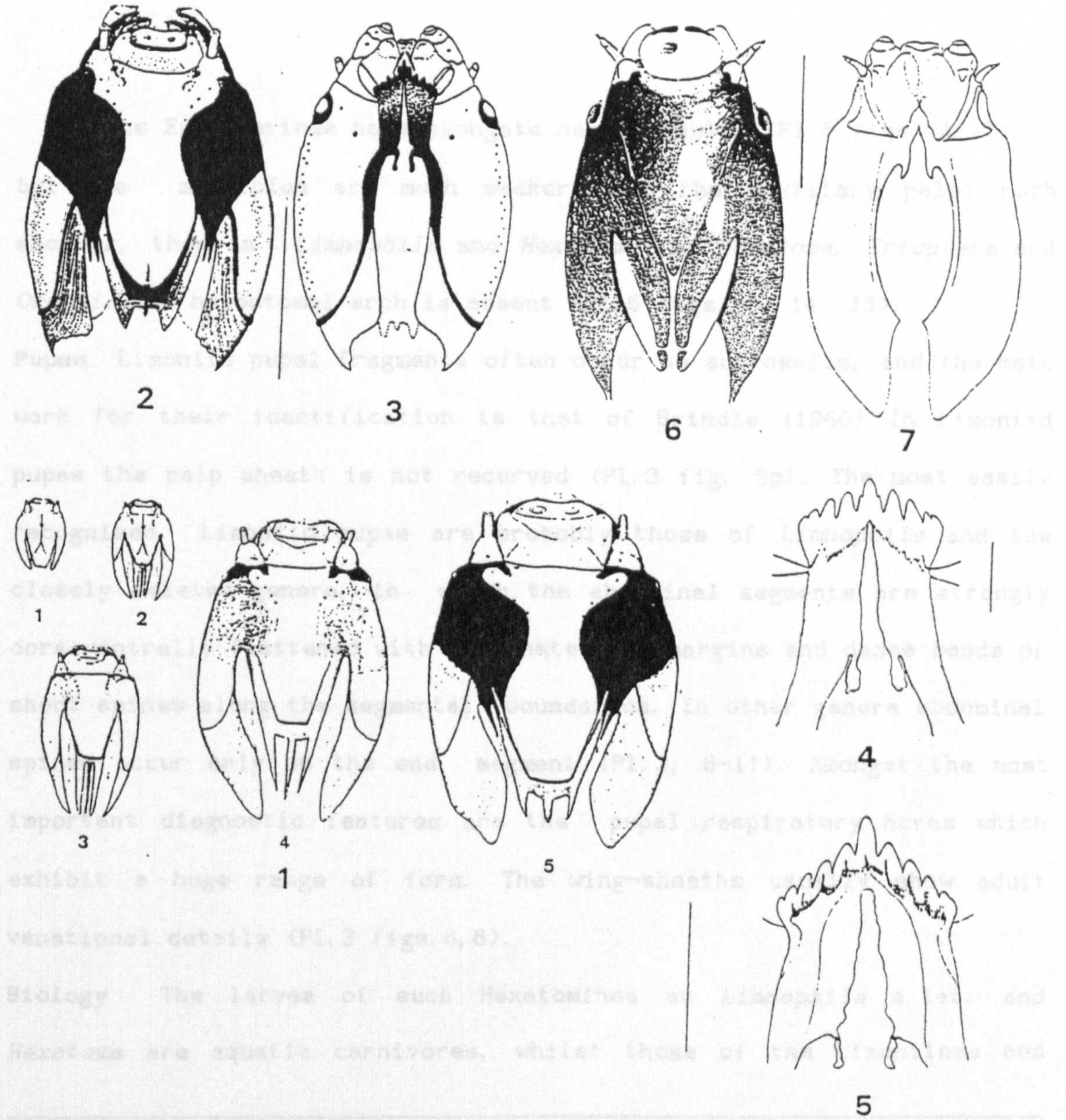


Plate 4

Plate 4 *Limoniidae* 1 *Dicranomya modesta*, larval head-capsules of first (1,2), second (3), third (4) and fourth (5) instars; 2 *Limonia macrostigma*, head-capsule of final instar larva (dorsal view); 3 same (ventral view); 4 same, hypostomium; 5 *D. modesta*, hypostomium; 6 *Helius flavus*, head capsule of final instar larva (dorsal view); 7 same (ventral view) (Scales 1-3, 6,7 0,5mm; 4,5 0,1mm) (6,7 orig; rest after Lindner)

The Eriopterinae have elongate head-capsules (Pl.5 figs. 14-17), but the mandibles are much weaker, and the maxillary palpi much shorter, than in *Limnophila* and *Hexatoma*. In *Hexatoma*, *Erioptera* and *Ormosia* the hypostomal arch is absent (Pl.5 figs. 8, 14, 15).

Pupae Limoniid pupal fragments often occur as subfossils, and the main work for their identification is that of Brindle (1960) In Limoniid pupae the palp sheath is not recurved (Pl.3 fig. 9p). The most easily recognised Limoniid pupae are probably those of *Limnophila* and the closely related genera, in which the abdominal segments are strongly dorsoventrally flattened with carinate side-margins and dense bands of short spines along the segmental boundaries. In other genera abdominal spines occur only on the end segment (Pl.3; 6-11). Amongst the most important diagnostic features are the pupal respiratory horns which exhibit a huge range of form. The wing-sheaths usually show adult venational details (Pl.3 figs.6,8).

Biology The larvae of such Hexatomines as *Limnophila* s.lat. and *Hexatoma* are aquatic carnivores, whilst those of the Limoniinae and

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Plate 5 *Limoniidae* Head capsules of final instar larvae. 1 *Austrolimnophila ochracea*, left (dorsal), right (ventral); 2 *Epiphragma ocellaris*, left (dorsal), right (ventral); 3 and 4 same, showing details of left side of labrum; 5 same, mandible (dorsal); 6 same (ventral); 7 same, hypostomium; 8 *Hexatoma bicolor*, left (dorsal), right (ventral); 9 same, cardo, maxilla and base of maxillary palp; 10 same, antenna (left) and maxillary palp (right); 11 *Limnophila punctata* antenna; 12 same species, left (dorsal), right (ventral); 13 same, maxilla, cardo and palp; 14 *Ormosia haemorrhoidalis*, left (dorsal), right (ventral); 15 *Erioptera pilipes*, left (dorsal), right (ventral); 16 same, mandible (dorsal); 17 same, clypeolabral region and antennae. (Scales 1 0.5mm; 2-7,8,12,14,15 0.25mm). (1 and 14 after Lindner; rest orig.)

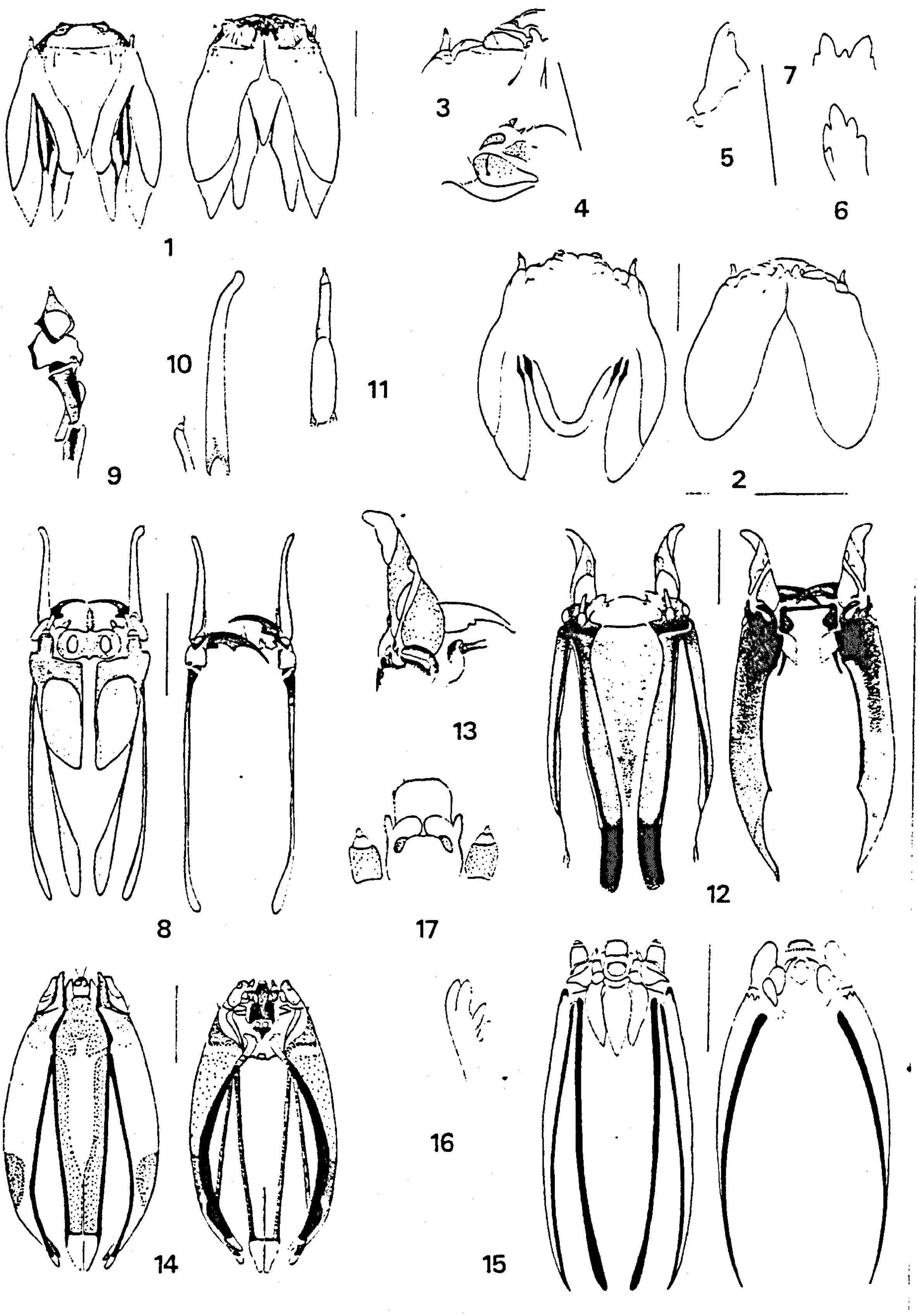

Plate 5

Eriopterinae are mostly humicoles and detritivores.

Taxa represented

Limonia (s. str.) ?*trivittata*(Schummel) (Pupal fragments from site 21)

L. (Dicranomyia) ?modesta (Meigen) Larvae mostly breed in wet moss or in waterlogged muddy places by streams etc. (Larval heads from sites 5; 21; 26; 27)

Limoniine spp. indet. (Larval and adult heads from site 19)

Limnophila (Euphylidorea) ?meigeni Verrall Breeds in wet peat. (Pupal fragments from sites 5; 21; 26; 27;)

Pilaria discicollis (Meigen) (Adult head from site 19)

Erioptera (s. str.) lutea v. taenionota Meigen Larvae among plant roots and decaying vegetation in mud. (Pupal fagments and wings from sites 19 and 27)

E. sp. indet. (Pupal fragment from site 19)

?*Molophilus* sp. indet. (Adult head from site 21)

Tipuloid indet. (Various fragments from sites 15; 25; 26; 27).

Superfamily PSYCHODOIDEA (Plate 6)

This superfamily was represented in this study by only two families, viz. the Psychodidae and the Ptychopteridae

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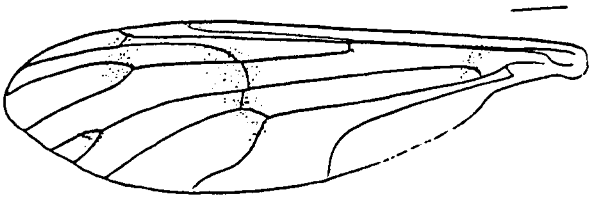
Plate 6 *Ptychopteridae* 1 *Ptychoptera contaminata* wing; 2 same, head of adult; 3 same thorax (dorsal view); 4 same, back of head and anterior part of thorax (lateral view); *Psychodidae* *Psychoda* sp. 5 pupa (ventral view); 6 same (dorsal view); 7 same, head and prothoracic region (lateral view); 8 wing sheath, showing venation; 9 same, end segment lateral view); 10 wing (Scales 1 1.0mm; 2,3,9 0.5mm; 5-8 0.25mm) (Orig.)



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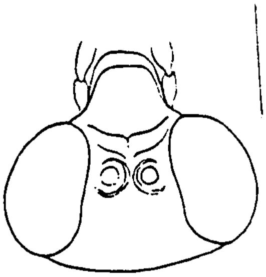

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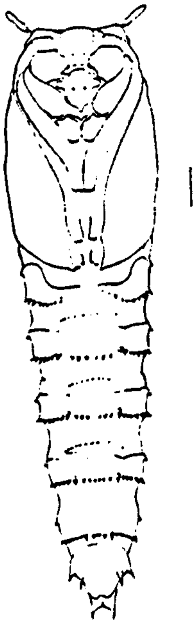

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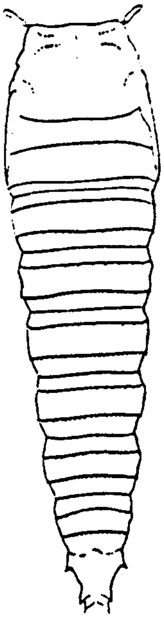

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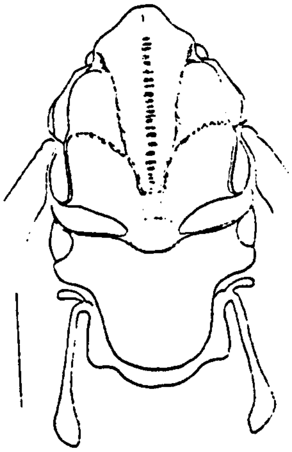

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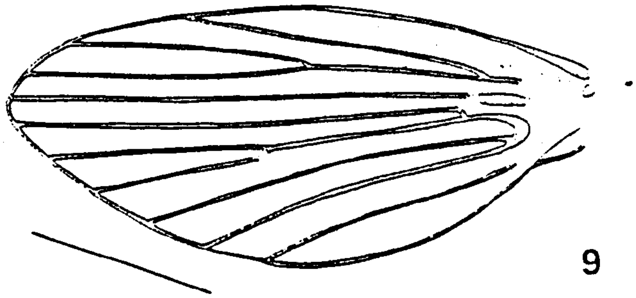

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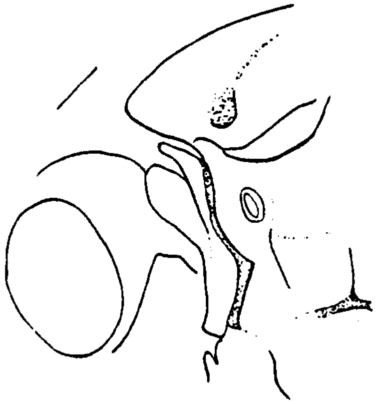

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Plate 6

Family PSYCHODIDAE Moth-flies (Pl.6 figs. 5-9) [c.50 British]

Adults The broad, pointed wings with the characteristic arrangement of many long, parallel wing-veins (fig.9), render these flies very easily recognisable. Specific identifications however are seldom possible as most species are distinguishable only on male genitalic characters.

Pupae Psychodid pupae are of rather distinctive form (fig.5-8) with strong pronotal respiratory horns, spiculate abdominal segmental margins and pointed wing-sheaths on which the wing-venation is usually clearly seen.

Biology With few exceptions, Psychodids mainly develop in wet situations containing a high concentration of decaying organic matter (eg.sewage, sodden decaying compost, manure heaps, dung-slurry, cess-pits etc.).

Taxa represented

Spp.indet. (Pupal fragments from sites 3; 7; 12; 14; 15; 17a; 21; 22; 24; 26; 27; 28)

Family PTYCHOPTERIDAE (False Crane-flies) (Plate 6) [7 British]

Adults A few fragments of adults only have been recovered from subfossil material examined during this study. Ptychopterid adults somewhat resemble moderate-sized craneflies but show many characteristic features. They are mainly aeneous black marked with orange. Head without ocelli (fig.2), and thorax with unmistakable arrangement of transverse and longitudinal sutures (fig.3); pronotum very small, hidden from dorsal view by front margin of mesonotum (fig.4). Wing venation as in fig.1 though the dark clouds on the cross-veins may be indistinct. Specific identifications rely mainly on wing venation, especially relative length of vein Rs, and on male genitalic features. The latter were present in both species recovered here.

Biology The biology of these flies has been fairly well-researched so that the ecological requirements of the British species are known in some detail (Stubbs 1993). All breed in water or saturated mud, where the larvae feed on detritus.

Taxa represented

Ptychoptera albimana (Fabricius) (Adult fragments from site 7)

P. minuta Tonnoir (Adult fragments from site 7)

Superfamily CULICOIDEA (Plate 7)

Family CULICIDAE (Mosquitoes) (Pl. 7; 8-12) [34 British]

Adults This important family was represented by only a few fragments of adults from Nipáatsoq in Greenland (site 40). Probably one of the best-worked of all Dipterous families owing to the medical and veterinary importance of many of its members, the treatment and bibliography given by Smith (1989) should serve as an introduction to

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Plate 7 *Chironomidae Chironomus* sp. 1 head-capsule of final instar larva; 2 thorax of adult (dorsal); 3 wing. *Simuliidae Simulium* sp. 4 head of subfossil adult (anterior) (antennal sockets in black); 5 thorax (lateral); 6 wing. *Ceratopogonidae ?Palpomyia* sp. 7 anterior half of subfossil pupa from Thorne Moor (lateroventral). *Culicidae* 8 *Culex pipiens* wing; 9 *Aedes impiger/nigripes*, incomplete head of subfossil adult (mouthparts missing); 10 *Culex pipiens*, adult thorax (dorsal); 11 same, showing details of scutellum; 12 same, thorax (lateral view) (Scales 1,4,5,7,9 0.25mm; 2,10,12 0.5mm; 3,6,8 1.0mm) (Orig.)

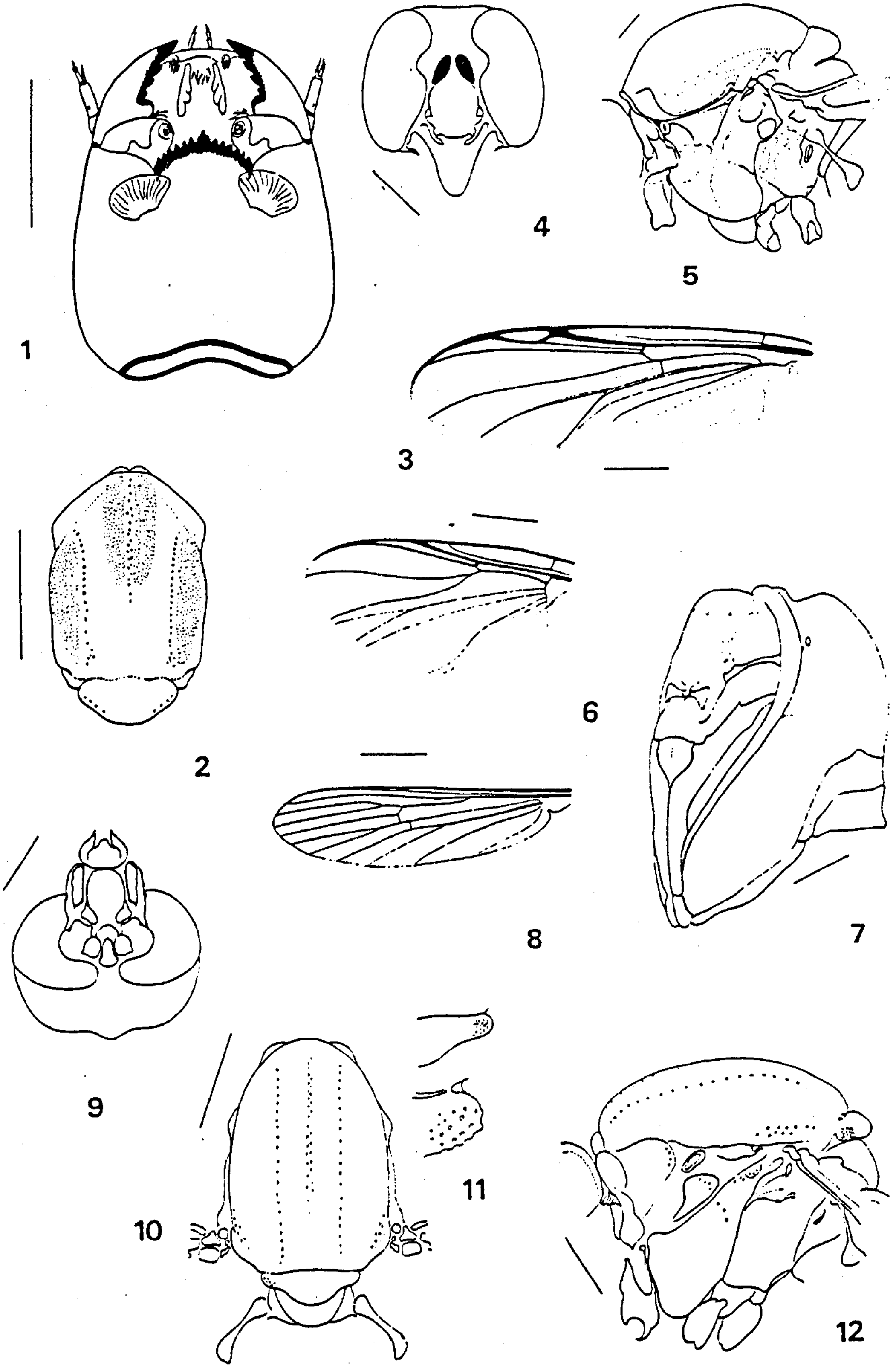

Plate 7

the field. Culicid wing-venation is rather uniform throughout the family and is highly characteristic (fig. 8). The head is adapted to a bloodsucking habit and bears a very long piercing proboscis and palpi; these have been lost in the subfossil head shown in fig. 9 but their points of origin in the anterior part of the head-capsule are clearly visible. A characteristic feature of many Culicids is the peculiar shape of the scutellum (figs. 10, 11). Also in lateral view the arrangement of the pleural sclerites is diagnostic for the family (fig. 12), and the bristles of the prospiracular region provide very important taxonomic characters.

Biology The species found in the present study, whether *Aedes impiger* or *nigripes*, is an Arctic mosquito which breeds in pools on the tundra.

Taxa represented

Aedes (Ochlerotatus) impiger Walker or *nigripes* Zetterstedt (Adult heads from site 40 evidently belonged to one of these two ubiquitous Greenlandic species and had entered the habitation for bloodmeals from the occupants.)

Family CERATOPOGONIDAE (Biting midges) (Plate 7; 7) [c. 154 British]

Apart from several possible adult thoraces, this large family was represented in the material studied by just two incomplete pupae (fig. 7) from peat-bog sites. These possess the peculiar "bow-tie" form of the palpal region of the facial mask of *Sphaeromias* (see Smith, 1989, fig. 1119), and are here tentatively referred to the large genus *Palpomyia* which often abounds in peat-bogs and fens, and includes some of our commonest larger Ceratopogonids. The immature stages of this genus have not been described, but the adults prey on other small insects. This family exhibits a great range of morphology and ecology in all developmental stages and Smith (op. cit.) should be referred to for further details.

Taxa represented

Gen., spp. indet. Larvae of *Culicoides obsoletus* live amongst mosses in bogs, but numerous biotopes are utilised by the family as a whole so the ecological requirements of the species represented here cannot be ascertained. (Adult thoracic fragments from sites 19; 26; 27)

?*Palpomyia* sp. (Pupal fragments from sites 5 and 15)

?*Forcipomyia* sp. *Forcipomyia* adults feed on blood of invertebrates and breed in a range of situations including manure. The genus is known from Iceland (Lindroth et al., 1973) and Ellesmere Island (McAlpine 1965a), but not from Greenland. (Adult thoraces 21; ?41, the identity of the three thoraces from Sandnes is very uncertain. They seem to agree with *Forcipomyia* rather than *Culicoides*, the only Ceratopogonid genus known from Greenland. Moreover since adult females of that genus feed on mammalian blood their occurrence could have been expected in human habitations).

Family CHIRONOMIDAE (Non-biting midges) (Plate 7; 1-3)
[over 450 British]

This huge family was virtually unrepresented in this study since the vast majority of species breed in water and the bulk of the subfossil deposits studied were from "dry" situations. In those few which were from "wet" locations however, the unmistakable head-capsules of Chironomids (fig. 1) were present in small numbers, along with adult thoraces (fig. 2) and fragments of wings (fig. 3). Smith (1989) provides a valuable overview of this family which is particularly important in limnological studies, especially in monitoring changes in water quality. In recent years extensive research in this field has led to great advances in taxonomic and ecological studies of all developmental stages (Walker, 1987)

Taxa represented

Chironomus ?plumosus (Linnaeus) (Larva heads and adult thorax from site 19)

C. (s. lat.) sp. (Adult thorax from site 7)

Chironomids s. lat. (Larval heads and adult thoraces from sites 5; 7; 12 (3 spp.); 15; 21; 27 (aquatic Orthocladiines); 36)

Family SIMULIIDAE (Buffalo gnats) (Plate 7; 4-6) [c. 33 British]

This small family of flies was mainly represented in material from West Greenland. These were clearly recognisable as Simuliids on the structure of the head (fig. 4), and the transverse sternopleural suture (fig. 5). The wing-venation (fig. 6) cannot be mistaken for any other Dipterous family. Simuliids breed in lotic waters, preferring rapids or cascades, but sometimes frequenting lake outflows. The female adults are bloodsuckers and many are important as vectors of disease. Smith (1989) reviews the family and provides valuable references.

Taxa represented

Simulium arcticum Muller or *vittatum* Zetterstedt (Adult heads and thoraces from sites 38; 39; 41; 42; 43). These were all from indoor deposits whence the flies, all females, had presumably entered for blood-meals. Then, as now, they were common in Greenland.

Simulium (s. lat.) spp. indet. (Adult fragments from site 21)

Superfamily TRICHOCEROIDEA

Family TRICHOCERIDAE (Winter Gnats) (Plate 8) [9 British]

Adults Head with distinct ocelli(fig. 10). Thorax resembling Tipuloid form with dorsal v-shaped transverse (fig. 4t), but suture between mesonotum and scutellum incomplete (fig. 4ds). Pronotum moderately long (fig. 3p) and lateral sensory pit (fig. 4sp) situated on shelf-like post-pronotum (fig. 4pp). Wing venation (fig. 5) very Tipuloid but with very short, recurved anal vein (an) and with cross-vein *m-cu* at outer end of discal cell (dc). *Diazosma* is aberrant in many respects, not least in the sinuate anal vein. Apart from *Trichocera maculipennis* in which the wings have all of the cross-veins clouded (fig. 5), and *T. annulata* which has a conspicuously banded abdomen, there is considerable difficulty in separating other members of the genus without recourse to genitalic differences. The key in Coe, Freeman & Mattingley (1950) is unreliable, and the works of Dahl (1966, 1967a and b) should be used for identification of adults. *Metatrichocera* species tend to replace *Trichocera* in higher latitudes and no members of the genus has been recorded from Britain, where several species of *Trichocera* are

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Plate 8 *Trichoceridae* 1 *Trichocera regalationis*, head of adult (dorsal view), showing a antennal socket, c compound eye, l labellum, o ocellus, p palp; 2 same, (ventral view); 3 same, head and thorax (lateral view), showing front (1), mid (2) and hind coxae (3), p sensory pore, w wing-base; 4 same, thorax (dorsal view), showing t transverse u-shaped suture; 5 *T. maculipennis*, wing; 6 same, head-capsule of final instar larva (dorsal view), showing a antennal complex, c postmarginal carina, m mandible; 7 same (ventral view), showing x maxillary complex; 8 *T. hiemalis* labrum of final instar larva (ventral view) (Scales 1-4 0,25mm; 5 1,0mm; 6,7 0,20mm) (Orig.)

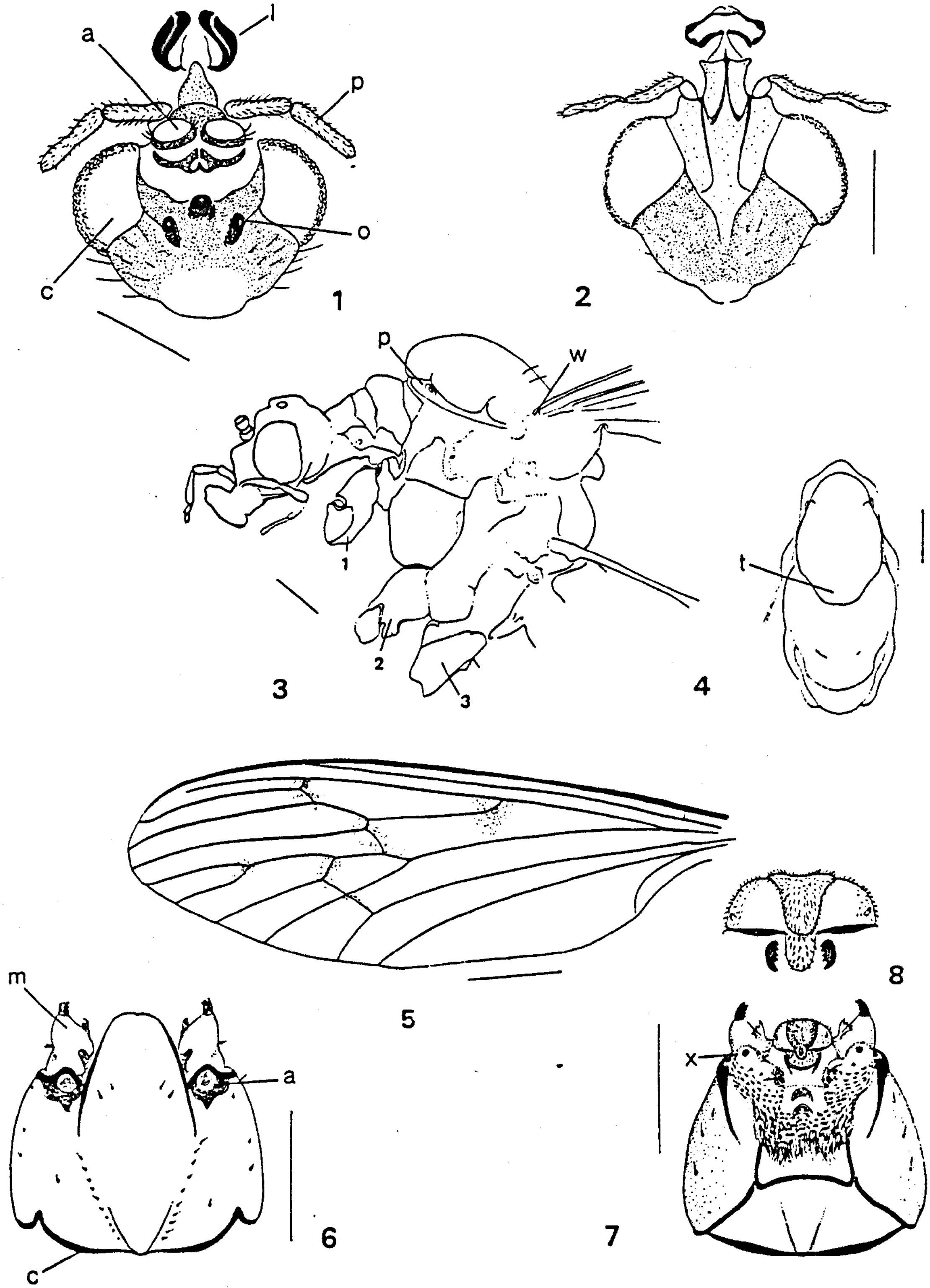


Plate 8

ubiquitous.

Larvae Amphipneustic. Head well-developed (fig. 6, 7), very distinctive and most nearly resembling *Sylvicola* (Anisopodidae). In both the posterior margin is complete (fig. 6, 7pm), ventrally forming a pigmented bridge between the posterior ends of the tentorial rods (fig. 7tr). This bridge is gently curved in Trichocerids but sharply angled in Anisopodids. Mandibles conspicuous (fig. 7m) and labrum with a median ventral setose area which has a posterior hirsute lobe (fig. 7, 8e), the shape of which is important in distinguishing species. On the dorsal surface the antennal regions appear as large, darkened eye-like features immediately behind the mandibular bases. The frontal sutures (fig. 6 c) meet at the hind margin of the head so that the epicranial plates meet at a fine point. Brindle (1962) and Smith (1986, 1989) provide keys for regional species of *Trichocera (annulata, hiemalis, maculipennis, regelationis* and *saltator*). Laurence (1956) however expressed some uncertainty regarding the identity of the species which he described and referred to *T. saltator*. Dahl (1967a) gave some anatomical details of the fourth instar larva and pupa of the nearctic *T. columbiana*.

Pupae No adequately detailed figures and descriptions have been published of a Trichocerid pupa, the figures in Keilin & Tate (1940), Laurence (1956) Brindle (1962) and Smith (1989) showing only the lateral view in outline. On the other hand, Karandikar (1931) and Dahl (1967a) figure the end-segments of *T. maculipennis* and *T. columbiana* respectively, showing that the sexes are clearly distinguishable in that stage.

Biology This family includes two genera (ie. *Trichocera* and *Metatrichocera)* which are notable for the high levels of resistance to extreme cold shown by some of their members, whose range extends into the most hostile climates of the High Arctic. The other genus, *Diazosma* is unknown in the immature stages, but the adults of the single known species, *D. hirtipenne* occur in woods. Brauns (1954) summarises Trichocerid larvae as being terrestrial and aquatic, feeding mainly in decaying organic matter, such as leaf-litter, rotting wood, putrifying fungi and animal dung in pastures. They are phytosaprophagous, or sometimes coprophagous. They commonly attack young plants, including crop species, where they may cause considerable damage. According to Keilin (1940) they are most readily found in potatoes, turnips, and, especially mangold-wurzels which have partly decayed when stored in pits during the winter, where they are usually accompanied by larvae of *Scatopse,* Lonchaea, Stratiomyiids and Sapromyzids. As stated above they reach the highest latitudes, and Brauns records them up at altitudes of up to 2800 metres in the Alps.

Taxa represented. (Including the available data on regional species.)

Trichocera annulata Perris (1847) found larvae in profusion in rotting gourds and fungi, with adults, from October to December in the south of France, whilst in northern England, Erzinçlioğlu (1980) found them feeding on carrion from January to late February. [He noted that this
Broadhead (1980) found Trichocera larvae in a human corpse.
was the only positive instance known to him of necrophagous habits in this family.] Keilin (1912) said that they breed in decomposing fungi and leaf-litter, whilst Stubbs & Chandler (1978) give fresh and decaying fungi amongst other media.

T. hiemalis(Degeer) According to Kidd & Brindle (1959) the larvae have been found in decaying plant refuse and owl pellets. Keilin (1912) says they breed in similar situations to *T. annulata* and *regelationis*. In Iceland, Andersson (1976) found adults in a farm cow-shed, in waste places and on a bird-cliff, in June and July.

T. maculipennis Meigen Although this fly does occur in open situations, as noted by Nielsen et al. (1954) and Dahl (1967), it is more often found in caves, mine-workings and dark interiors of buildings. Brauns (1954) found it in the Segeberger Kalbergher Höhle in Schleswig Holstein, breeding in bat-dung at a constant temperature of about 8 degrees Centigrade, and an air humidity close to 100%. Kidd & Brindle (1959) record it from a Derbyshire cave and a Cheshire copper mine, whilst I have found it in the cold, dark interior of a long-abandoned house at an altitude of 1000 feet on the Lancashire Pennines. Karandikar (1931) provides an exhaustive account of the biology and morphology of the larva and pupa. His material came from a whiskey distillery in Scotland where the fly, along with *Psychoda severini*, was breeding in the semi-fluid waste from malt yeast residues. Larvae and adults were found together from mid-March to late September, but none of any stage from October to mid-March. The entire life-cycle took 40 to 42 days at a constant room temperature of about 60 degrees Fahrenheit. Nielsen et al. (1954) state that the species is probably mostly synanthropic in Iceland although it has been recorded from bogs. Adults swarm around house-gables, even at midnight, and have been noted from March to September, and in December. Lindroth et al (1973) record it from stables, farm buildings, canyons and cliffs, where adults may occur amongst *Archangelica* etc. The species occurs throughout Iceland, except in the Central Highlands, and it has occurred on Heimaey and

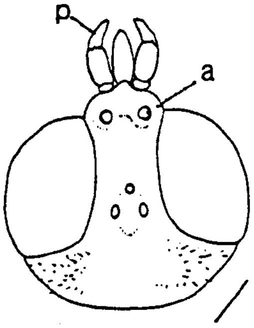
Surtsey (Lindroth et al. 1973). Through commerce the species has become almost cosmopolitan, having reached New Zealand and Kerguelen (Dahl, 1970). Greenlandic records mentioned by Dahl (1967a) no doubt referred to indoor captures. (Larval heads, pupal wing-sheaths and adults' wings from sites 28; 35; 36)

T. regelationis (Linnaeus) Rhynehart (1924) found eggs and larvae of this species amongst rotting swedes and decaying parts of their roots all year round. In the Treshnish Islands (West Scotland), larvae were found in soil under decaying vegetation in June, the adults frequenting adjacent cliffs and caves; the species is also recorded from fresh and decaying fungi (Stubbs & Chandler 1978). Adults are most abundant in winter but can be found throughout the year. De Meijere (1910) records it in abundance above 82 degrees north in Greenland, but Dahl (1967a) suggests *that T. borealis* Lackschewitz was the species concerned.

T. saltator (Harris) (=*fuscata* Meigen) According to Cuthbertson (1929) this occurs mainly amongst stream-side vegetation. Laurence (1956) found larvae, thought to belong to this species, breeding in cow-dung in pastures from October to March. They then entered diapause until September or even later. The adults are mainly active during winter . Hackman & Meinander (1979) bred this species from the fungi *Tricholoma impricatum, Stropharia hornemanni* and *Cortinarius trussiphorus.*

Trichocera sp. (Larval heads from sites 19; 24; 26; 39)

Plate 9 *Anisopodidae Sylvicola cinctus* 1 head of adult (dorsal view), showing a antennal sockets, p palp; 2 same, wing. *Sciaridae* 1 *Sciara thomae*, head of adult (dorsal view); 4 same, thorax (lateral view); 5 *Bradysia brunnipes*, wing; 6 same, head-capsule of final instar larva (ventral view), *Cecidomyiidae* 7 *Mayetiola* sp., "false puparium" (Scales 1,3-7 0,25mm; 2 1,0mm.) (Orig.)



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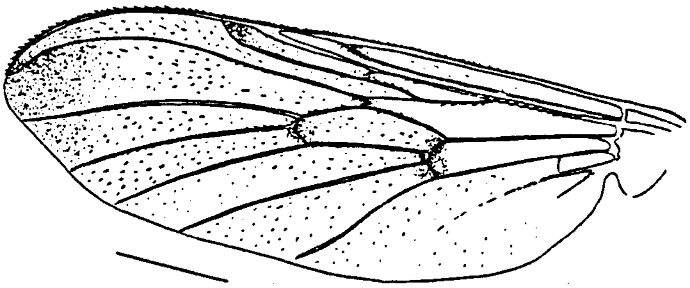

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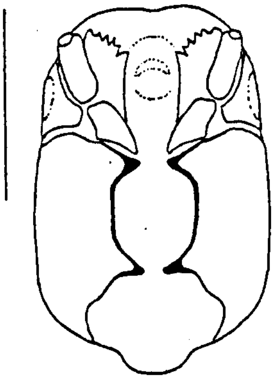

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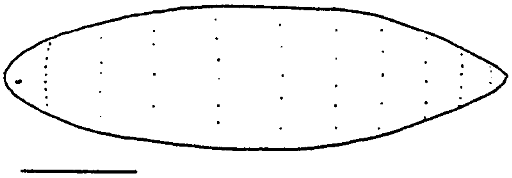

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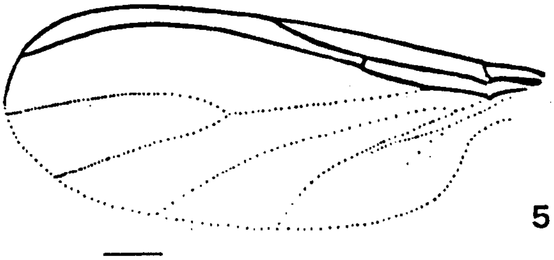

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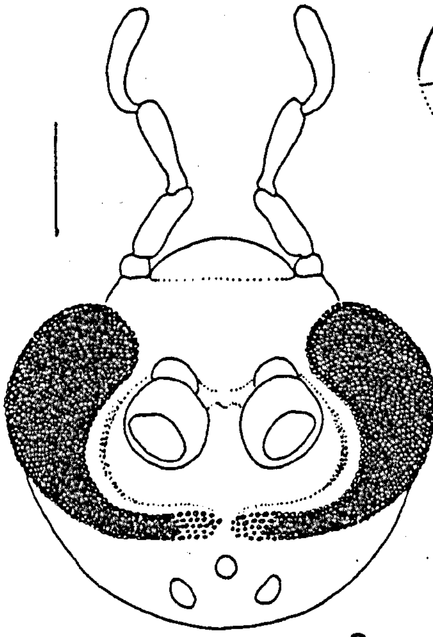

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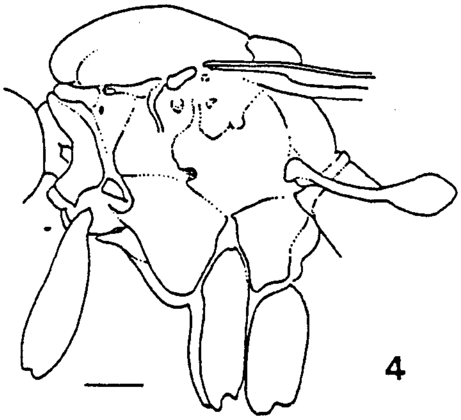

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Plate 9

Superfamily ANISOPODOIDEA

Family ANISOPODIDAE (Window gnats) (Plate 9; 1-2) [5 British]

Adults This very small family was represented by just one wing of *Sylvicola ?cincta*. Head with ocelli as in Trichocerids, but wing-venation is very different (fig. 2).

Larvae The larval head-capsule closely resembles that of *Trichocera* but the posteroventral marginal carina is sharply angulate between the distal ends of the tentorial rods (see *Trichocera*, Pl. 7; 7).

Pupae Similar to Trichocerids, but more strongly spiculate on head, thorax and abdominal segments. An examination of the pupae of several Anisopodid species during this study revealed striking differences. The findings will be published elsewhere.

Biology Anisopodids breed in a very wide range of decaying organic matter especially of vegetable origin, so they occur commonly in middens or accumulations of dung or sewage. The scarcity of the family in the material studied in this programme is therefore surprising. *S. punctatus* is only known to breed in cow-dung, whilst *S. zetterstedtii* develops commonly in rotten root-stocks of *Heracleum* and *Angelica*. Larvae of *S. fenestralis* often occur in profusion in sewage-bed filters.

Taxa represented

Sylvicola cinctus (Fabricius) or *fenestralis* (Scopoli) (wing from site 11)

Superfamily BIBIONOIDEA

Family BIBIONIDAE (Fever flies, St, Mark's flies) (Plate 10) [20 British]

Adults Fragments of adult Bibionids, especially heads, thoraces and wings, occur commonly as subfossils and should pose no problems in referring to the correct family, or often genus. Males have holoptic eyes with a sharp lateral demarcation between the enlarged dorsal and much smaller ventral facets (fig. 1). The eyes in the female are much smaller with the post ocular regions correspondingly enlarged (fig. 2-5). The relative lengths of the head before and behind the eyes differs greatly between species; thus, in *Dilophus febrilis* (fig. 3) the anterior part of the head is relatively much longer than in *D. femoratus* (fig. 4). In most species of *Bibio* this part is even shorter (fig. 5). In *Dilophus* the front part of the thorax has two transverse rows of strong spinose tubercles, which are particularly well-developed in the female (fig. 1, 2 and 7). These are absent in *Bibio* (fig. 8). The wing-venation (fig. 6) is highly characteristic, somewhat reminiscent of the much smaller Scatopsids in that the subcostal, costal and radial veins are usually much darker than the remainder.

Plate 10 *Bibionidae* *Dilophus febrilis* 1 head and thorax of male adult (lateral view); 2, same, of female (lateral view); 3 head of female (anterior view); 7 thorax of female (dorsal view); 4 *Dilophus femoratus*, head of female (anterior view); 5 *Bibio nigriventris*, head of female (anterior view); 6 *B,johannis*, wing; 8 *B,marci*, thorax of male (dorsal view) (inset shows front thoracic margin of female); *Bibio* larvae 9-11 ventral, dorsal and lateral views respectively; 12 head-capsule of final instar (dorsal view); 13 same (ventral view); *Dilophus* larvae 14 head and thorqacic segments (dorsal view); 15 same, posterior abdominal segments (dorsal view); 16 head-capsule of final instar larva (ventral view); 17 same (lateral view), (Scales 1-7 0,20mm; 8 1,0mm; 9,11,14,15 0,6mm; 12,13,16,17 0,5mm,) (Orig,)

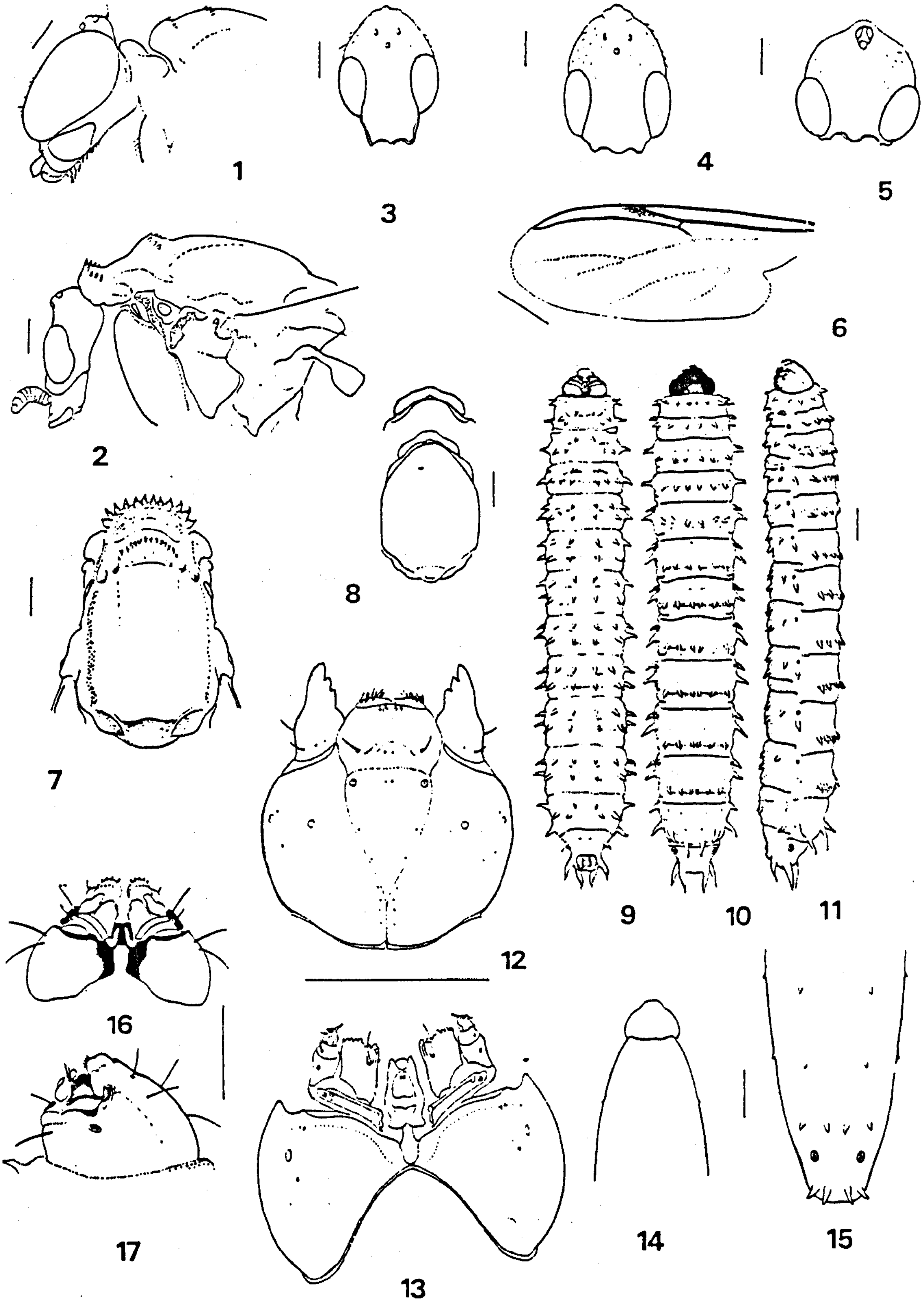


Plate 10

Larvae Holopneustic, having the primitive arrangement of spiracles on all body segments (fig. 9-11). The skin is rather durable, and almost complete subfossil skins have been found. The non-retractile head-capsule is of unmistakable form (fig. 12, 13, 16 and 17). All body segments have spiniform processes, but these are much stronger in *Bibio* (fig. 9-11) than in *Dilophus* (fig. 14, 15). The processes on the end-segment are long in both genera, but the posterior spiracles have three respiratory slits in *Dilophus* and two in *Bibio*.

Pupae No Bibionid pupae were found during this programme. For morphology see Smith (1989).

Biology Bibionids breed mainly in humus soil, compost and decaying plant matter, but will also attack roots of herbaceous plants where they may reach pest status. The adults are short-lived, most species being univoltine with a spring swarming period. A few however fly during summer or autumn. The bivoltine *Dilophus febrilis* swarms in spring and summer.

Taxa represented

Bibio ?johannis (Linnaeus) (Wing from site 21)

B. marci Linnaeus (Adult thorax from site 1)

B. ?nigriventris Haliday (Adult fragments from sites 21; 25; 27)

B. pomonae (Fabricius) (Complete larval skin from site 35)

Dilophus febrilis (Linnaeus) (Adult fragments from site 5)

D. femoratus Meigen (Adult fragments from sites 19; 26; 27)

D. febrilis/femoratus (Adult fragments from site 36)

Spp. indet. (Larval heads and adult fragments from sites 11; 12; 25; 27)

NB. Thoraces of a *Dilophus* were found commonly in deposits from the Falkland Islands where no member of the genus is currently known.

Superfamily SCIAROIDEA

A huge superfamily comprising five families regionally and over 1000 species. Most are fungicolous in the larval stage. Despite their great abundance in most terrestrial environments however, they seldom appear in subfossil assemblages, as most are extremely fragile in pupal and adult stages. Although a few more eurytopic species can tolerate aquatic conditions, no truly aquatic Sciaroid appears to be known.

Family SCIARIDAE (Fungus midges) (Plate 3-5) [over 100 British]

Adults Adult Sciarids are characterised by the "eye-bridge", a narrow extension of the compound eyes across the frons, immediately behind the antennal bases (fig.3b). The wing-venation (fig.5) is highly uniform throughout the family, the main differences between taxa being the relative length of the costal section preceding the intersection of the radial vein and the arrangement of bristles on the base of the radial vein, and on the distal sections of the median and cubital sectors. The thoracic pleurae have a characteristic mid-pleural pit (fig.4p).

Larvae Subfossil Sciarid larval head-capsules have been scarce in this study. The familial characteristic is seen on the ventral surface, where the epicranial plates(genae) meet narrowly at two points(basally and medially) by virtue of two narrow bridges (fig.6x). Freeman (1983) figures the larval head-capsule of *Lycoriella solani*, whilst Smith (1989) figures that of *Bradysia brunnipes*. They appear to be identical and it is possible that there is very little diversity in cephalic structure throughout the family.

Pupae Sciarid pupae appear not to have been studied in any detail. The basal segment of the antennal sheath bears a strong curved spine, at least in several species including *Bradysia brunnipes.*

Biology Typical breeding situations for Sciarids include mammal dung, rotting wood, decaying fungi and decaying vegetable matter and humus in which fungal mycelia have permeated the medium.. Many occur in beds of cultivated mushrooms and potted house-plants, where they often reach pest status. Bird and mammal nests are also commonly colonised by Sciarids.

Taxa represented

Lycoriella/Bradysia sp. indet. Larvae of these genera are typical inhabitants of decaying compost and manure heaps. (A wing from site 27 belongs to a larger Sciarid with the radial vein meeting the costa opposite the median fork; several species of appropriate size and venation in both of these genera)

Bradysia sp. (A wing, length 3.7mm., from site 41)

?*Scatopsciara vivida* (Winnertz) Nielsen et al. (1954) regard this as a synanthropic species in Iceland, found in houses or in old hay. Widespread in Britain north to the Faroes, Iceland and recorded from West Greenland. (Wings with venation identical to that figured by Freeman (1983) for this very common species, but rather larger than normal, from site 27.)

Gen. spp. indet. (Adult heads and wings from sites 3; 14; 21; 27; 28; 36; 37; 41)

Family SCATOPSIDAE (Plate 11) [37 British]

Adult Small flies of highly characteristic appearance (fig. 2, 3), somewhat resembling Bibionids but much smaller. Similarly, the wings (fig. 2) have the costal, subcostal and radial veins blackened, the remainder clear. By far the commonest Scatopsid in archaeological deposits is the largest British species, *Scatopse notata*, in which the darkened veins far surpass the middle of the wing (fig. 2)

Larvae Peripneustic, with spiracles on prothorax and most abdominal segments (fig. 5). Larval head-capsules, wich are quite common in subfossil assemblages, with ventral median space between inner margins of epicranial plates on ventral surface (fig. 9). In *Scatopse notata*, and perhaps all members of this family, the larval skin is not shed when pupation occurs, but remains intact. It cannot however be regarded as a puparium since it remains soft and pliable, and, being devoid of melanin, its translucence persists. The larval integument bears a pattern of short setae arranged in a pattern which differs in all species described so far. In *S. notata* (fig. 5) each thoracic segment, and abdominal tergites 1 to 7, has five longitudinal dorsal rows. The end-segment (fig. 5-7) has two long, black, horn-like posterior spiracular processes, whilst the anal region (fig. 7) has a circlet of strong black spinose bristles.

Pupae *Scatopse notata* pupae (fig. 11, 12) are normally enclosed in the unmistakable final instar larval skin (fig. 5), but even when found free

Plate 11 *Scatopsidae* *Scatopse notata* 1 adult male genitalia (ventral view); 2 head and thorax of adult (lateral view); 3 same (dorsal view); 4 wing; 5 final instar larva (dorsal view); 8 head-capsule of same (dorsal view); 9 same (lateroventral view); 10 pupal prospiracular process; 11 pupa (ventral view); 12 same (dorsal view); 13 pupal end-segments (posterior view) a male, b female. (Scales 1-3, 10, 13 0,25mm; 4, 6, 7 0,5mm; 5, 11, 12 1mm; 8, 9 0,1mm.) (Orig.)

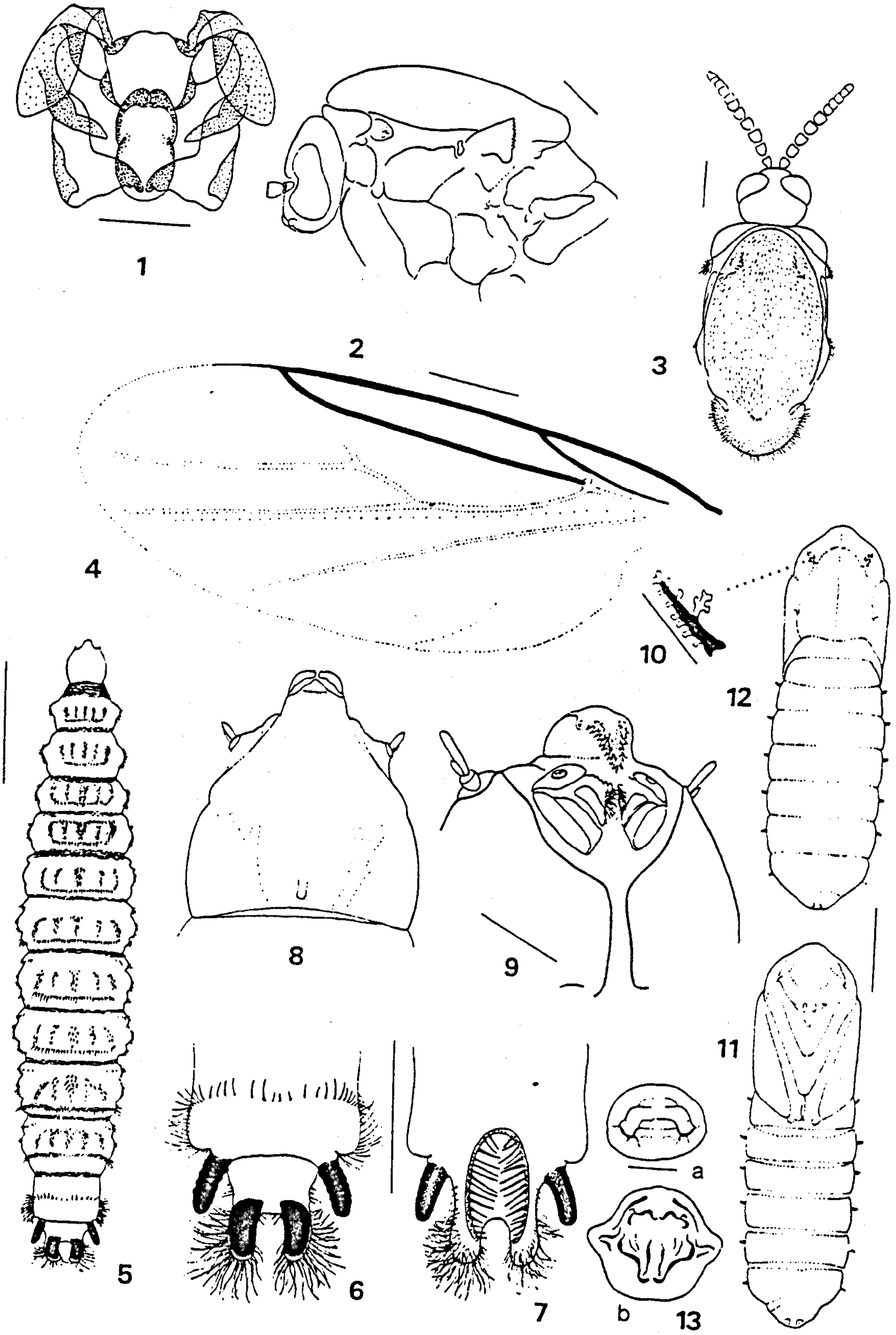


Plate 11

they should be readily referable to this family. They are rather fllattened dorsoventrally and have short spiracular processes on each abdominal segment (fig. 11, 12). The prospiracular processes are shortly plumose (fig. 10, 12). Very often the head and thoracic sections are missing, indicating that the flies had emerged, but even the end segments alone (fig. 13a, b) are distinctive.

Biology By far the commonest regional Scatopsid in archaeological deposits is *Scatopse notata*, and it is the only one known so far from Iceland and Greenland. It has been bred from wasps' nests, flower bulbs, onions, fruit-canning and wine-making residues, dung and rotting fungi (Smith 1989), decaying vegetation, carrion, guano, etc. It is a typical member of the fauna of cess-pits, manure heaps, middens, garbage-dumps and compost heaps. However, it also occurs far from human habitations, in such places as guano accumulations below bird-cliffs (Nielsen et al. 1954). The biology and morphology were reviewed by Morris (1918). Throughout much of the North Atlantic region it is hemisynanthropic and has been found in many of the samples from archaeological excavations examined from Britain and Iceland.

Taxa represented

Scatopse notata (Linnaeus) (Larval and pupal fragments from sites 3; 10; 11; 14; 16; 19; 22; 27; 28; 35; 36)

Rhegmoclema cookii Hutson (Pupal fragment, with complete male genitalia from site 19)

Family CECIDOMYIIDAE (Gall-midges) (Plate 9; 7) [c.600 British]

This huge family was represented by only a few "false flax seeds"- the "false puparia" of certain Cecidomyiid genera. The vast majority of these midges produce galls on a very wide range of plants, and many are extremely host-specific. Uniquely, amongst the Nematocera a small number of species form puparia reminiscent of those found in the Cyclorrhapha. However it appears that in some species the entire third larval instar is spent within this structure, which is actually the chitinised skin of the second instar larva. It cannot therefore be regarded as a true puparium. Indeed in *Sitodiplosis mosellana* the final instar larva vacates this "false puparium" to pupate outside (Barnes 1946-56). According to Barnes "false-puparia" occur mainly in the Oligotrophine genus *Mayetiola* , but also in *Dasyneura pyri* (Bouché) and in the cecidomyines *Sitodiplosis mosellana* (Géhin) and *Contarinia tritici* (Kirby). Apart from *Dasyneura pyri* all of these affect grasses. Superficially the Cecidomyiid "false puparia" very closely resemble Cyclorrhaphous puparia, especially those of the Ephydrid genus *Hydrellia*, but lack posterior spiracles and larval mouthparts. At present it is not possible to identify "false puparia" to genus.

Taxa represented

?Mayetiola sp. ("False puparia" from sites 3; 15; 19; 34; 36)

(Indetermined Nematoceran pupae from site 19).

(BRACHYCERA)

Superfamily TABANOIDEA

Family STRATIOMYIIDAE (Soldier flies) (Plate 12; 1-9) [50 British]

Puparia Almost uniquely amongst the Brachycera, Stratiomyiid pupae are enclosed in puparia- the hardened final larval instar skin. Almost all British species are fairly well-known in this stage so identification of complete specimens is relatively straightforward using Rozkošný (1973). Important diagnostic characters are general body form (fig. 1, 7), shape and chaetotaxy of the head-capsule (fig. 2-4) and body segments (fig. 1, 6, 7), and the underside of the end-segment (fig. 5, 9).

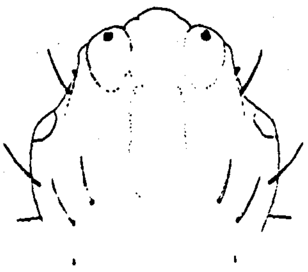
Biology Apart from the Pachygastrinae, which breed under the bark of dead trees, or in sap-runs, Stratiomyiids develop either in water, rich in detritus, in decaying vegetable matter, or in dung.

Taxa represented

?Oxycera sp. *Oxycera* larvae live amongst mosses, algae etc. usually in alkaline, nutrient-rich water. (Puparial fragments from site 3)

Chloromya formosa (Scopoli) Breeds mainly in dung. (Puparia from sites 3 and 19)

Plate 12 *Stratiomyiidae* 1 *Chloromyia formosa*, final instar larva (dorsal view); 2 head-capsule of same (ventral view); 3 same (dorsal view); 4 same (lateral view); 5 same, end segment (ventral view); 6 same, abdominal tergite showing surface sculpture and pattern; 7 *Oxycera* sp., final instar larva (dorsal view); 8 same, head capsule (dorsal view); 9 same, last two abdominal segments (ventral view). *Tabanidae Haematopota* sp. 10 pupa (ventral view); 11 same (lateral view); 12 same, end-segment (posterior view). (Scales all 0.5mm) (Orig.)



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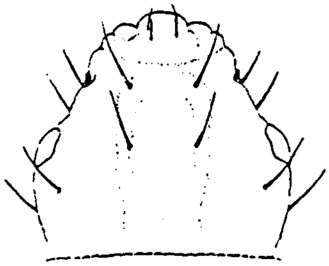

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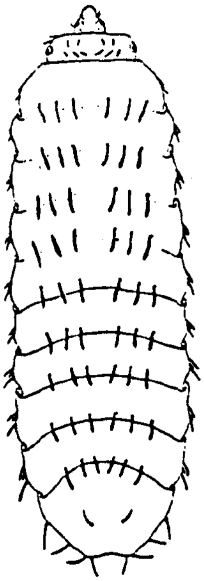

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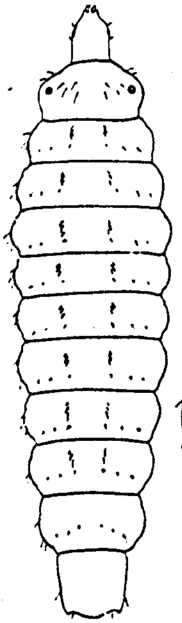

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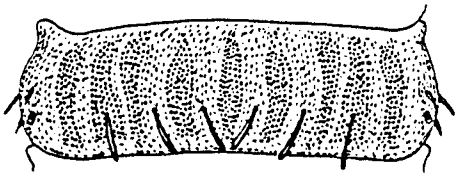

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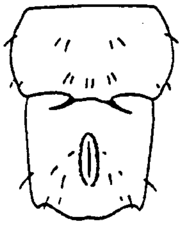

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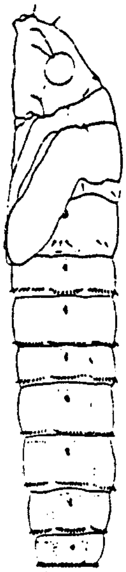

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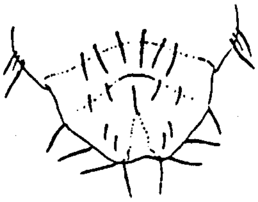

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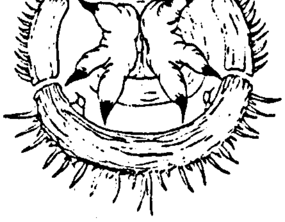


12

Plate 12

Family TABANIDAE (Horse-flies, Clegs etc.) (Plate 12; 10-12)

[29 British]

Pupae No detailed review of British Tabanid pupae exists, but the two pupae found in this study, appear, on details of facial mask, tergal spiculation and structure of the end-segment, to belong to *Haematopota* or *Chrysops*.

Biology *Chrysops* larvae are wholly aquatic whilst *Haematopota* also breed in drier soils, often far from water (Smith, *lc.*). Adult female tabanids feed on mammalian blood.

Taxa represented

Chrysops/Haematopota sp. (pupal fragments 19; 27)

Superfamily EMPIDOIDEA

Family HYBOTIDAE (Plate 13; 1,2 and 4) [170 British]

Adults Only two Hybotid taxa have been found during the present study, namely *Stilpon sublunatum* (fig. 1,2) and *Trichina clavipes* (Fig. 4). The former is a minute, shiny blackish fly, with a remarkable head structure and highly distinctive venation and wing markings. In *Trichina*, the wing venation resembles that of several related genera and members of the largest Empid genus, *Hilara*.

Biology All adult Hybotids are probably predaceous but the immature stages are almost entirely unknown. *Stilpon sublunatum* is only known to occur in lowland peat bogs, where it may be found in great profusion.

Taxa represented

Stilpon sublunatum Collin (adult heads, wings etc. from site 5)

Trichina clavipes Meigen (wing from site 21)

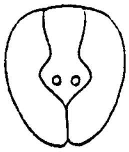
?*Trichina* sp. ("Empid pupa 1") Short-spined pupae; tergal spine-bands comprising of a median row of minute spines and an apical row of longer ones which are of various sizes, some being twice as long as others. Larger, more isolated spines on penultimate segment. Abdominal spiracular openings obscure but prothoracic ones peculiar, being oval with wavy median transverse region delineated. Inner region of front metatarsal cover strongly dentate. pupae, one complete with adult 21)

Family EMPIDIDAE (Plate 13; 3,5-8) [206 British]

Pupae Very few Empid pupae are known but several were found in this study. The typical form, found in *Rhamphomyia* and *Empis* is shown in fig.5 and 6. Distinctive features include the facial mask with its pronounced proboscis-sheath, the hind leg-sheaths which protrude shortly beyond the wings, and the abundant clothing of long bristles on the abdominal segments. *Hemerodromia* pupae are remarkable on account of the eight pairs of extremely long respiratory filaments arising from the thoracic and abdominal spiracles (fig.7,8). Too little is known at present to distinguish Hybotid from Empid pupae.

Adults Empid adults, which exhibit great diversity of form, were only represented by two specimens in the current study, namely a wing of *Hilara chorica (fig.4)* and a thoracic fragment of an unidentified *Empis*

Plate 13 *Hybotidae* 1 *Stilpon sublunatum*, adult (lateral view) showing wing-markings; 2 same, head (anterior view), *Empididae* 3 *?Empis/Rhamphomyia* sp., incomplete thorax from specimen from peat on Thorne Moor; 4 *Hilara chorica*, wing; 5 *Rhamphomyia* sp., pupa (ventral view); 6 same (lateral view); 7 Hemerodromiine pupa (dorsal view); 8 same, single abdominal segment (anteroventral view). (Scales 1,2,4 0,20mm; 3,7,8 0,25mm; 5,6 1,0mm) (7 after Brindle, rest orig.)



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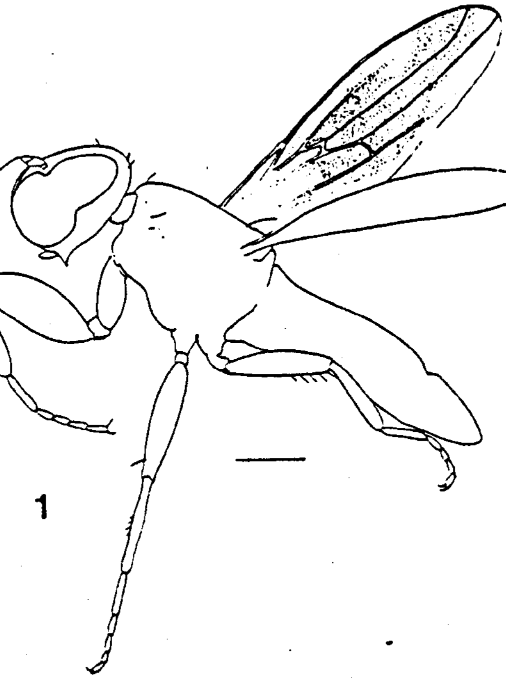

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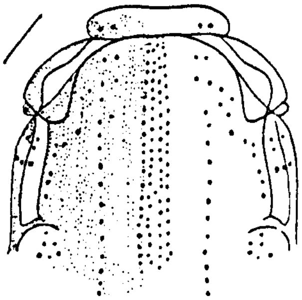

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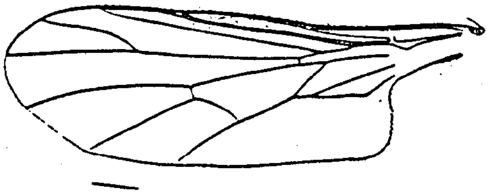

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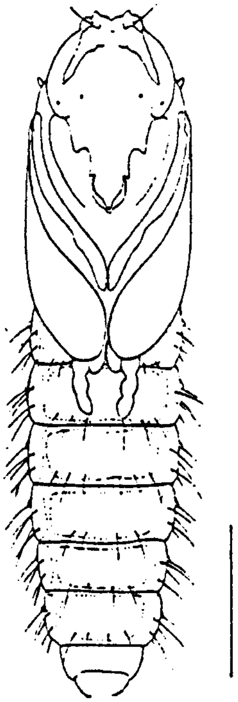

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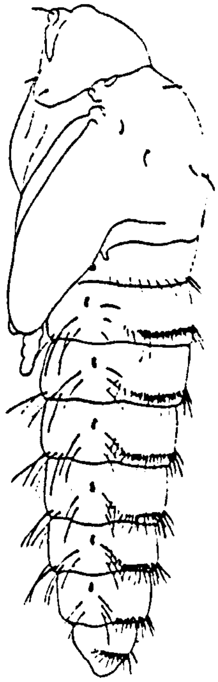

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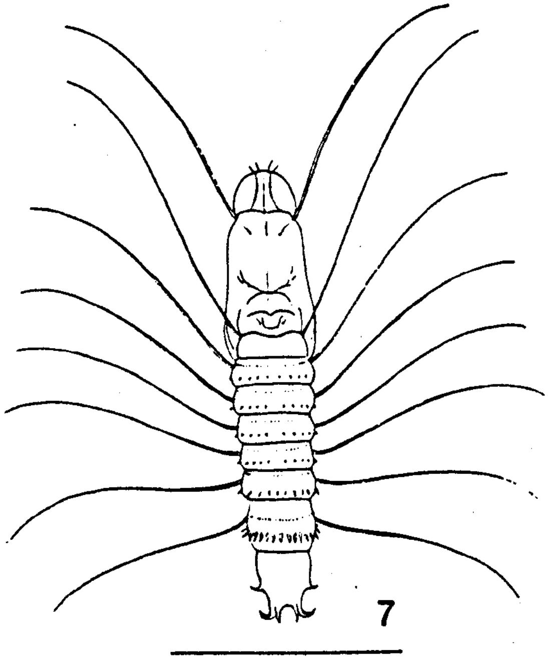

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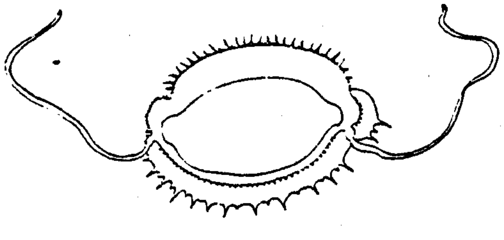

8

Plate 13

or *Rhamphomyia* (fig. 3). The former is distinguished from its congeners by its small size and darkened costal stigma. The structure and chaetotaxy of the thorax in *Rhamphomyia* and *Empis*, is rather distinctive.

Biology Adult Empids, like Hybotids, prey on other insects. Again, the immature stages of very few species are known. The Hemerodromiinae are mostly aquatic in the preimaginal stages, some pupae being remarkably well adapted to this purpose. Other common biotopes for immature Empids include humus soil or organic mud, mosses and decaying wood.

Taxa represented

Rhamphomyia ?simplex Zetterstedt (Pupal fragment from site 35)

?R. sp. (Pupal fragments from site 21)

Empis or *Rhamphomyia* sp. (Adult thoracic fragment from site 15)

Hilara chorica (Fallén) (Wings from sites 19 and 21)

"Hemerodromiine sp." ("Empid pupa 2a") Tergites only found; spine-bands as in sp. 1 but apicals much stronger, fewer, more widely-spaced; spiracles with very long filamentous processes. Several from site 21).

"Empid pupa 2b (= ?front half of 2a). No overlapping fragments to prove that a and b belong to same species, but b has identical very long filaments arising from prothoracic and first abdominal spiracles. Several from site 21)

"Empid pupa 3" ("long-haired type") No median tergal spine-band and tergal hind margins irregularly serrate with tips of the teeth endingin long fine bristles. Spiracles obscure. Several from site 21)

Family DOLICHOPODIDAE (Long-headed flies, "Dollies") (Plate 14)

[c.270 British]

Pupae Although very few Dolichopod pupae have been described, all are very alike in the highly characteristic facial mask. This has a central longitudinal channel traversed by three irregular transverse ridges of which the anterior pair are in the antennal region (fig. 1, 2, 6 and 7). The prothoracic horns are very long and apico-ventrally flattened (fig. 1, 4), the leg-sheaths reach at least to the middle of the abdomen (fig. 1), and the tergites have at least one row of serrations along their apical margins (fig. 1, 3 and 5). Too few pupae are known yet for a generic key to be prepared, but the facial mask shows diversity in the form of the transverse ridges (see figs. 2, 6 and 7), and a range of form is also found in the shape of the prothoracic horns.

Adults The wing-venation is remarkably constant in this family (fig. 8) and rather distinctive by virtue of the absence of the median cross vein found in the otherwise similar Cyclorrhaphous type (cf. Pl. 17; 9, etc.). The head also is often very characteristic, with the sunken vertex and swollen bases of the large vertical and ocellar bristles (fig. 9, and 10). Most Dolichopodid adults, unlike other Empidoids,

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Plate 14 *Dolichopodidae* 1 *Dolichopus plumipes*, pupa (lateral view); 2 same, anterior part showing facial mask and prospiracular horns (ventral view); 4 same, prospiracular horns; 5 same, details of armature on tergal margins; 7 same, details of facial mask (left side only); 9 same, adult head (anterior view); 10 same (dorsal view). 3 *Rhaphium* sp., armature on pupal tergal margins; 6 same, facial mask of pupa. 8 *Sympycnus desoutterri*, wing. (Scales 1,2 0.5mm; 6,7,9,10 0.25mm; 3 0.20mm; 8 0.2mm)) (Orig.)

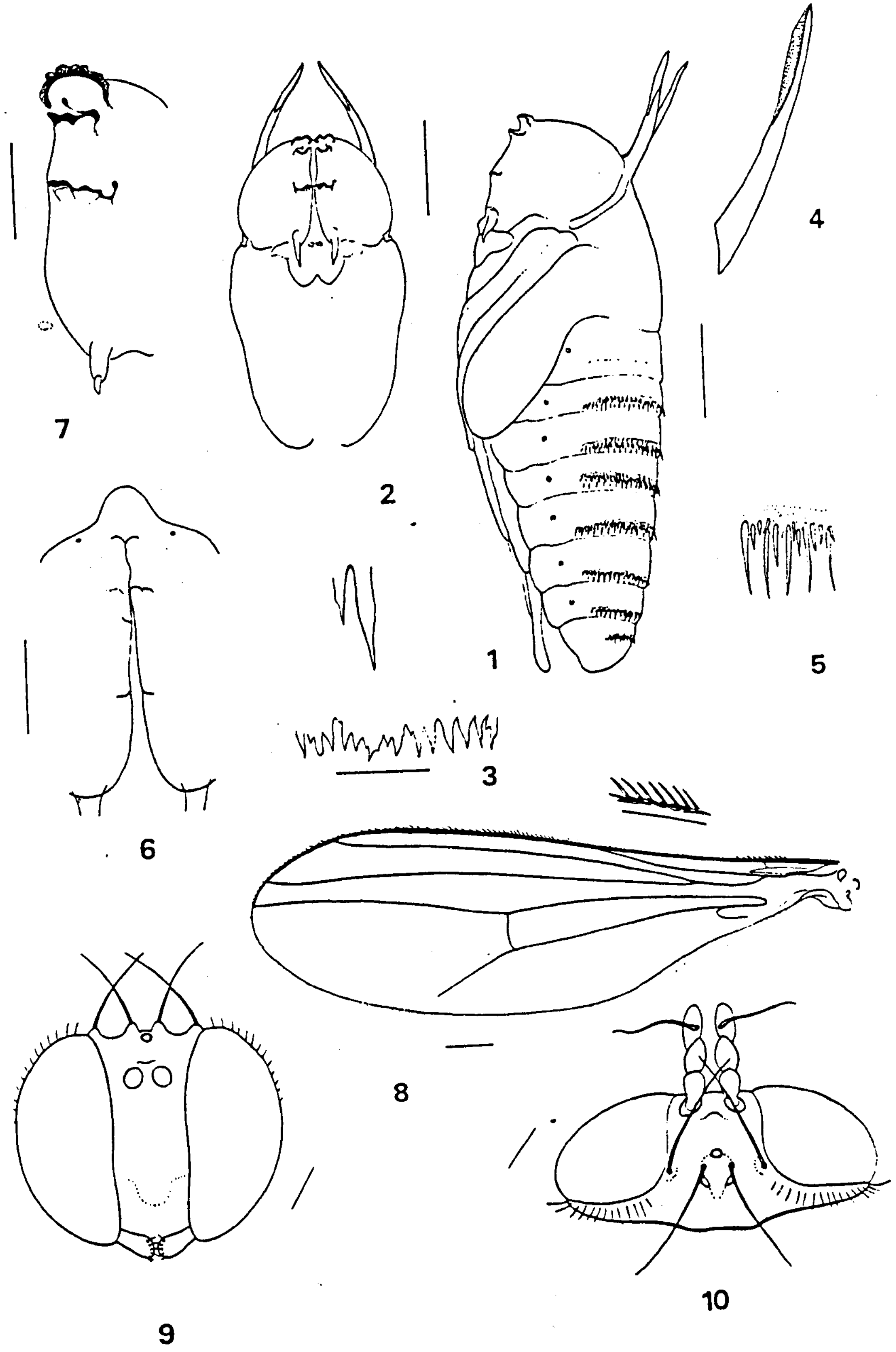

Plate 14

Empidoids, are of a bright metallic colour. These colours often survive in subfossil material.

Biology The main biotopes for larval Dolichopodids are decaying parts of trees (including workings of lignicolous insects and sap-runs), humus soil (including decaying vegetation etc), and water or mud with a high detritus content. Many species develop in mud or wet sand in inland or estuarine marshes, or in the littoral zone. *Aphrosylus* species are marine carnivores whilst *Thrypticus* are leaf-miners.

Taxa represented

Dolichopus plumipes (Scopoli) (Pupal fragments from sites 28 and 35)

Rhaphium sp. (Adult head from site 21)

Campsicnemus loripes (Haliday) (Wing from site 21)

Sympycnus desoutteri Parent (Wing from site 27)

Gen. spp. indet. (Adult fragments from sites 5; 19; ?21)

"Dolichopodid pupa 1" (Apical tergites only; no spine bands but basal half of tergites densely spiculate-tuberculate with region of isolated very long bristles behind. Apical segment conical with rounded apex bearing 2 outwardly divergent hooks. Several from site 21)

?*Rhaphium* sp. ("Dolichopodid pupa 2") (Tergal margins strongly dentate with irregular long teeth; spiracles obscure. Facial mask with conspicuous groups of spines on inner margins of eye-covers. Several from site 21)

(CYCLORRHAPHA ASCHIZA)

Superfamily LONCHOPTEROIDEA

Family LONCHOPTERIDAE (Pointed-winged flies) (Plate 15; 4) [7 British]

Adults On wing-venation alone (text-fig. 3 and Pl. 15 4) these flies cannot be confused with any other Diptera. Moreover, even the sexes differ in the shape of the anal vein.

Biology Adults and larvae of the monotypic genus *Lonchoptera*, are found amongst damp, decaying vegetable matter.

Taxa represented

Lonchoptera lutea Panzer (wings 21; 27)

Superfamily PHOROIDEA

Family PHORIDAE (Plate 15; 1-3)

[c. 300 British]

Puparia Far too few Phorid puparia are known to produce a generic key so positive identification of empty puparia is impossible at present. A number of puparial forms are distinguishable however. In *Conicera* and *Diplonevra* there are rows of strong lateral (and often dorsal) processes on all body segments (fig. 2), giving a strong superficial resemblance to the totally unrelated Fanniidae (see Plate 27; 13 and 14). The main differences are in the long pupal respiratory horns in Phorid puparia, and in the different shapes and situations of the posterior spiracles. In the huge genus *Megaselia*, two puparial forms

Plate 15 *Phoridae* 1 *Megaselia "nigra* type", puparium (dorsal view); 2 *Conicera/Triphleba* puparium (dorsal view); 3 *Megaselia* sp., wing. *Lonchopteridae Lonchopter lutea* 4 wing of female (inset shows anal veins of male). *Syrphidae* 5 *Eristalis tenax* puparium (dorsal view); 6 same (ventral view); 7 *Platycheirus clypeatus* aggr., adult male (dorsal view) showing abdominal markings; 8 head of same (anterior view) (Scales 1-3,5,6 1,0mm; 4 0,5mm; 7,8 0,25mm) (Orig.)

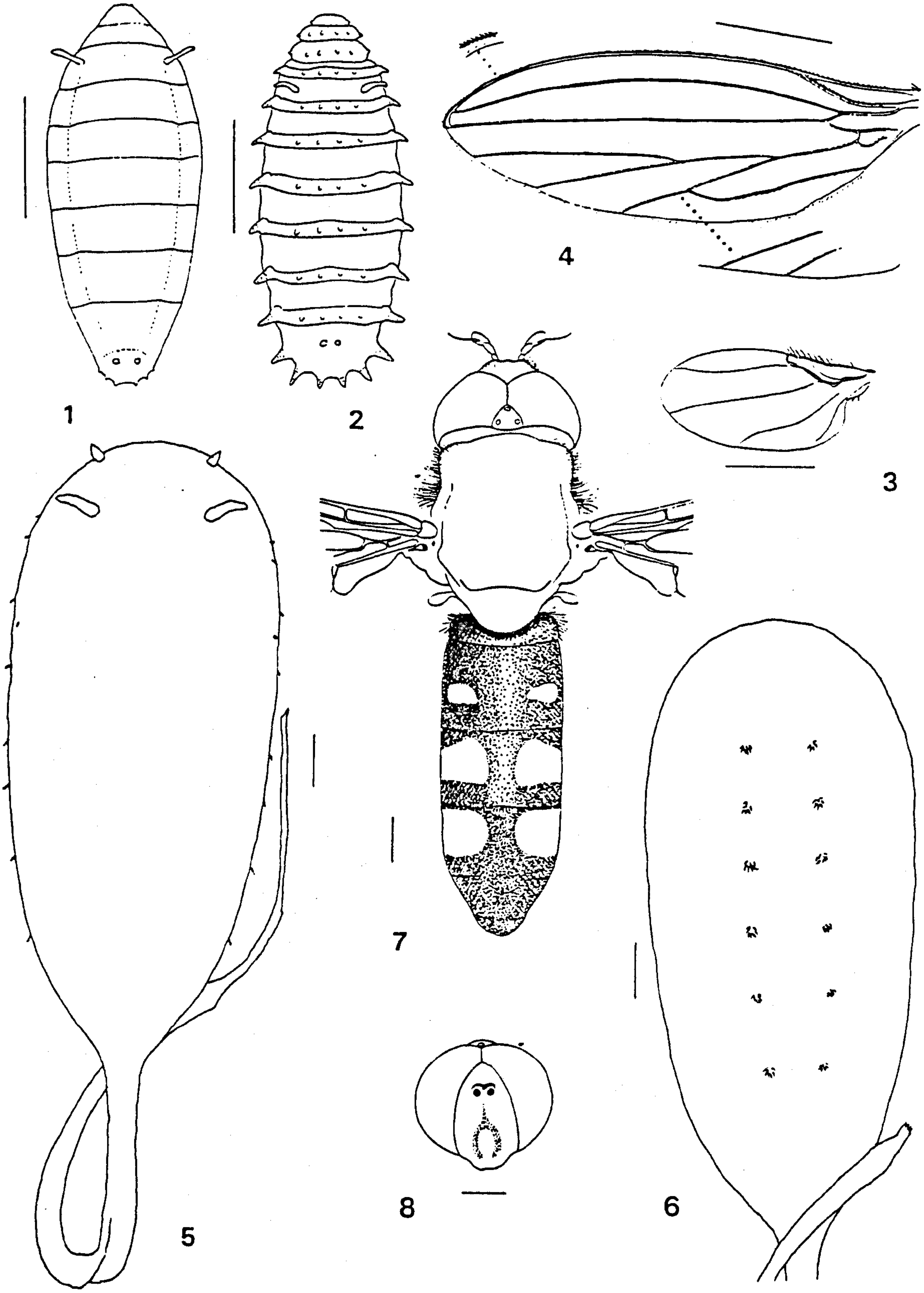

Plate 15

have long been recognised; in the *M. rufipes* type the end-segment has three pairs of tiny marginal tubercles (fig. 1), which are absent in the *M. nigra* type. *Metopina* puparia are unusually small in size.

Biology *Megaselia* species breed in decaying plant and animal matter, dung etc., and sometimes parasitise other insects (Smith *lc.*).

Adults In this huge and taxonomically difficult family, identification of adults relies largely on genitalic and other features which do not survive subfossilization. The Phorid type of wing-venation (fig. 3) however is quite different from that found in any other dipterous family, and these have been found in several deposits during this study.

Taxa represented

?Conicera/Diplonevra sp. (Puparia from site 8)

Megaselia "nigra" type puparia. (Puparial fragment from site 35. (*M. (Aphiochaeta) groenlandica* Lundbeck, the only Phorid known from the Nuuk (Godthaab) area, is unknown in the puparial state)

M. "rufipes" type puparia. (Puparial fragments from sites 9; ?11; 35)

M. spp. indet. (Puparia and wings from sites 3 (at least two species); 21; 28; 30; 35; ?41)

?Metopina sp. (Puparia from site 8)

Gen. spp. indet. (Puparial fragments from sites 1 and 24)

Superfamily SYRPHOIDEA

Family SYRPHIDAE (Hover-flies, Drone-flies etc.) (Plate 15; 5-8)

[242 British]

Puparia This family contains a wide range of puparial forms, but the only type found in this study was the "Rat-tailed maggot", *Eristalis* *tenax*. In this type (fig. 5 and 6) the anal spiracles are located at the end of a very long respiratory siphon and there are prominent anterior respiratory horns. There are six pairs of ventral abdominal false-legs crowned with strong curved spines (fig. 6). The major work on the ecology, biology and morphology of immature stages of Syrphidae is Rotheray (1993).

Adults Many adult Syrphids are mimics of bees and wasps, often being boldly marked in black and yellow (fig. 7). Tergites of such hoverflies have been recovered during this study. Heads of Syrphid adults can sometimes be recognised amongst subfossil assemblages by their relatively large size, facial protuberance and the absence of a ptilinal suture. The heads of other British Schizophora are smaller than most Syrphids and lack the facial prominence.

Biology A very wide range of ecological niches are occupied by members of this large and well-studied family (see Rotheray *op. cit.*)

Taxa represented

Platycheirus clypeatus s. lat. Larvae probably general scavengers in leaf litter (Rotheray *op. cit.*). (Adult tergal fragment from site 21)

Brachyopa ?scutellaris Robineau-Desvoidy Larvae in sap-runs on sickly trees (Rotheray *op. cit.*). (Adult thorax from site 15)

Eristalis abusivus Collin or *arbustorum* (Linnaeus) Larvae in organic mud or amongst waterlogged, decaying vegetation; often in water with high faecal content. (Adult head and thorax from site 19).

E. tenax (Linnaeus) Breeds in places with a high animal sewage content such as farmyard drains etc. (Smith 1989). Also in cess pits and amongst liquified domestic garbage, where the telescopic respiratory siphon allows the larvae to penetrate deep into anaerobic areas. (Puparia from site 3).

?Syrphid sp. indet. (Puparial fragment from site 27)

(CYCLORRHAPHA SCHIZOPHORA)

(ACALYPTERAE)

Superfamily TEPHRITOIDEA

Family *Otitidae* (Plate 16; 1) [20 British]

Puparia An unusual feature of all known Otitid larvae is the dorsal scar on the posterior spiracle (fig. 1).

Biology The immature stages and biology of *C. urticae*, puparia of which were found in this study, were discussed by Lobanov (1964), who found the larvae in manure and rotting vegetation. Other Otitid larval pabula include decaying parts of herbaceous plants, compost heaps and beneath the bark of dead trees.

Taxa represented

Ceroxys urticae(Linnaeus) (puparia 19)

Superfamily MICROPEZOIDEA

Family MICROPEZIDAE (Stilt-legged flies) (Plate 16; 5-9) [8 British]

Puparia Posterior spiracle with strong dorsal tooth and respiratory

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Plate 16 *Otitidae* 1 *Ceroxys urticae*, postspiracular region of puparium (posterior view). *Psilidae* 2 *Loxocera* sp., end segment of puparium (posterior view); 3 same (lateral view); 4 same, posterior spiracle. *Micropezidae* 5 *Calobata cibaria*, puparium (ventral view), showing detail of prospiracular process; 6 same (dorsal view); 7 same, end segment (posterior view); 8 posterior spiracle; 9 end segment (lateral view) (Scales 1, 0.6mm; 2,3,7-9 0.25; 4 0.12mm; 5,6 0.8mm) (Orig.)

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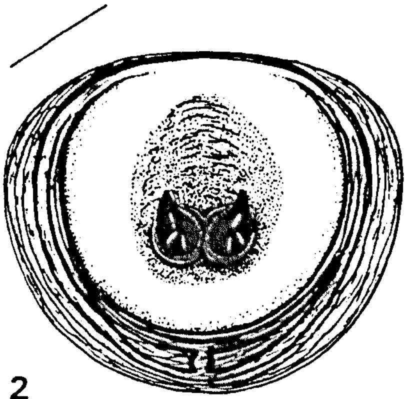

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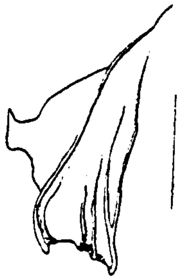

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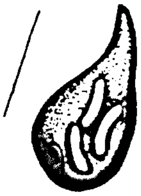

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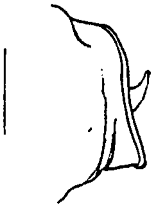

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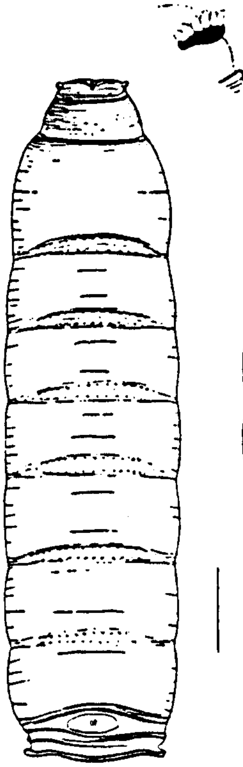

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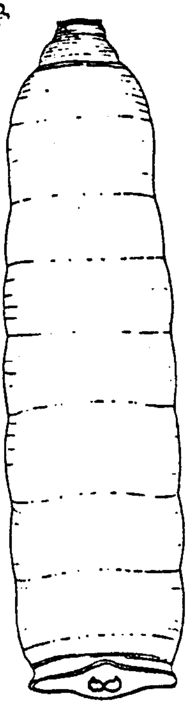

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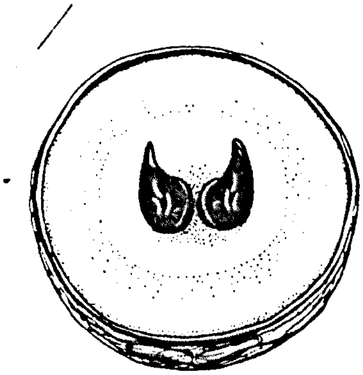

7

Plate 16

slits with unusual allignment (fig.7,8). In some *Calobata* species, they are crescentic to U-shaped, and the end-segment has a prominent rim around the perispiracular field (fig.5-9).

Biology *Calobata* larvae have been found about plant roots in riverside sand-banks, decayed grass-heaps (Brindle 1965) and mineralised pig-manure (Lobanov 1960).

Taxa represented

Calobata petronella (Linnaeus) (puparium from site 27)

Superfamily TANYPEZOIDEA

Family *Psilidae* (Carrot-flies etc.) (Plate 16; 2-4) [27 British]

Puparia. Distinctive features of Psilid puparia are the dorsal spiniform processes on the posterior spiracles and the unusual arrangement of the respiratory slits (fig.2-4), which converge towards the median scar, unlike those of Micropezids.

Biology. Psilids are phytophages, affecting a wide range of vascular plants (eg. Orchidaceae, Asteraceae etc.), and in conifer resin. *Psila rosae* attacks various Umbelliferae.

Taxa represented

?Loxocera sp. Larvae mine in stems of *Juncus*. (puparia 19)

Superfamily SCIOMYZOIDEA

Family SEPSIDAE (Plate 17; 1-11) [27 British]

Puparia. In *Orygma* the puparium is large and relatively unmodified, save for the massive posterior spiracles (fig.10) whose slits are arranged in a very similar manner to *Coelopa* (fig.11). In the other genera the seventh segment is often densely spiculate, and the conical end-segment has tubercles arranged in a distinctive manner and is produced behind into spiracular processes (fig. 1-7).

Adults. Wings of adult Sepsids have been found in this study. Those of *Sepsis* have an apical dark spot.

Biology. *Orygma luctuosum*, morphologically and ecologically the most aberrant regional Sepsid, is an abundant and widespread member of the wrack-bed fauna, occurring throughout the North Atlantic including Greenland. Many *Sepsis* species breed in dung herbivore dung, whilst *Themira* and *Nemopoda* often abound in cess-pits (esp. *T. putris*), rotting sodden vegetation, and masses of goose dung and algae on lake shores.

Taxa represented

Themira ?dampfi Becker (Puparial fragments from site 36)

T. ?leachii Haliday (Wing from site 21)

T. ?putris (Linnaeus) (Puparia from sites 6 and 7)

T. sp. indet. (Puparium and wing from sites 11 and 18)

Orygma luctuosum Meigen (Puparial fragments from sites 22; 27; 41)

Gen. spp. indet. (Puparial fragments from sites 3; 10; 14; 16, 19; 21; 36;)

Plate 17 *Sepsidae* 1 *?Themira* sp., puparium (ventral view); 2 same (dorsal view), showing detail of prospiracular process; 3 same (lateral view); 4 same, posterior spiracle; 5 same, puparium (ventral view) showing detail of prospiracular process; 6 same (dorsal view); 7 same, end segment (lateral view); 8 same, posterior spiracle; 9 *Sepsis punctum*, wing; 10 *Orygma luctuosum*, puparium (dorsal view), showing detail of posterior spiracular process; 11 posterior spiracle. *Sciomyzidae* 12 *Tetanocera elata*, head of adult (lateral view); 13 same (dorsal view). (Scales 1,2,3,11 0.25mm; 5,6,9 0.6mm; rest ?) (Orig.)

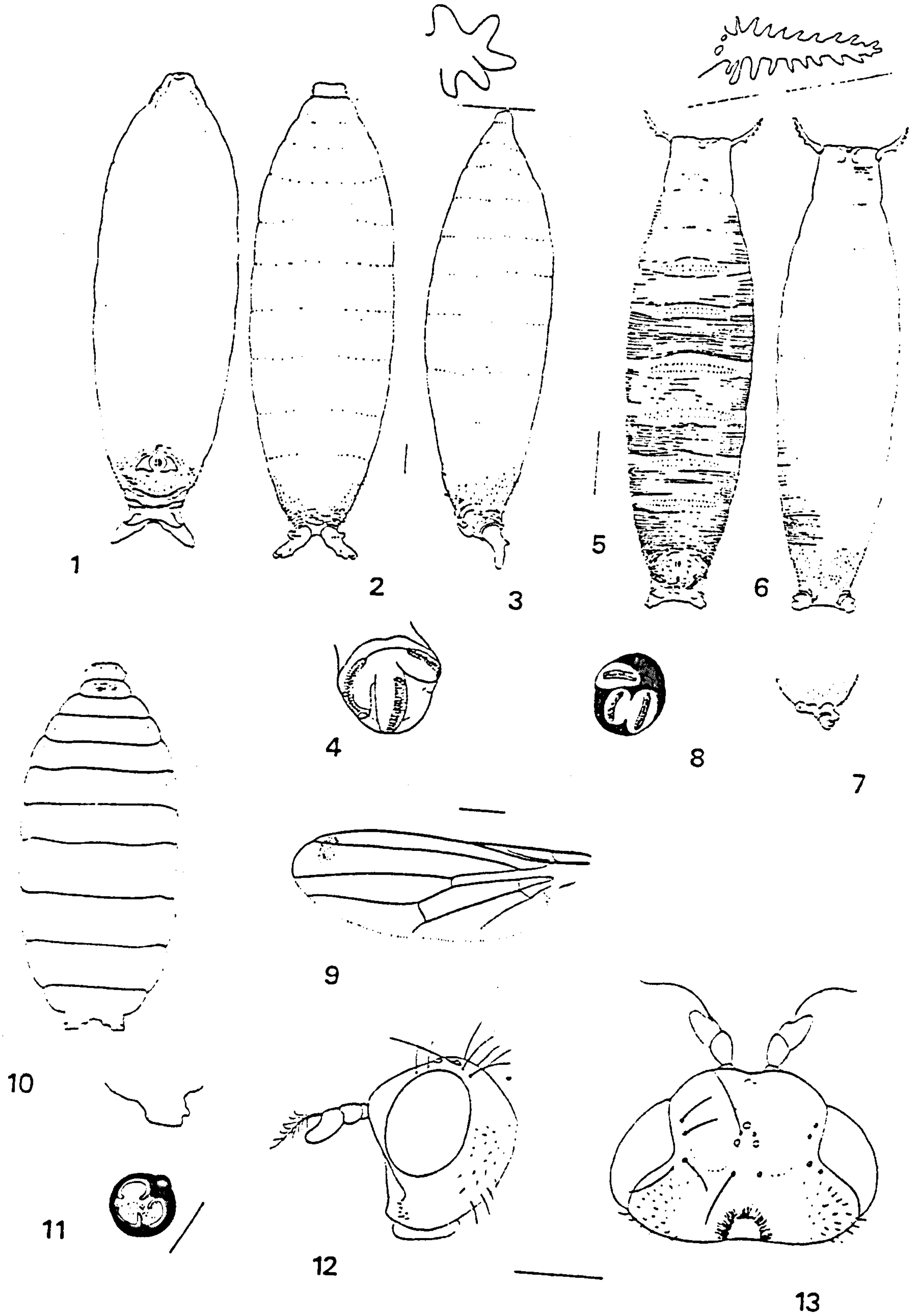

Plate 17

Family SCIOMYZIDAE (Snail-killing flies) (Plate 17; 12, 13) [65 British]

As the name suggests, these flies parasitize snails, some attacking only the egg-masses, whilst others are apparently free-living predators on small aquatic snails.

Taxa represented

Tetanocera sp. (adult head fragment from site 12)

Superfamily HELOMYZOIDEA

Family *Coelopidae* (Shore flies) (Plate 18) [3 British]

Puparia. The puparium of *Coelopa(fig. 6-8)* differs from that of any other genus of flies in the huge, remote, posterior spiracles (fig. 9), whose slits are arranged very like those of *Orygma (fig. 10)*.

Adults Adult *Coelopa* possess many rather distinctive features, including the strongly concave face(fig. 1) and the leathery, closely shagreened thorax (fig. 4, 5)

Biology. Coelopids are characteristic members of the wrack-bed fauna where they often breed in utmost profusion. *C. frigida*, whose biology is the subject of much research pioneered by Egglishaw (1960); (Smith 1989), occurs throughout coastal regions of the eastern North Atlantic,

Plate 18 *Coelopidae, Coelopa frigida* 1 head of adult (lateral view); 2 same (dorsal view); 3 wing, showing detail of costal vestiture; 4 thorax (dorsal view); 5 same, showing detail of surface scupture and tubercular alveoli; 6 puparium (dorsal view); 7 same (ventral view); 8 same, showing anal region; 9 puparial end segment (posterior view); 10 posterior spiracle. (Scales 1,2,9,10 0.25mm; 3,4,6,7 0.5mm) (Orig.)

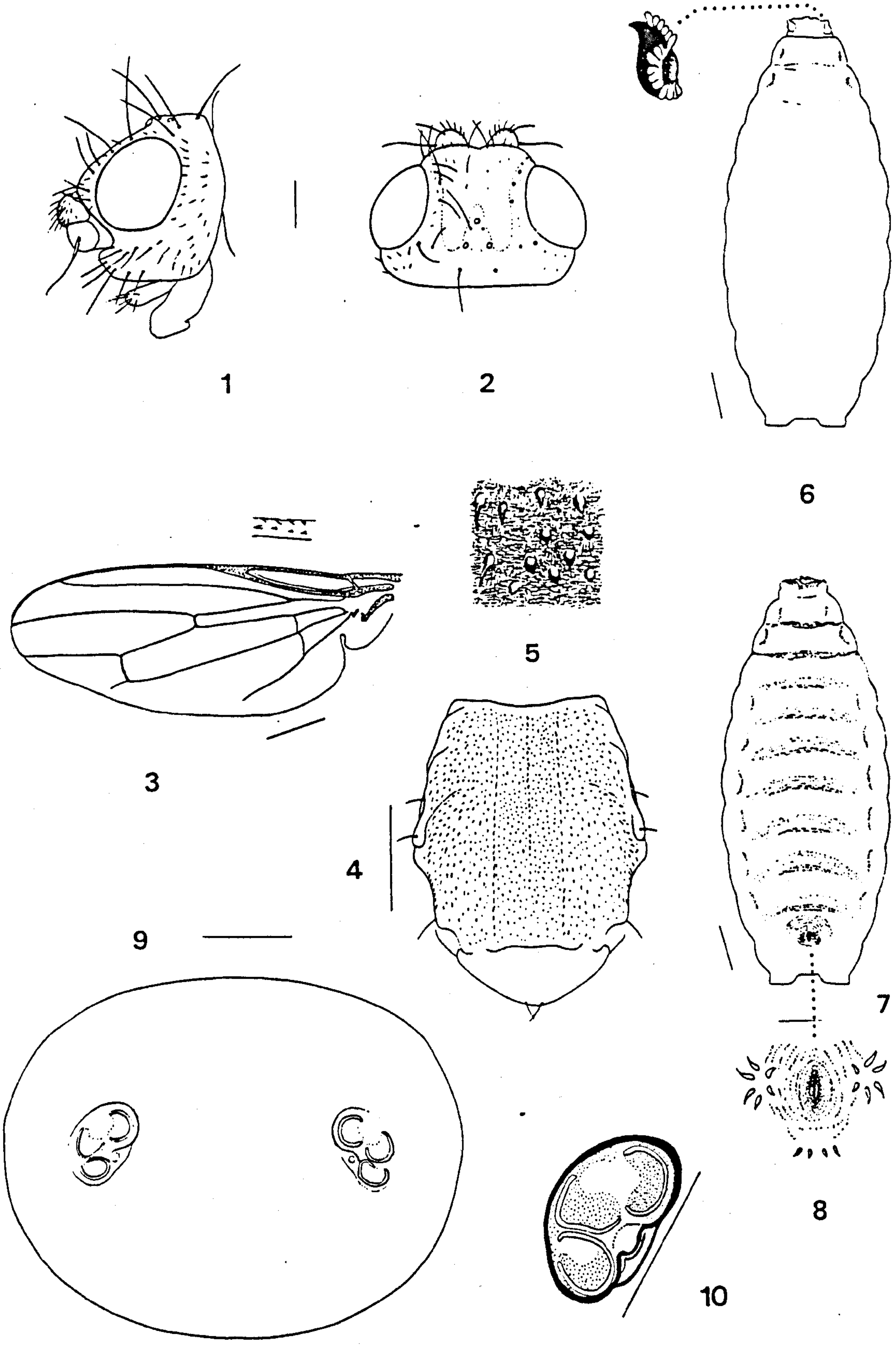

Plate 18

including Iceland. The genus is absent however from Greenland.

Taxa represented

?Malacomyia sciomyzina (Haliday) (Adult fragment from site 27)

Coelopa frigida (Fabricius) (Puparia and adult fragments from sites 21 and 27)

Family Helcomyzidae [2 British]

Puparia In *Heterocheila buccata* the posterior spiracles are relatively smaller than in Coelopids or *Orygma;* the peritreme is unmodified and the slits converge towards the median scar. In *Helcomyza ustulata* the peritreme is produced into a strongly curved dorsal tooth.

Biology. Both species are only known to breed in decaying seaweed on the coast, but exhibit stark differences in choice of microhabitat (see Smith 1989). Unlike *Helcomyza ustulata, Heterocheila buccata* does not belong to the wrack-bed fauna, but breeds in *Laminaria* buried in the sand.

Taxa represented

Heterocheila buccata (Fallén) (Puparium from site 27)

Family HELEOMYZIDAE (Plate 19, 20; 1-5) [61 British]

Puparia In *Heleomyza* the puparium is usually strongly transversely ridged and the posterior spiracles are prominent, peg-like (Pl. 20; 1-4); the end-segment lacks perispiracular tubercles but there is a ventral, postanal pair (Pl. 20; 4). In *Neoleria* there are a pair of dorsolaterals. In *Neoleria, Tephrochlamys, Scoliocentra* and small specimens of *H. borealis*, the transverse ridges are absent, but the end-segment is very similar in all genera (Pl. 20; 1-4) Identifications should be confirmed by male genitalic characters (Pl. 19; 8-14).

Adults Wings of *Heleomyza* were abundant in some samples, the most distinctive feature being the strong costal spines (Pl. 19; 5, 6). In denuded examples the alveoli of the larger spines can usually be distinguished from those of the smaller ones.

Biology This family contains two major subfamilies of which the Suillinae are fungicolous flies, none of which has been encountered in this study. The Heleomyzinae on the other hand include the two most abundant species in the current research project, *Heleomyza borealis* and *serrata*. Heleomyzines are primarily necrophagous, some breeding only in carrion. More often however they appear to breed in excrement of omnivorous or carnivorous birds and mammals. Most have a marked preference for breeding in shaded, or entirely dark, situations, so that many breed only in caves or mammal burrows (ie. *Eccoptomera*, *Aecothea* and *Scoliocentra*). *Neoleria inscripta* is unusual in apparently

Plate 19 *Heleomyzidae* 1 *Heleomyza captiosa*, head of adult (lateral view); 2 same (dorsal view); 3 same, thorax (dorsal view); 4 same (lateral view); 5 same, wing; 6 same, detail of costal vestiture; 7 *Scoliocentra caesia*, male genital segment (lateral view); 8 same (internal view); 9 same (posterior view), showing posterior gonapophyses (a and b); 10 *?S. fraterna*, posterior gonapophysis from puparium from Sandnes; 11 *Neoleria inscripta*, male genital segment in a, lateral, b, posterior and c, interior view; 12 *Heleomyza captiosa*, male genital segment in a, lateral, b, posterior and c, interior view; d shows internal side of surstylus; 13 *Heleomyza borealis*, male surstylus from puparium from Sandnes; 14 *Heleomyza serrata*, male surstylus from puparium from Stóraborg. (Scales 1-5 0,4mm; 7-9, 11, 12 0,2mm; 10, 13 0,12mm; 14 0,25mm) (Orig.)

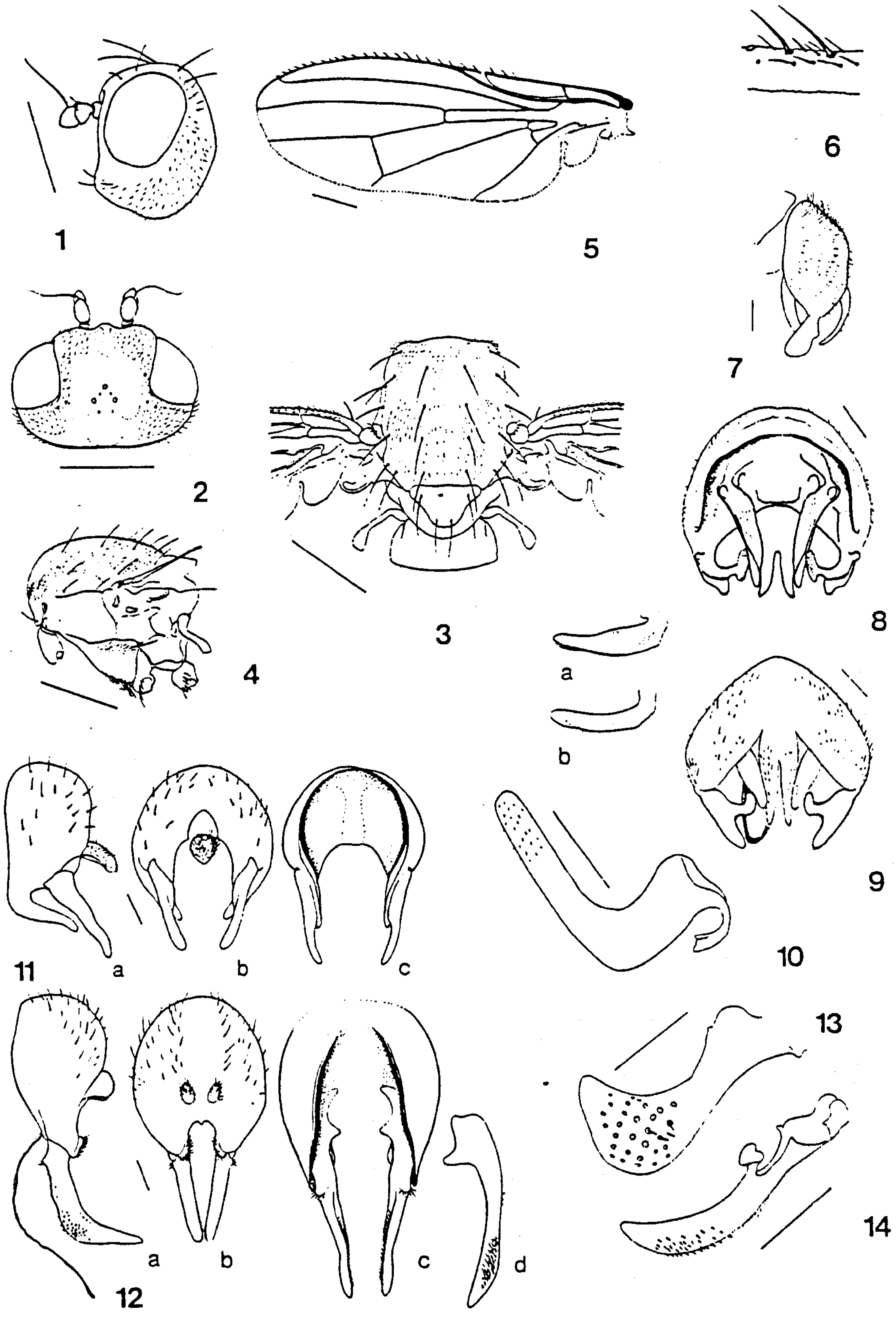

Plate 19

preferring carrion lying in unshaded places (eg. dead animals on keepers' gibbets). Whilst *Heleomyza* species sometimes breed in sunlit places such as guano heaps below bird-cliffs, or chicken manure dumps outside battery-farms, they more often inhabit shaded cess-pits, cave entrances and old buildings in which rotting animal matter has accumulated. Some Heleomyzines are very tolerant of low temperatures. Thus, *Heleomyza borealis* is one of the very few acalypterate flies which breed commonly in the High Arctic.

Taxa represented

Neoleria prominens (Becker) (Puparia from sites 37; 39; 40; 41)

Tephrochlamys rufiventris (Meigen) (Puparium from site 3)

Heleomyza borealis Boheman (Puparia and adult fragments from sites 19; 25; 30; 35; 36; 37; 38; 39; 40; 41; 43)

H. captiosa Gorodkov (See under next species)

H. serrata (Linnaeus) (Puparia and adult fragments from sites ?3; ?19; 28; ?30; 36; ?38; ?39; ?43) (Specimens from British localities probably all *H. captiosa*)

Plate 20 *Heleomyzidae* 1 *Heleomyza serrata*, puparium from Stóraborg (ventral view); 2 same, detail of ventral ambulatory welt on abdominal segment 4; 3 same, apical segments (dorsal view); 4 same, end segment (ventral view), showing detail of papillae of anal region; 5 *?Scoliocentra fraterna*, posterior spiracle of Sandnes specimen. *Sphaeroceridae* 6 *Copromyza equina*, wing; 7 *?Leptocera fontinalis*, wing; 8 *"Limosina sp."* wing; 9 *Thoracochaeta zosterae*, puparium (ventral view); 10 same, detail of ventral ambulatory welt of abdominal segment 4. (Scales 1,6,8,9 0.6m; 2,4,5 0.25mm) (Orig.)

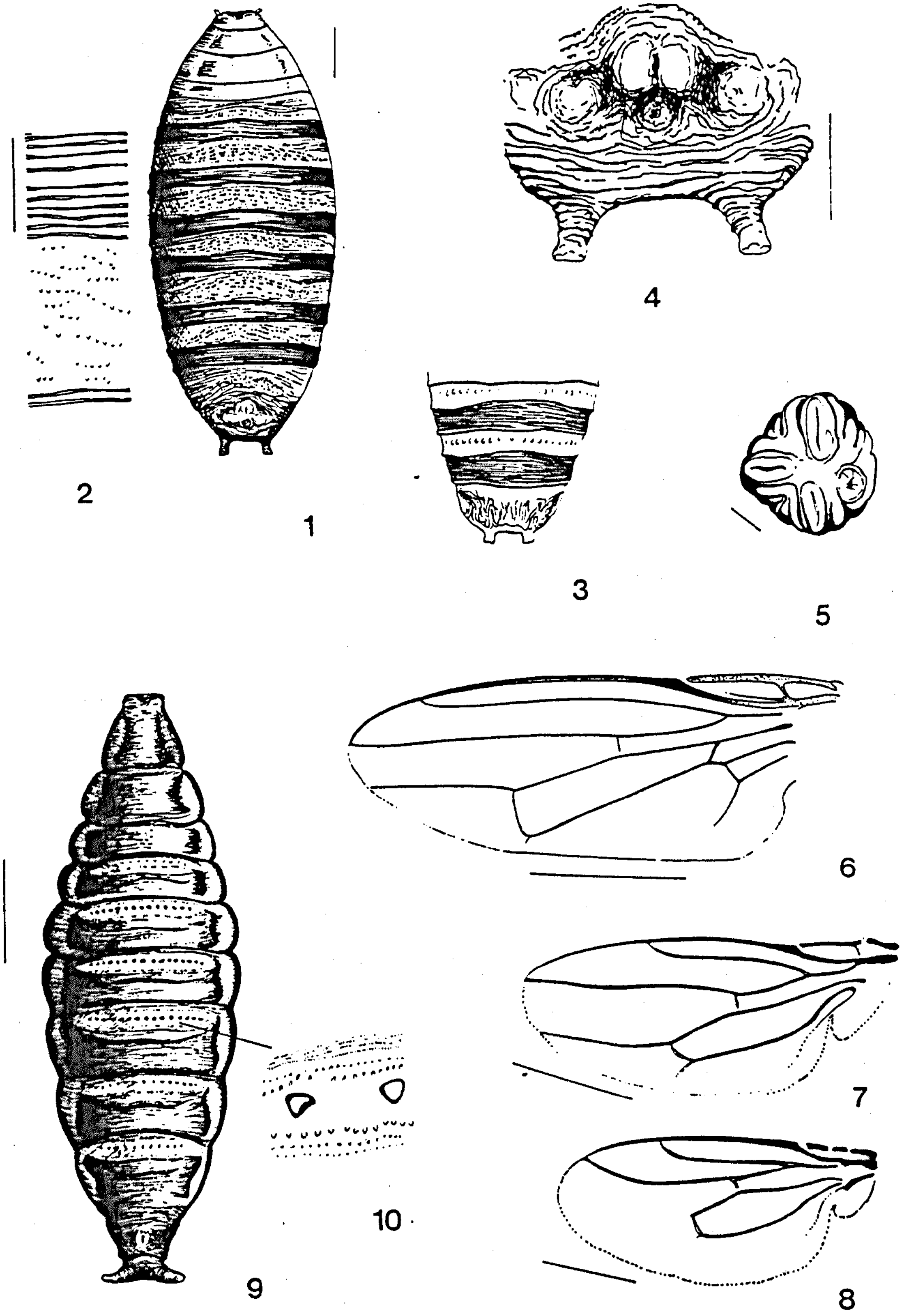

Plate 20

?Scoliocentra fraterna Loew (Puparia from site 40. Recorded from Greenland by Gill 1962. Male genital characters from a Nipáatsoq puparium checked)

Heleomyzines indet. (41; 16; 24)

Family SPHAEROCERIDAE(Lesser Dung-flies)(Plate 20; 6-10) [107 British]

Sphaerocerid puparia are extremely common in archaeological deposits and a major review of these was carried out during this study (Skidmore 1992, see Appendix 1). One of the most distinctive puparia is that of *Thoracochaeta zosterae* (fig. 9, 10), whose abundance in many archaeological excavations is discussed fully in Skidmore (*op. cit.*). Sphaerocerid wings are often common in deposits and conform to the patterns shown here (Pl. fig. 6-8). *Copromyza* wings often have a conspicuous black suffusion towards the base of the costal vein above the costal break (fig. 6) but most species cannot be positively identified on venational features. Sphaerocerids breed in decaying organic matter, some displaying strong preferences for animal matter (eg. *Telomerina flavipes*), seaweed (eg. *Thoracochaeta*) or dung. Several limosinines (eg. *Herniosina bequaerti, Terrilimosina racovitzai* and *Telomerina flavipes,* etc.) are strongly troglodytic.

Taxa represented

Sphaerocera curvipes Latreille (Puparia and adult fragments from sites7; 14; 27)

Ischiolepta ?pusilla (Fallén) (Puparia from sites 3; 7; 14; 19)

Copromyza (s. s.) equina (Fallén) (Adult thoraces from site 27)

C. similis (Collin) (Adult thoraces from site 27)

C. (s. s.) sp. (Puparia from sites 28 and 36)

C. (s. lat.) sp. (Puparia from sites 7; 14; 19; 21; 28; 30; 35; 36; ?41)

Crumomyia nitida (Meigen) (Puparia from site 36)

Leptocera fontinalis (Fallén) (Puparia and adult fragments from sites 22; 27; 28; 36)

L. sp. (Puparia from sites 16; 19; 28)

Limosina silvatica (Meigen) (Puparia from sites 19; 22; 27; 28)

Opacifrons humida (Haliday) (Wing from site 27)

Herniosina bequaerti (Villeneuve) (Puparia and adult fragments from sites 19; 28; 36)

Thoracochaeta zosterae (Haliday) (Puparia from sites 3; 10; 13; 14; 16; 22; 27; 28)

Minilimosina (s. str.) *?fungicola* (Haliday) (Puparia from site 27)

Opalimosina liliputana (Rondani) (Puparia from sites 7; 27; 36)

Terrilimosina racovitzai (Bezzi) (Puparia and adult fragments from site 24)

Pullimosina heteroneura (Haliday) (Puparia from site 27)

Spelobia clunipes (Meigen) (Puparia from site 27)

S. ?rufilabris (Stenhammar) (Puparia from site 27)

S. sp. (Puparia and adult fragments from sites 14; 25; 36)

Telomerina flavipes (Meigen) (Puparia from sites ?3; ?14; 19; ?22; 28; 36; 38; 39; 40; 41; 43)

Trachyopella coprina (Duda) (Puparia from site 27)

T. ?lineafrons (Rondani) (Puparia from site 18)

T. sp. (Puparia from sites ?3; 19; ?22; ?35; ?36)

Limosininae indet. (Puparia and adult fragments from sites 7; 14; 16; 19; 22; 28; 36)

Sphaerocerid spp. indet. (Puparia and adult fragments from sites 19 and 36)

Superfamily OPOMYZOIDEA

Family LONCHAEIDAE (Plate 21; 1) [31 British]

Puparia Lonchaeid puparia have a strongly margined perispiracular region, the posterior spiracular peritreme has at least a slight dorsal tooth and the respiratory slits are convergent (fig. 1).

Biology Lonchaeids mainly breed under the sodden bark of dead trees, but a very few will utilize decaying vegetable matter in compost heaps or masses of rotting vegetables in manure or domestic garbage dumps.

Taxa represented

?Lonchaeidae (Puparia ?19, or psilid)

Family PIOPHILIDAE (Cheese-skippers) (Plate 21; 2-8) [13 British]

Puparia Apart from the aberrant Neottiophilinae, Piophilid puparia have a characteristic arrangement of papillae in the posterior spiracular region (fig. 2-8). Hennig (1948-52) drew attention to the paired lobes above and below the spiracles. These are perispiracular in position, being on the eighth segment, not the anal segment, as has

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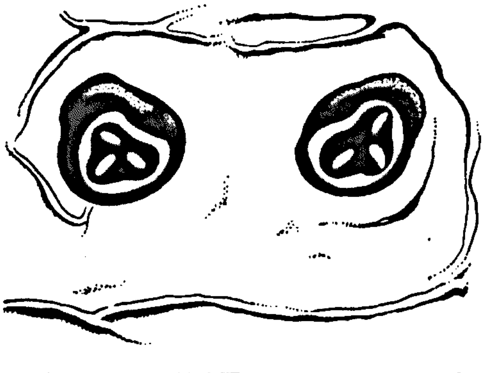
Plate 21 *Lonchaeidae* 1 *Lonchaea* sp., puparium, postspiracular region, *Piophilidae* 2 *Allopiophila vulgaris*, puparium (dorsal view); 3 same, end segment (dorsal view); 4 same (ventral view); 5 same (laterodorsal view); 6 *Lasiopiophila pilosa*, end segment of puparium (dorsal view); 7 same (ventral view); 8 same (laterodorsal view), *Agromyzidae* 9 *?Cerodontha* sp, puparial end segment (dorsal view), (Scales all 0,25mm) (Orig.)



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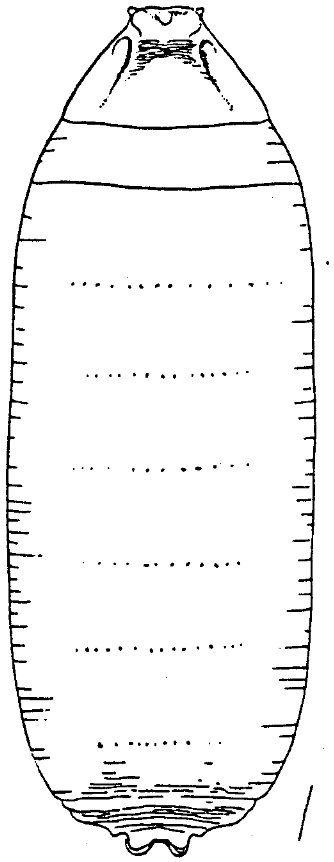

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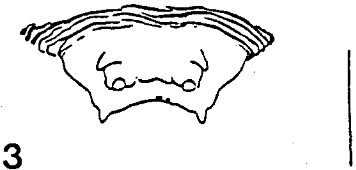

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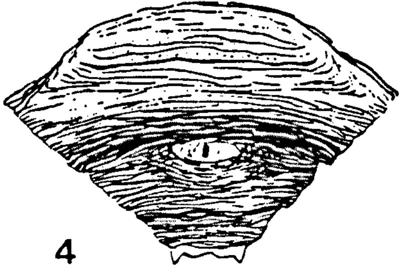

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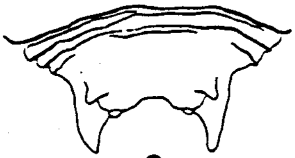

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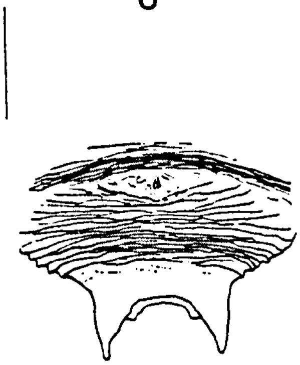

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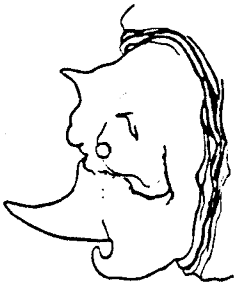

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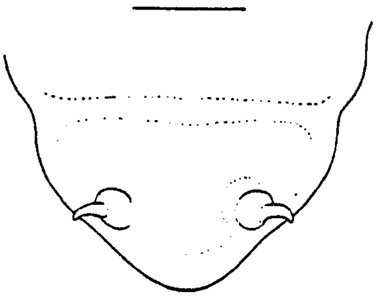

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Plate 21

been claimed by some later authors. In some species, notably *Lasiopiophila pilosa* (fig. 6-8), and, to a lesser extent, *Piophila casei and Arctopiophila arctica*, the ventral pair are much longer than the dorsal. Brindle (1965) provides a key to the larvae of four species based on the number of prospiracular lobes (ie. 4 in *Mycetaulus bipunctatus*, 6 in *Piophila varipes* and *vulgaris*, and 10 in *P. casei*. Smith (1986) revised the key, adding *P. foveolata* which has 12 such lobes. The number of these lobes in *A. arctica* and *L. pilosa* is not known.

Biology Another family noted for the extreme resistance to very low temperatures shown by many species, several of which range into the High Arctic (eg. *Arctopiophila arctica, Lasiopiophila pilosa, ?Piophila affinis, Stearibia nigerrima* etc.) The popular name of "cheese-skippers" alludes to the characteristic jumping habit of the larvae. The mechanism is described by Brindle (lc.) and Smith (lc.) and involves the larva suddenly gripping its ventral perispiracular papillae by the mouth-hooks, then releasing and straightening the body. This habit enables the larvae to escape predators and to spring clear of the breeding matrix for the purposes of pupariation. Possibly the enlarged ventral papillae in the species mentioned above gives them a greater capablity in this activity. By far the most important Piophiline pabulum is carrion in a dry, advanced stage of decay, and hence these are amongst the final wave of colonisers. Commonly, huge populations of Piophiline larvae are found in larger bones of long-dead corpses (eg. dessicated remains of beached whales and seals), where they feed on the marrow remnants. Other media however are commonly utilised, such as milk and cheese, dried meat, birds' nests, dead snails etc. More unusual pabula include decaying fungi, compost and rotten wood (Smith 1986). Infestation of carrion by Piophilines usually occurs after Calyptrates such as Calliphorids and Sarcophagids have ceased to breed, and they are usually regarded as exophilic heliophiles. Instances however are known of Piophilines having been found in buried corpses, including Egyptian mummies (Smith *op. cit.*) but such reports are scarce, and often possibly open to questions of interpretation. It is conceivable that infestation could have occurred before entombment or during museum storage.

Taxa represented

Allopiophila vulgaris Fallén (Puparia from sites 25; 37; 39; 41)

Lasiopiophila pilosa (Staeger) (Puparia from sites 37 and 39)

Piophila sp. (Puparia and adult fragments from sites 19; 28; 30; 36)

Family OPOMYZIDAE (Plate 22; 1,2) [14 British]

Adults Single wings of two very common and unmistakable Opomyzids have been found during this study, as stated below.

Biology The larvae feed in the basal tillers of various grasses, including cultivars, where they sometimes reach pest status.

Plate 22 *Opomyzidae* 1 *Geomyza balachowskii*, wing; 2 *Opomyza germinationis*, wing. *Anthomyzidae* 3 *Anthomyza gracilis* aggr., puparium (dorsal view), showing a prospiracular process, b posterior spiracular process, c ventral surface of end segment; 4 same, cephalopharyngeal skeleton. *Carnidae* *Meonura neottiophila* 5 puparium (dorsal view) showing a, prospiraclar process, b, posterior spiracle; 6 same, end segment (lateral view); 7 same (ventral view). (Scales 1,2 0,8mm, 3,4 0,25mm, 4b 0,02mm, 5 0,5mm, 6,7 0,2mm) (Orig.)

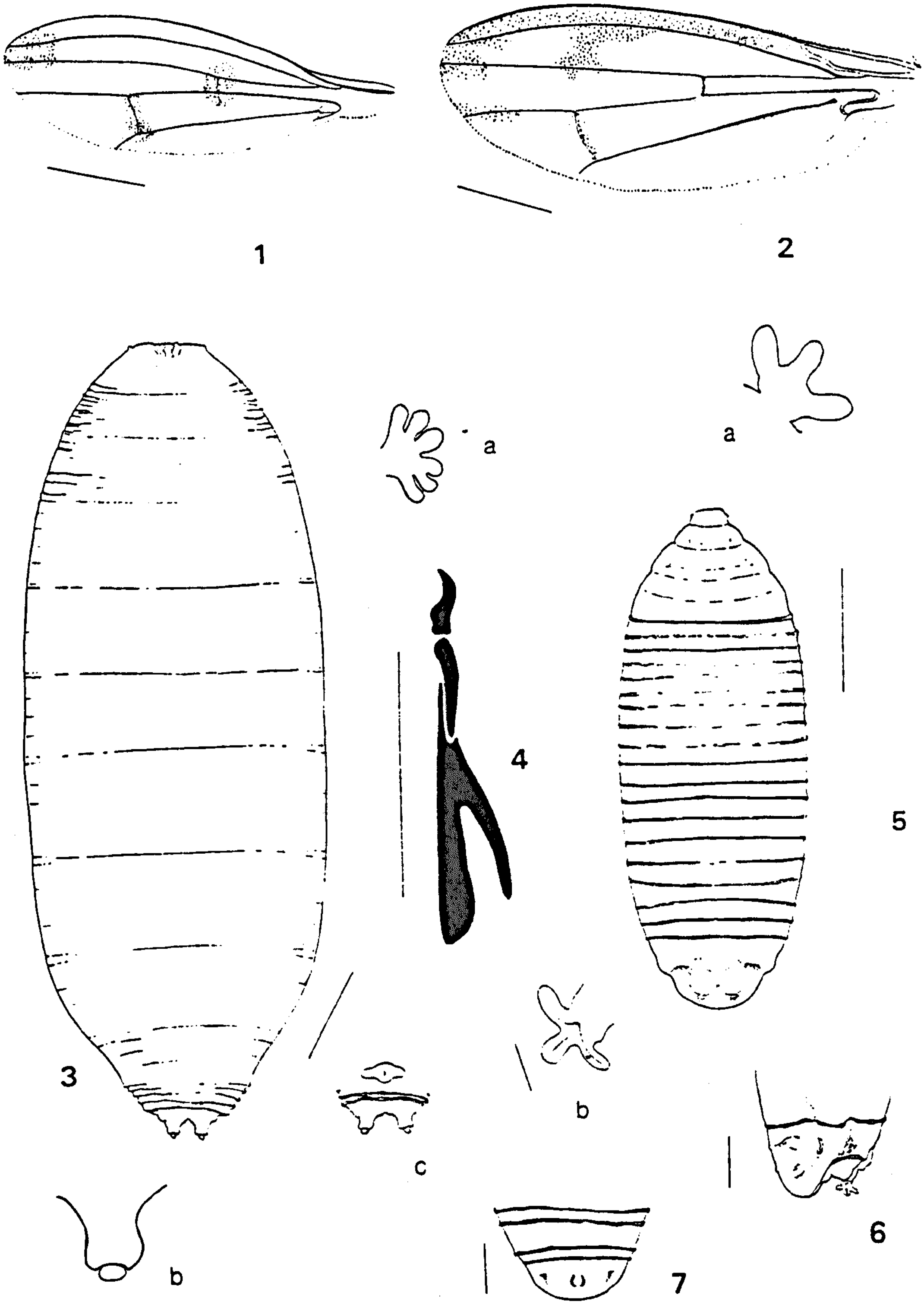

Plate 22

Taxa represented

Geomyza balachowskii Mesnil (Wing from site 21)

Opomyza germinationis(Linnaeus) or *petrei* Mesnil (Wing from site 26)

Family AGROMYZIDAE (Plate 21; 9) [c.360 British]

This very large family of small flies was almost unrepresented in this study. The larvae are leaf or stem-miners in vascular plants, many species being extremely host specific whilst others are polyphytophagous. Agromyzid puparia are very poorly researched and hence even the genus cannot be positively determined for the three different taxa recovered in this study. The puparia exhibit a great range of form, especially in the posterior spiracles, which are sometimes surmounted on tubular or conical processes on the dorsal surface of the end-segment (fig.9). Mature larvae usually vacate the mines to pupariate on the ground, but sometimes pupariation may occur in the larval mine.

Taxa represented

?Agromyza sp. (Puparia from sites 40 and 41)

Phytomyza sp. (Puparia from site 41)

Agromyzid spp.indet. (Puparia from sites 3; 7; 19; 36)

Superfamily ASTEIOIDEA

Family ANTHOMYZIDAE (Plate 22; 3,4) [16 British]

A few empty puparia were tentatively referred to this family. The most distinctive features of these puparia were the form of the posterior spiracles and the absence of any perispiracular papillae (fig.3,4). The larvae develop in a wide range of grasses, sometimes in the workings of other insects.

Taxa represented

?Anthomyzid sp. (Puparia from site 19)

Superfamily DROSOPHILOIDEA

Family EPHYDRIDAE (Marsh flies) (Plate 23) [134 British]

Several genera have been found during this study, some in large numbers, but the family exhibits such diversity of form in all stages of development that an overall description is impossible.

Puparia. In *Hydrellia* the puparium differs from other known Ephydrids in its smooth shiny integument and tubular form with contractions at each segment. But for the minute pointed posterior spiracles on the narrow end segment, it bears a strong superficial resemblance to the "false puparia" of *Mayetiola* (Cecidomyiidae). In other known Ephydrid puparia the integument is microscopically spiculate, giving a dull overall appearance. In many genera there are at least a pair of additional, larger spicules on most segments, as in *Teichomyza*, *Scatella*, *Thinoscatella* and *Scatophila* which are figured here (fig. 3-9). In *Philygria* each abdominal segment has several of these larger

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Plate 23 *Ephydridae* 1 *Scatella stagnalis*, wing; 2 *Hyadina ?guttata*, wing; 3 *Scatella* sp., puparium (dorsal view); 4 same, end-segment (dorsal view); 5 *Scatophila ?cribrata*, puparium (dorsal view); 6 same, end-segment (dorsal view); 7 same, larval pharyngeal sclerites (lateral view); 8 *Philygria vittipennis*, puparium (dorsal view of posterior half); 9 same (ventral view); 10 same, thoracic segments (dorsal view, showing detail of prospiracular process); 11 *?Thinoscatella quadrisetosa*, puparium (dorsal view); 12 same, posterior end (dorsal view) (Scales all 0,25mm) (Orig.)

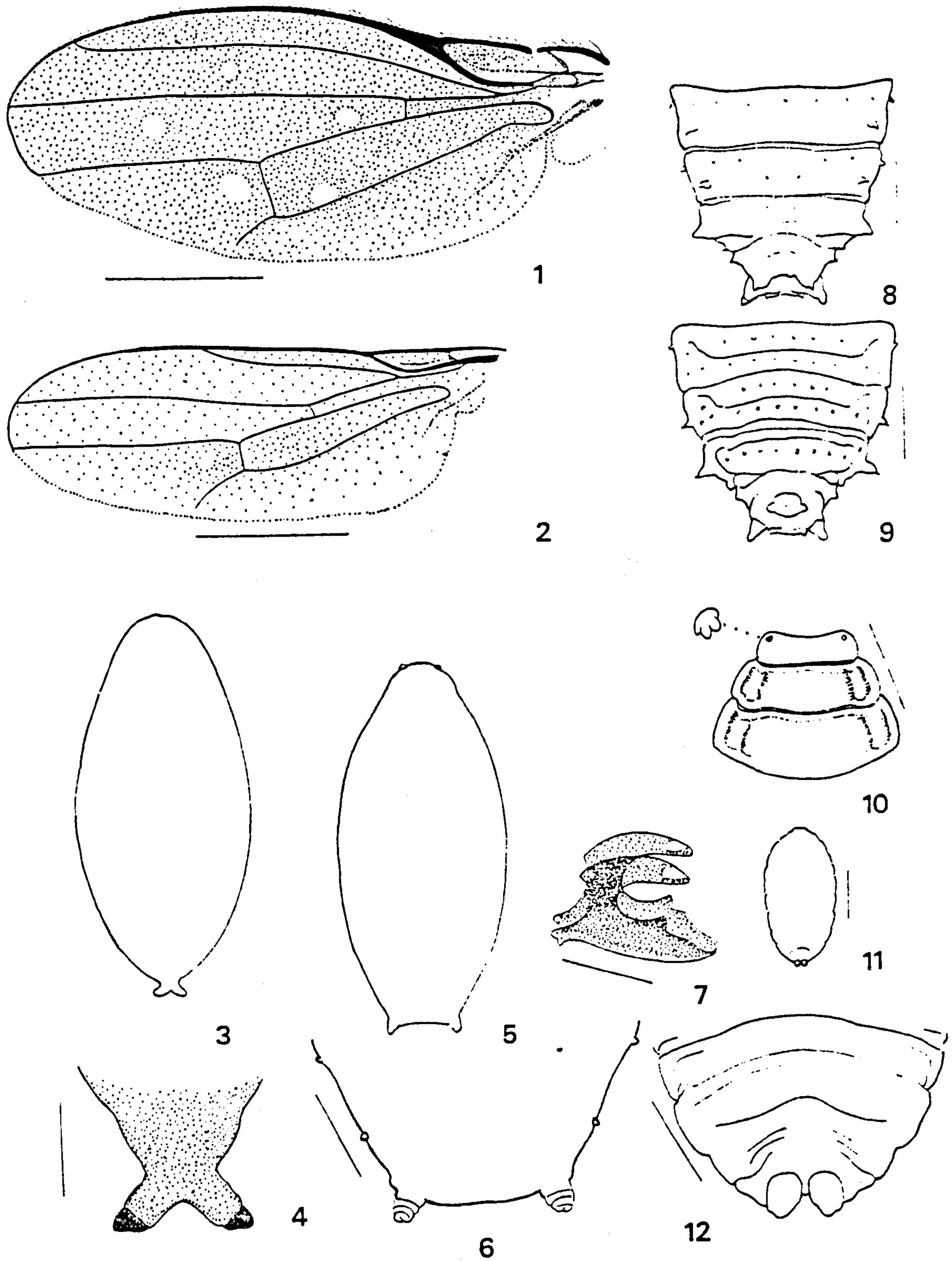

Plate 23

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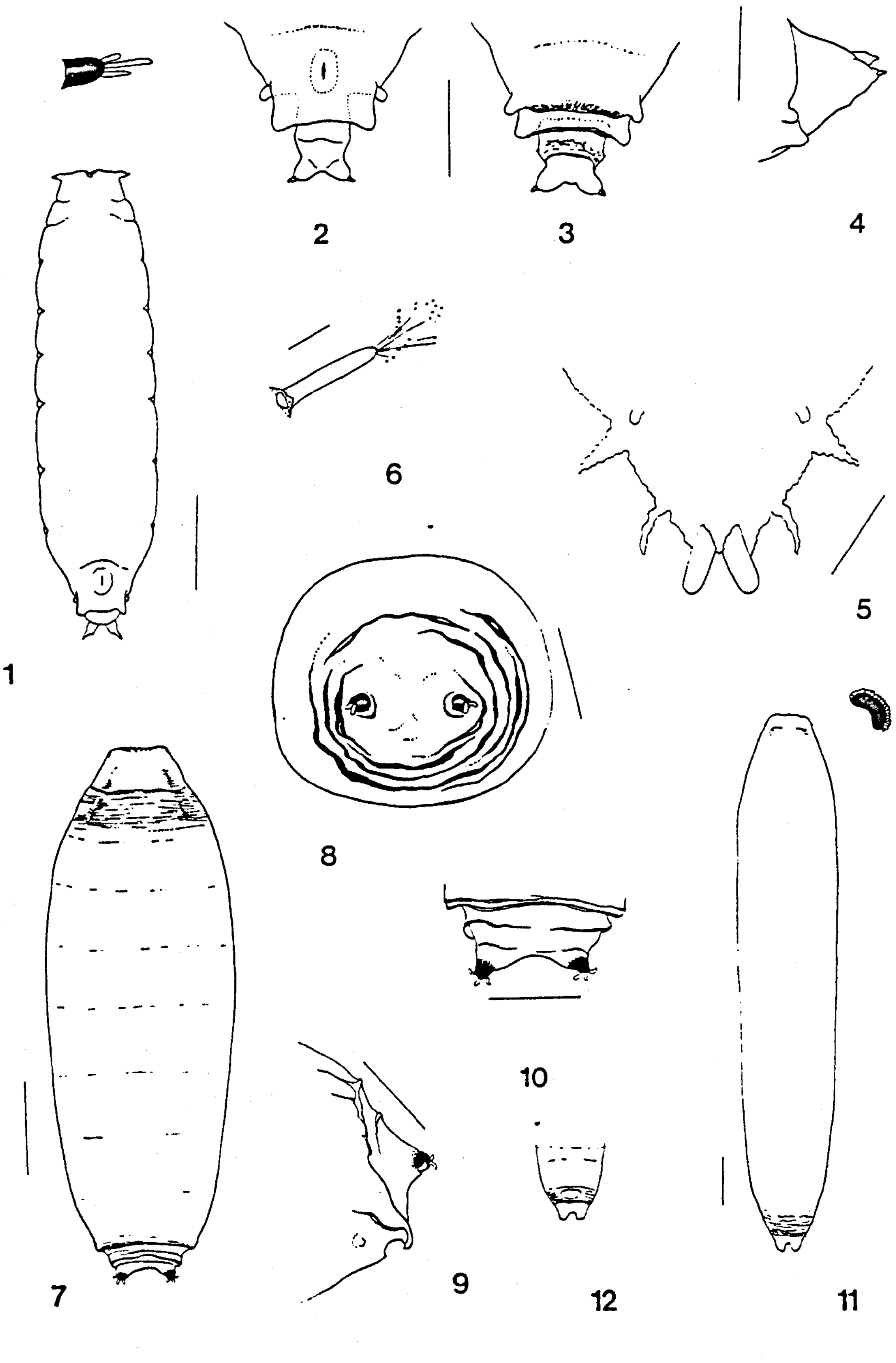

Plate 24

habitations, and hence their scarcity in the present study is surprising.

Taxa represented

Scaptomyza graminum (Fallén) (Puparia and adult fragments from site 27)

S. sp. (Puparia from sites 26; 36)

Drosophila sp. (Puparia from sites 3; 19; 35; 36)

Family MILICHIIDAE [12 British]

Only one possible Milichiid puparium was recovered from the material studied here. Milichiids breed in faeces, carrion and in ants' nests but the morphology of the early stages is almost unknown. Smith (*1989*) notes that the genus *Madiza* is associated with primitive sanitary conditions, but it also abounds in putrid organic matter in garbage dumps.

Taxa represented

?Madiza sp. (Puparium from site 14)

Family CARNIDAE (Plate 22; 5-7) [13 British]

Puparia Two puparia have been tentatively referred to *Meonura* on the basis of the stellate posterior spiracles situated on the posterodorsal surface of the end-segment, so being invisible from below (fig. 5-7).

Biology Carnids are mainly associated with birds' nests but are also thought to breed more widely in animal dung and carrion (Smith *op. cit.*)

Taxa represented

?Meonura sp. (Puparia from site 36)

Family CHLOROPIDAE (Frit-flies etc.) (Plate 24; 7-12) [166 British]

Puparia The few described Chloropid puparia suffice to show that a very wide range of forms occur in this family. *Meromyza* are noteworthy on account of their very long, narrow shape, stout, contiguous posterior spiracles, and multi-lobed prospiracular processes (fig. 11, 12). In certain other genera (eg. ?Chloropisca) (fig. 7-10), the posterior spiracles are stellate as in *Meonura*.

Adults Chloropid adults are commonly boldly marked in black and yellow and some may be identifiable at least to genus on the thoracic markings alone (eg. *Cetema* species).

Biology With very few exceptions, Chloropids develop in various grasses, where some of the stem-borers induce galls.

Taxa represented

Meromyza sp. (Puparia from site 19)

Cetema sp. (Adult thorax from site 21)

Chloropid spp. indet. (Puparia from sites 3 and 12)

Acalypterae indet. (Puparia from sites 19; 21; 28; 36)

Superfamily MUSCOIDEA

Family SCATHOPHAGIDAE (Dung-flies etc.) (Plate 25-26) [53 British]

Puparia Only two genera were recovered during this study, namely *Cordilura* and *Scathophaga*. These are totally dissimilar, the former being smooth and shining, with poorly-developed perispiracular papillae, and strongly produced postspiracular slits, whose margins project as spines beyond the peritreme (pl. 25 figs. 6-10). *Scathophaga* (pl. 25 figs. 1-5), on the other hand is dulled by a dense vestiture of fine short setae and the perispiracular papillae are large and conical. It very closely resembles certain Anthomyiids, especially *Botanophila fugax* and its close congeners, but in *Scathophaga* the posterior spiracles are relatively slightly larger and the scar is strictly median, not slightly supramedian as in *Botanophila.* Also the vestiture in *Scathophaga* is rather coarser and darker in colour. *Scathophaga furcata* and *stercoraria* differ from *S. litorea* in possessing two pairs of subequal subspiracular papillae. Wharton & Moon (1979) state that *furcata* puparia differ from those of *stercoraria* in the relative sizes of the first and second perispiracular papillae, but these vary greatly in both species. In *litorea* the median subspiracular papillae are greatly enlarged possibly due to coalescence with the lateral subspiraculars which appear to be absent (fig. 5)

Adults Fragments of adult *Scathophaga* species occur rather commonly in some deposits. *S. litorea* and *calida* are distinguished from other members of the genus by the strong propleural and stigmatical bristles

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Plate 25 *Scathophagidae* 1- 7 *Scathophaga furcata,* adult; 1 head and thorax (dorsal view), showing chaetotaxy as follows- *fr* frontals, *or* orbitals, *oc* ocellars, *v* verticals, *po* postorbitals, *h* humerals, *ac* acrostichals, *dc* dorsocentrals, *ia* intraalars, *pa* prealar, *sa* supraalars, *no* notopleurals, *sc* scutellars (NB. bristles only shown on left side); 2 head (anterior view) showing *pa* palps, *pr* proboscis and *vb* vibrissae; 3 same (lateral view); 4 thorax (lateral view, wing bases only indicated), showing bristles as in fig. 1 plus *me* mesopleurals and *st* sternopleurals; 5 wing (showing detail of vestiture on costal vein); 6 male internal forceps (ventral view); 7 male surstylus. 8, 9 *Scathophaga litorea*; 8 detail of propleuron showing *pt* prothoracic and *st* stigmatical bristles. 9 male internal forceps (ventral view). (Scales all 0.25mm) (Orig.)

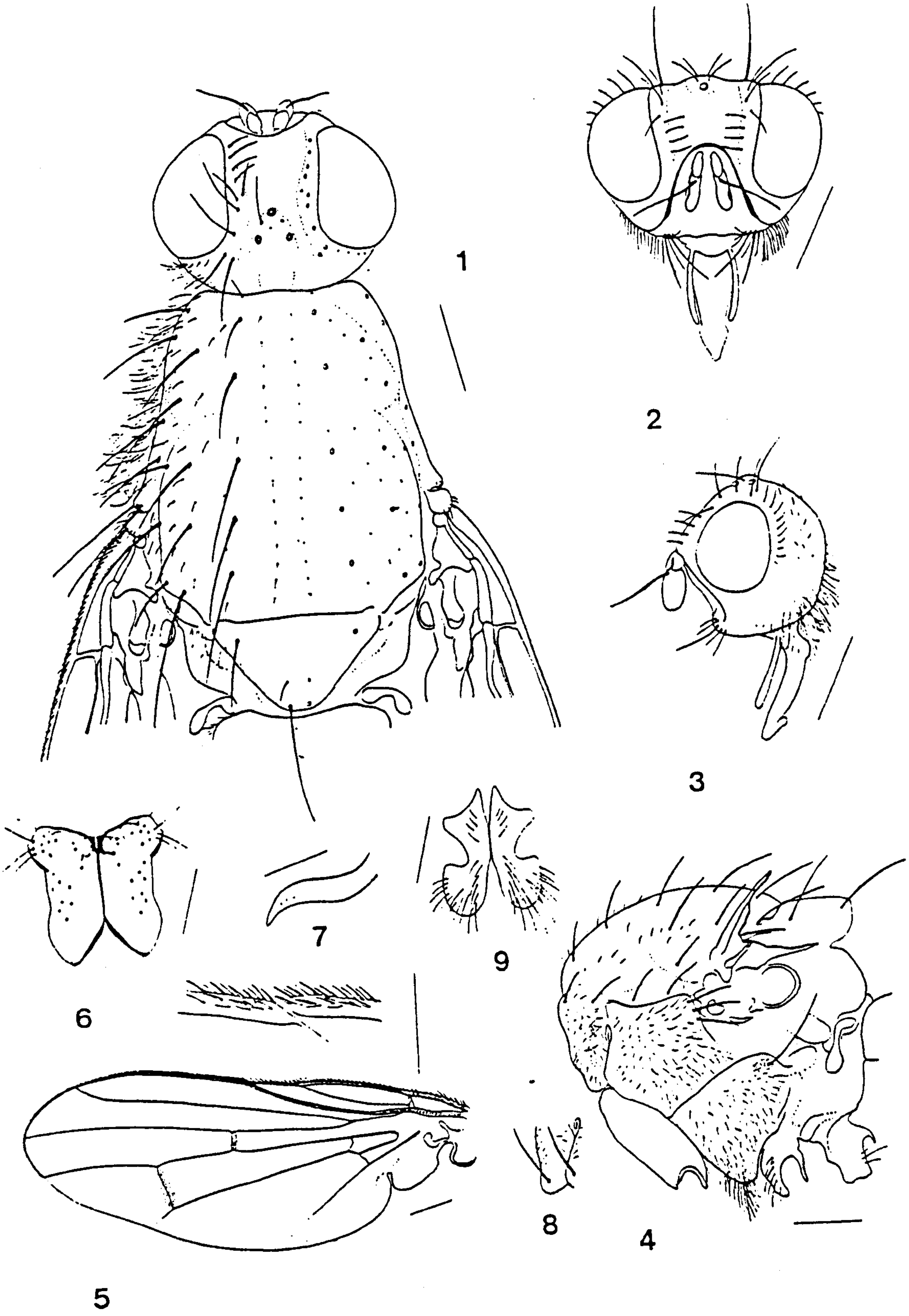

Plate 25

(plate 25 fig. 4, 8).

Biology Larval pabula in Scathophagids include living and sodden, rotting plants, and dung. The family is best represented in cool temperate, or subarctic regions.

Taxa represented

Cordilura sp. [*Cordilura* larvae mine stems of *Carex*, *Scirpus* and *Juncus* in marshy situations.] (Puparia from sites 15 and 26)

Scathophaga furcata Say [Larvae mainly in dung of ungulates, often breeding in abundance in sheep-dung in moorland areas. Apart from dung of cow and sheep (Skidmore 1978, 1991) and pig (Coffey 1966), it is also recorded from dog dung and owl pellets (Disney 1976). But it must also breed in other materials (eg. decaying vegetation), as it may occur abundantly where no dung is present. An ubiquitous species of the cooler temperate regions, this fly ranges into the High Arctic (Spitsbergen, Jan Mayen etc.). In Iceland, Nielsen et al. (1954) state

Plate 26 *Scathophagidae* 1 *Scathophaga stercoraria*, puparium(dorsal view) showing detail of prospiracular process; 2 same, end segment (ventral view), showing arrangement of papillae, *pa* postanal, *ea* extraanal, *ms* median subspiracular, *ls* lateral subspiracular, *p5* fifth perispiracular, *ap* anal plate; 3 same (posterior view), showing *sp* posterior spiracular plate, *p1*- *p5* first to fifth perispiracular, *ms* median subspiracular, *ls* lateral subspiracular, *pa* postanal, *ea* extraanal; 4 same, pharyngeal sclerite; 5 *Scathophaga litorea*, puparial end segment (posterior view); 6 *?Cordilura ciliata*, puparium (dorsal view) showing prospiracular process; 7 same(ventral view) showing prospiracular process (in lateral view); 8 same, end segment (lateral view); 9 same, postspiracular region (posterior view); 10 posterior spiracles of *Cordilura* puparium from Buiston, (Scales- 1,6,7 0,6mm., 1a,2,3,4,5,8,9 0.25mm.) (Orig.)

Plate 26

that *furcata* is eurytopic and that the flight period extends from early June to early September. In the High Arctic *S. furcata* is partially replaced by *S. apicalis* Curtis, the biology and immature stages of which are unknown.] (Puparia and adult fragments from sites 27; 39; 40; 41; 43; probably belonging to *furcata* rather than *stercoraria*, but specific identification impossible.)

S. litorea Fallen [There appears to be some confusion as to the normal larval pabulum of this fly. Whilst Backlund (1945), Lindroth *et al. (1973)*, Stubbs & Chandler (1978) and others state that it breeds in heaps of moist rotting seaweed, this is evidently not the preferred habitat. Despite extensive searches I have never found a single larva or puparium of *S. litorea* in this situation, even where the fly was present in profusion. Moreover, in his detailed studies on the wrack-fly fauna of the Holy Island area of Northumberland, Egglishaw (1960) also failed to find the immature stages of this fly. Again, Hackman (1956) was unable to find larvae or adults in wrack-beds on the coasts of Uppland. On the other hand, the puparia can invariably be found about the high tidal zone on the landward side of salt marshes, amongst piles of grass, dead crabs and marine and littoral shells. I have repeatedly found them in such places, including the precise localities in Northumberland where Egglishaw carried out his researches. Interestingly, Séguy (1934) records *litorea* (sub nom. *impudica* (Reihe)) breeding "dans un amas de débris de buccins" on the French coast. Hackman (1956) carried out a detailed study of *S. litorea* and *impudica* and concluded that the latter was merely a pilose form found mainly in more northerly areas. Nielsen *et al.* (1954) record *S. litorea* all round the coasts of Iceland, more rarely inland and on home fields, the adults flying from early June to mid September. In Greenland, Carpenter & Roman (1938) found it on drift-line seaweed on shore at Utorqait in Amerdloq in mid July. Common on coasts throughout the North Atlantic area, the Greenlandic range of *S. litorea* extends to 68°40'in the west and 70°N in the east; otherwise it occurs from France to Novaya Zemlya, and in Labrador. The closely related arctic species *S. nigripalpis* Becker, which ranges along the Arctic Sea coasts of Siberian coasts and across the Canadian Low Arctic, replaces it in parts of northern Greenland.] (Puparia and adult adult fragments from sites 39 and 41)

S. calida Curtis or *litorea* Fallén [The biology of *calida* is unknown but it doubtless very closely resembles that of *litorea* as they usually occur together.] (Adult fragment from site 28)

S. sp. (Puparia and adult fragments from sites 14; 19; 22; 25; 28; 30; 31; 35; 36; 37; 41)

Family ANTHOMYIIDAE (Plate 27 figs. 1- 12) [c.220 British]

This very large family is taxonomically the most difficult in the superfamily, both in adult and immature stages. Puparia are common in subfossil assemblages.

Puparia The typical Anthomyiid puparium, as exemplified by *Botanophila fugax* (fig. 8) and its close relatives has the complete complement of perispiracular papillae characteristic of the Muscoidea and is extremely similar to *Scathophaga*. Further papillae are found in the perianal region. The postspiracular slits are strongly convergent to radiate and the scar is supramedian. In some *Pegomyia* species the margins of the respiratory slits protrude from the peritreme to form spiniform processes (fig. 1), somewhat as in the Scathophagid genus

Cordilura. Also in some *Pegomyia*, but also in *Fucellia, Zaphne* and some *Delia* the perispiracular papillae are ill-defined or apparently absent (figs. 5,9,10). *Delia fabricii* (figs.10- 12) is one of the most spectacular of all regional Muscoid puparia in having the median subspiracular papillae massively enlarged, blackened, and arising from a shining black plate.

Biology Anthomyiids frequent a very wide range of media including those utilised by the Scathophagidae.

Taxa represented

Fucellia spp. [Larvae in coastal wrack-beds, but on Amsterdam Island, Trehem et al. found *Fucellia fucorum* breeding in cow-dung in pastures. *Fucellia fucorum* ranges through the British Isles to Shetland, Faroes, Iceland, to Jan Mayen, West Greenland and Spitsbergen. Four species of *Fucellia* occur in West Greenland, namely *ariciiformis* (Holmgren), *fucorum* (Fallen), *pictipennis* (Becker) and *tergina* (Zetterstedt). At present the puparia of the Greenlandic species cannot be distinguished, but specimens from the middens of three of the Norse farmsteads show

Plate 27 *Anthomyiidae* 1 *Pegomya* sp., puparium (posterior view); 2 same, posterior spiracle (dorsal view); 3 same, pharyngeal sclerite; 4 posterodorsal pharyngeal cornu of another species of *Pegomya* (from Sandnes); 5 *Fucellia* sp., puparium (posterior view); 6 same, posterior spiracle; 7 same, pharyngeal sclerite; 8 *Botanophila fugax*, puparium (posterior view); 9 *Zaphne* sp., puparium (posterior view); 10-12 *Delia fabricii*, puparium; 10 (ventral view); 11 (dorsal view); 12 (posterior view); 13 same, larval mouthparts. *Fanniidae* 14 *Fannia manicata*, puparium (dorsal view), showing prospiracular process (inset); 15 *Fannia scalaris*, puparium (dorsal view). (Scales 1,3-5,8,9,13 0.25mm; 10,12 0.6mm; 14,15 1.0mm) (Orig.)

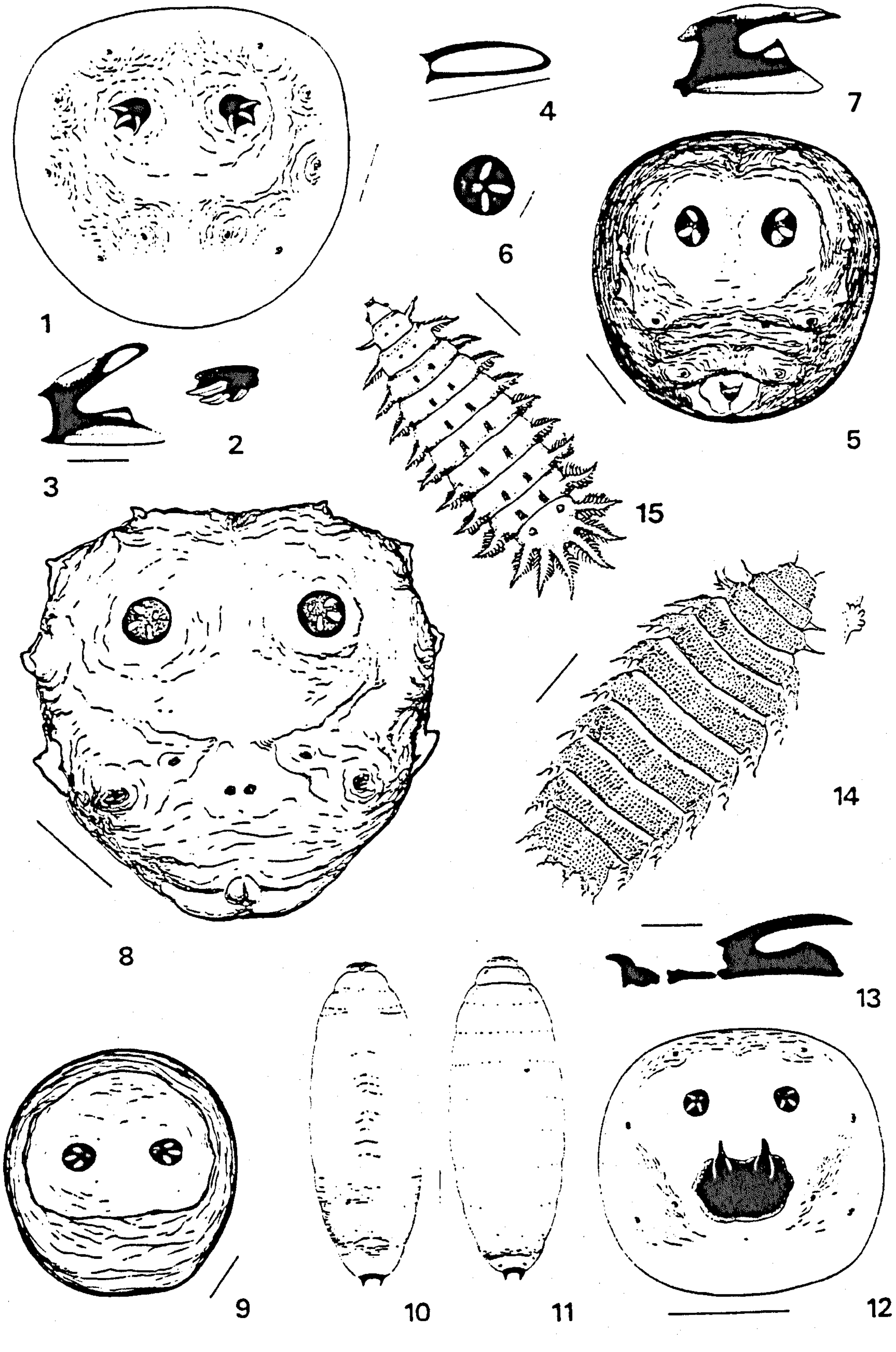

Plate 27

slight differences from British examples of *tergina* examined by the writer. Sharov (1948) describes and figures the larval morphology of *F. fucorum*, whilst Egglishaw (1960) deals with the biology and morphology of *F. maritima* (Haliday). Both of these occur widely around the coasts of Iceland, whilst *F. tergina* is only known from Heimaey and Surtsey (Lindroth et al. 1973). Madsen (1936) notes that *F. ariciiformis* breed in "clay-flats" near river mouths and lagoons in Greenland with *F. pictipennis* and *fucorum*. Nielsen et al. (1954) record *fucorum* indoors in Reykjavik from March to August, and outdoors from early June to early September; the very early dates for flies indoors requires some explanation. The Norse settlement puparia are here referred tentatively to *fucorum*.] (Puparia from sites 27 *(fucorum)*; 37; 39; 41 *(?fucorum)*; 42 *(?fucorum)*

Botanophila fugax (Meigen) [*B. fugax* is recorded as a stem-miner in various living and decaying herbaceous plants, including many crop species, but is also recorded from mouse-droppings (Ferrar 1987; Smith *1989*). The puparium and biology are described by Stork (1936) and Miles (1950). In Iceland, *fugax* is common throughout the country and is eurytopic. Three other species, *profuga* (Stein), *rubrigena* (Schnabl) and *tuxeni* (Ringdahl) occur in Iceland, the last-named regarded as an endemic.] (Puparia ?3; 30; 35)

B. betarum (Lintner) [According to Huckett (1965), this Nearctic species replaces *fugax* in Greenland (Greenlandic sites). Amongst the material from the Norse farms there appear to at be at least two species of *Botanophila*. In one of these types, here tentatively referred to *B. betarum*, the postanal papillus appears as a conspicuous wart surmounted by two small tubercles below the four subspiracular papillae, as in *fugax*, figured by Stork (*1*936) and confirmed by an Icelandic puparium from which an adult male was dissected. The biology of *betarum* presumably resembles *fugax*, but other species are phytophages, affecting leaves, stems, fruits, etc., whilst others have been associated with various smut fungi (Ferrar 1987).] (Puparia from sites 39 and 41)

B. ?profuga (Stein) [The puparia of the second *Botanophila* species from the Norse farms are extremely similar to the preceding but have simple postanal papillae. They probably belong to *profuga*, the only other common Greenlandic *Botanophila* according to Huckett (1965), although two others are recorded from West Greenland (ie. *moriens* Ringdahl and *sobrina* (Collin).] (Puparia from sites 39; 41; 42)

Botanophila sp. (Puparia from sites 3 and 19)

Zaphne caudata (Zetterstedt) [*Zaphne* breed in organic silt and mud in marshes and by lakes and rivers] (Puparium containing male adult 21)

Z. ?frontata Zetterstedt [Specific identity cannot be stated but these Greenlandic puparia differ from *Z. divisa* in the shape of the postspiracular slits. Since *Z. frontata* is the commonest species in West Greenland, this seems a probable candidate. In Iceland (Lindroth et al. 1973) it frequents Salix heath and fell-fields especially in colder and more northerly parts; in Scandinavia it is characteristic of the *regio arctica* (Ringdahl 1954-59). Within the Greenlandic fauna, *Zaphne* puparia are rather distinctive by virtue of the sunken posterior spiracles. In this respect they most closely resemble those of the muscid *Hydrotaea anxia*, but there the respiratory slits are quite differently orientated and the perispiracular papillae, which may be distinct sometimes in *Zaphne*, are totally wanting. Four other species occur in West Greenland, namely *brunneifrons* Zetterstedt (= *teste* (Walker)), *divisa* (Meigen) and *verticina* Zetterstedt.] (Puparia from sites 39 and 41))

Zaphne sp. (Puparium 37)

Pegomya spp. [The specific identity of the *Pegomya* puparia from the Greenlandic sites is unknown but will probably be either *pilosa* Stein, *zonata* (Zetterstedt) (=*rufipes* (Fallen) or *tenera* Zetterstedt (= *obscurior* Collin), all of which are known from West Greenland. All three breed in boleti; Hackman & Meinander (1979) record them from *Leccinum carpini, scabrum* agg. and *versipillis* agg. and from *Boletus edulis* agg. Another species (*P. hyoscyami* (Panzer), which mines the leaves of a wide range of herbaceous plants, including beet and spinach (Ferrar, 1965), was recorded widely as far north as 68°N in West Greenland by Nielsen (1954), but is not included in Huckett (1965) for West Greenland. *P. haemorrhoa* (Zetterstedt) likewise was not given in Huckett *(op. cit.)* for West Greenland, though a specimen which I took at Narssassuaq on 13 July 1963 agreed well with this species, whose larvae mine leaves of *Rumex*. There is a rather remarkable range of form in puparia of this genus in the development of the perispiracular papillae and postspiracular respiratory slits. .In *P. bicolor* Wiedemann the papillae are almost wanting whilst the slits project far beyond the peritreme margins. In the Norse farmstead specimens the papillae are well-developed and the slits do no project; the pharyngeal sclerite has a massive fenestra occupying almost the entire posterodorsal cornu (fig. 4).] (Puparia from sites 39 and 41)

?Lasiomma octoguttata (Zetterstedt) [This has been reared from birds' nests, bird pellets, bear dung and dead snails (Ferrar 1987) and the

puparium was figured and described by Stork (1936).] (Puparia from sites 39 and 41)

?Pegoplata (=Nupedia) infirma (Meigen) [Reared from Brassicas and "freshly-sown maize seeds" (Ferrar 1965). Puparium described and figured by Stork *(1936).]* (Puparia from site 30)

?Nupedia/Paregle sp. [Members of these genera have been recorded mainly from dung and decaying vegetation (Ferrar 1987).] (Puparia from sites 22; 25; 27; 28; 35; 36)

Delia fabricii (Holmgren) [Johansen (1988) gives a detailed and well illustrated account of the life-cycle, biology and economic importance of this fly. He found it to be a pest of *Poa pratensis* in northern Norway, where the grass is grown for seed-production. *D. fabricii* overwinters there in the egg stage and the highly characteristic larvae mature rapidly during spring, pupariate in the soil in early June and the adults fly in summer. In Iceland, where it occurs commonly only in the south, the flight period extends from mid-June to mid-August. In the Ameragdla middens this species was the commonest Anthomyiid and one of the most numerous Diptera, being present at five of the six farms. The success rate was over 90 per cent, but one puparium from Sandnes contained an Ichneumonid parasite. *Poa pratensis* occurs throughout Greenland and is a valuable component of arctic grazing lands, occurring commonly around human settlements. It is also a very important summer fodder plant for reindeer in Greenland (Sage 1986) and forms 5 per cent of their summer grazing lands in the Kangerdlugsuaq (Stromfjord) district, the northernmost recorded locality for this fly. *D. fabricii* occurs widely from the coniferous forest-belts into the lower tundra regions throughout the Northern

Hemisphere, having a range coincident approximately with the complex of sedge meadows and Polar semi-deserts (Sage 1986).

The puparium of this fly is the most distinctive one found in Greenland (fig. 10-13), by virtue of the subspiracular papillae, which are massively enlarged to form a pair of huge, blackened, spiniform processes. The nearctic species *Calythea micropyga* (Thomson) is somewhat similar according to Wharton & Moon (1979) though in that species the processes are much smaller and narrower. Indeed puparia of *fabricii* were tentatively queried as belonging to *micropyga* or a *Delia* in Buckland et al. (1983). In *Delia* species the median subspiraculars are normally, perhaps always, much larger than the laterals.] (Puparia from sites 37; 38; 39; 40; 41; 42)

D. platura (Meigen) [*Delia* puparia from Niáqussat and Sandnes agree well with descriptions of *D. platura* in Stork (1936). This species is polyphytophagous, the larvae attacking seedlings, growing points and cotyledons of a wide range of herbaceous plants, including various grasses, and also decaying plants and insects. In Iceland, where *D. platura* is common, it flies from mid June to late July in sandy bogs, grass fields, ruderal places and homesteads and on hill slopes. The larvae attack a number of kitchen-garden plants (Lindroth et al., 1973). Three other species are found in West Greenland, namely *D. angustifrons* Meigen, *D. echinata* (Séguy) and *D. icterica* Holmgren. Records of *D. florilega* (Zetterstedt) in Nielsen et al. (1954) presumably refer to *D. echinata.*] (Puparia from sites 39 and 41)

D. sp. (near *fabricii*) (Puparium from site 11)

Anthomyiids indet. (Puparia from sites 3; 11; 14; 15; 19; 21- 3 spp; 22; 30; 32; 36; 37; 41)

Family FANNIIDAE (Plate 27 figs. 14,15) [59 British]

Puparia Fanniid puparia should pose no problems in recognition, having a coarsely granulate or reticulate surface sculpture and simple to plumose processes on all body segments (figs. 13, 14). Certain Phorid puparia are superficially similar but the shape and location of the posterior spiracles are different. Also, Phorid puparia have distinct, and often very long, pupal respiratory horns which are always absent in fanniids. The taxonomy of Fanniid larvae and puparia relies mainly on the relative development of the processes, the surface sculpture and the location and shape of the posterior spiracles (Chilcott 1960; Lyneborg 1970). These are located medially (fig. 15) or laterally (fig. 14).

Biology Fanniids breed in a very wide range of decaying organic matter and dung. Other characteristic habitats for Fanniids are rotting fungi, carrion, birds'nests, accumulations of guano below bat roosts, nests of social insects and humus soil. Many species are restricted to one or other of these habitats.

Taxa represented

Fannia canicularis (Linnaeus) "The Lesser House-fly" [This has been bred from a wider range of media than any other insect except *Musca domestica*, but it favours dung and decaying plant and animal matter.] (Puparia from site 3)

F. ?postica (Stein) [This has been reared from decaying plant matter, dead wood and vertebrate carrion (Ferrar 1987).] (Puparium from site 36)

F. scalaris (Linnaeus) "The Latrine fly" [A classic cess-pit fly, and the characteristic inhabitant of primitive lavatories, this is much scarcer than formerly in Western Europe. It favours semi-liquid masses of faeces, including human, and urine-soaked substrates (Smith 1989). Specimens in a less corroded condition from the Leicester samples agreed well with this species, but many unidentifiable examples were also referred to this taxon.] (Puparia from sites 3 and ?24)

Family MUSCIDAE (Plate 28) [281 British]

Puparia Muscid puparia are mainly characterised by the possession of well-developed, paired accessory oral sclerites (fig. 6, 7) which are found in no other dipterous family. In the Muscini and Stomoxydinae which lack these the postspiracular respiratory slits are serpentine (fig. 2, 3). In most Muscids perispiracular papillae are absent, the "end-segment" being typically smoothly rounded or truncate. In some genera, notably in certain *Hydrotaea* species and in many of the Coenosiinae, the cuticle is finely, longitudinally striate. The

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Plate 28 *Muscidae* 1-5 posterior spiracles of 1 *Muscina stabulans*, 2 *Musca domestica*, 3 *Stomoxys calcitrans*, 4 *Hydrotaea dentipes*, 5 *Phaonia* sp; 6 *Hydrotaea dentipes*, larval mouthparts, showing *os* oral sclerites, *hs* hypopharyngeal sclerite and *ps* pharyngeal sclerite; 7 *Phaonia subventa*, oral sclerites, showing *d* dentate sclerite, h mouth hook and *aos* accessory oral sclerites comprising *a* anterior ribbon, *b* oral bar and *p* posterior ribbon,; 8-11 *Spilogona* spp.indet., 8 posterior spiracle of specimen from Sandnes; 9 posterior spiracle of specimen from NiEaqussat, 9 perispiracular region of Sandnes specimen, 11 perispiracular region of Niáqussat specimen. *Hippoboscidae* *Melophagus ovinus* 12 complete specimen (dorsal view); 13 head of subfossil specimen (dorsal view); 14 thorax of subfossil (ventral view); 15 puparium (dorsal view). (Scales 1-5,8,9 0.1mm; 6 0.25mm; 12-15 1.0mm) (Orig.)

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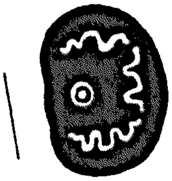

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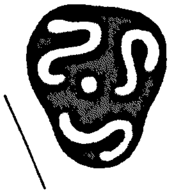

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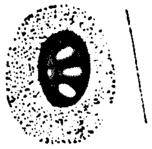

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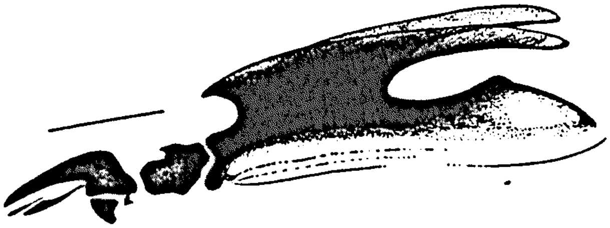

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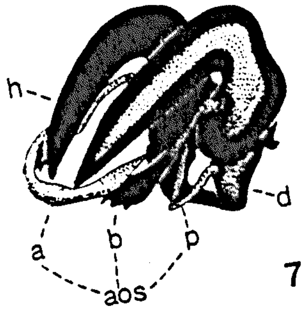

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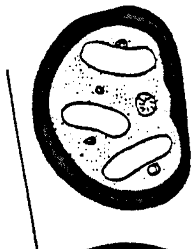

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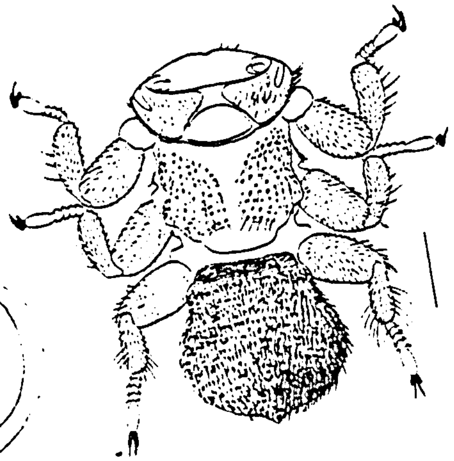

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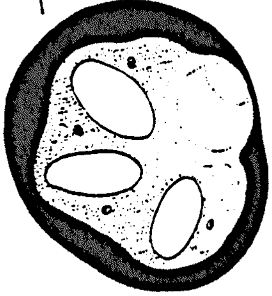

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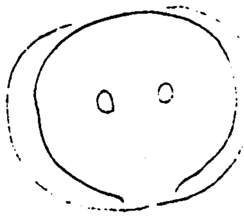

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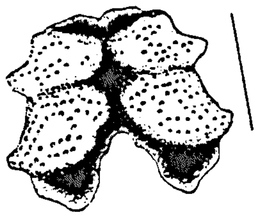

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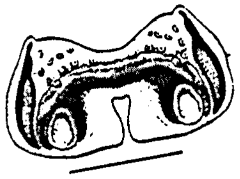

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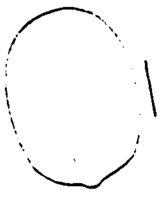

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Plate 28

posterior spiracles are often very small in relation to the puparial length (Skidmore 1984).

Biology The vast majority of Muscids, whose larvae possess accessory oral sclerites, lead a predatory mode of life, consuming larvae of other insects in a very wide variety of terrestrial or freshwater situation. A few occur in the littoral zone where they prey on marine arthropods. In those which lack the accessory oral sclerites, the larvae are wholly saprophagous or coprophagous. *Musca domestica* is omnivorous, having been bred from a wider range of media than any other insect. This species and *Stomoxys calcitrans* are believed to have originated in the Mediterranean region. From there they were transported by man to the North Atlantic area, where they are thermophilous eusynanthropes, incapable of maintaining permanent populations without his assistance. They require artificially heated biotopes in which the temperatures are maintained at high levels by bacterial fermentation. The major work on the biology and immature stages of the Muscidae is Skidmore (1984).

Taxa represented

Muscina stabulans (Fallén) [An exophilous eurytopic eusynanthrope in cool temperate regions whose larvae are major predators of those of *Musca, Stomoxys, Calliphora,* etc., but which can infest man and other vertebrates causing very serious myiasis (Skidmore 1984) (Puparia from sites 6; 9; 10; 16; 17)

Hydrotaea ?albipuncta (Zetterstedt) [Predaceous, in cow-dung; related species in humus, manure heaps etc.] (Puparium from site 19)

H. anxia (Zetterstedt) [The Arctic representative of the subgenus *Hydrotaeoides* (Skidmore op. cit.), and doubtless agreeing in biological habits with the very closely related *H. dentipes.* These flies are facultative carnivores in the larval stage, developing in a wide range of rotting organic matter. The adults are highly heliophilous.] (Puparia from sites 37; 38; 39)

H. dentipes (Fabricius) [Breeds in numerous media including dung, carrion, rotting vegetation etc., where the larvae prey on those of other flies (see Skidmore op. cit.)] (Puparia from sites 3; 9; 10; 14; 18; 22; ?36)

H. s. str. sp. (puparium 14)

?*Thricops* sp. [Larvae in humus soil, preying on other insect larvae.] (Puparia from sites 27; 36)

Eudasyphora cyanella (Meigen) [Coprophagous in cow, and possibly, sheep-dung] (Puparia from sites 19 and 22)

E. ?cyanicolor (Zetterstedt) (Puparium from site 19)

Neomyia cornicina (Fabricius) [Coprophagous in cow-dung.] (Puparia and adult fragments from sites 19; 21; 22)

Musca domestica Linnaeus "The House fly" [The classic communicative endophilous eusynanthrope (Greenberg 1971-3), combining dependence on man with a propensity for breeding in foul situations, contaminating his food and infesting his person when chance permits. The House-fly poses a major health threat where poor hygiene prevails, transmitting many pathogens and causing ocular, aural, urino-genital and intestinal Myiasis in humans. The immense literature on the biology and ecology of this fly is summarised by Skidmore (1985), the classic works including Hewitt (1914) and Greenberg (lc). The salient features are as follows. The female lays up to 2500 eggs over a period of weeks, preferring to oviposit in daylight though secreting the eggs in dark fissures in the medium. However, egg-laying may occur in total darkness. The egg has a low resistance to hydrostatic pressure so it is not laid in the wettest parts of the pabulum but the larvae require high temperature and humidity for healthy development. Such conditions prevail where bacterial fermentation is sustained by continual addition of further decaying material. This fundamental requirement of the House-fly was noted as early as the 1730s by the great French scientist Réaumur. Optimum breeding conditions for this fly occur in cess-pits, manure heaps, garbage-dumps, compost and lawn-clipping heaps, but it will utilize any decaying vegetable or animal matter where bacterial fermentation is taking place. As stated above larvae will also infest humans and other animals, causing Myiasis, where opportunities arise. Larval development under perfectly optimum conditions, such as in human faeces at high temperature and humidity, may take only three days, the puparial a further three. Pupariation occurs in drier parts of the biotope. In ideal conditions, there can be many generations per year and populations can reach enormous levels. Increasingly adverse conditions lead to dwarfism, infertility and an ever higher mortality until a threshold is reached below which survival becomes entirely unsustainable. The adults have a well- .developed migratory habit, dispersing randomly up to 20 miles from their emergence sites.

Thought to have originated in the Middle East, the fly has been spread by commerce throughout the World, but in temperate regions it cannot maintain populations without human aid. The date of arrival of this fly in northern Europe is highly conjectural but Lemdahl (pers. comm.) has found puparia in Neolithic deposits at Alvastra in Sweden. In Roman times it occurred widely throughout lowland Britain but its arrival in Iceland may have been as late as the 19th century.

Amongst the many enemies of the House-fly are several related muscids including *Muscina stabulans*, *Hydrotaea dentipes* and *Myospila meditabunda*, whose larvae devour those of the House-fly and can lead to local extinctions. Portchinsky (1913) suggested that by breeding with man however, the House-fly is partially protected against the attentions of its numerous foes. The presence of breeding populations of houseflies in Britain indicates human presence since suitable breeding situations with the required constant high temperatures and humidity do not occur here in nature.] (Puparia and adult fragments from sites 2; 14; 18; 19)

Stomoxys calcitrans (Linnaeus) "The Biting House-fly" [The biology of this fly has been extensively studied as it is an insect of economic importance. It has been reared from a very wide range of media and like *Musca domestica* it requires high temperatures for completion of the life cycle. Hence, in temperate regions it is dependent upon man for the creation and maintenance of such thermal values. Favoured breeding sites are steaming manure and sileage heaps, cess-pits, domestic refuse dumps and compost heaps etc.] (Puparia from sites 6; 14; 18)

Spilogona sp. [The larvae are obligative carnivores living in moss-cushions, mud, silt, sand or sandy humus, sometimes under shallow water (Skidmore 1985). At least two *Spilogona* species were present in the Greenlandic material studied (figs.8-11). In one of these the posterior spiracles were relatively much larger than in the other, suggesting perhaps a dimorphic larva, whilst the one with much smaller spiracles, was presumably monomorphic. *Spilogona* puparia are distinctive within the Greenlandic fauna, where no other Coenosiines occur, in their longitudinally fluted microsculpture, most clearly seen on the end segment where the striations converge upon the posterior spiracles. Those from Sandnes and Niáqussat occurred with peak populations of Ephydrids - a classic habitat and food source for *Spilogona* larvae. The genus is remarkably rich in species in Arctic regions and five have been recorded from Qugssuk, namely *Spilogona arctica* (Zetterstedt), *S. dorsata* (Zetterstedt), *S. malaisei* (Ringdahl), *S. opaca* Schnabl and *S. sanctipauli* (Malloch).] (Puparia of *Spilogona* or other Coenosiinae from sites 3; 11; 15; 18; 23; 26; 33; 35; 36)

Coenosia mollicula (Fallén.) [Biology not known but other members of genus breed in humus soil and in sickly plants attacked by other insects upon whose larvae these larvae feed. British Isles to Shetland; Faroes]. (Puparium and wing from site 27)

Helina evecta (Harris) [Larvae in humus soil, preying on other insect larvae. British Isles to Shetland; Faroes. Replaced in Iceland by the very similar *H. annosa* (Zetterstedt).] (Puparium and adult fragment from sites 19 and 27)

H. sp. (near *reversio* (Harris)) [Larvae of most Helina species live in humus soil.] (Puparia from sites 24 and 27)

Phaonia angelicae (Scopoli) [Larvae predaceous, in humus.] (Puparium from site 19)

P. ?errans (Meigen) [Larvae predaceous, in humus amongst trees] (Puparium from site 15)

P. ?incana (Wiedemann) [Larvae predaceous in humus.] (Puparia from sites 21 and 25;)

P. pallidisquama (Zetterstedt) [Like other members of *Phaonia* s. stricto (Skidmore, 1985) the larvae are obligative carnivores breeding in moss and humus soil. There can be little doubt that the *Phaonia* puparia from Sandnes and Niáqussat belong to this species, the only *Phaonia* recorded from this area of West Greenland. The minute posterior spiracles with their slightly convergent respiratory slits, the rather large size of the puparium and its smoothly rounded end segment are highly distinctive features within the Greenlandic Dipterous fauna.).] (Puparia from sites 39 and 41)

P. s. str. (Puparium from site 15)

Muscid indet. (Eggs from site 21; puparia from sites 26 and 27)

Family HIPPOBOSCIDAE (Louse-flies) (Plate 28 figs. 12-15) [13 British]

Taxa represented

Melophagus ovinus Linnaeus (fig. 12) "the Sheep-ked" [The only species found in this study. As in other Hippoboscids the entire larval stage is spent in the parental oviduct and the female deposits a single mature larva which immediately hardens to form the puparium (fig. 15). The adult cannot be confused with any other insect, even in the fragmented state in which it is usually found in subfossil assemblages (figs. 13, 14). An obligative ovine ectoparasite whose entire life is spent in the fleece of the sheep upon whose blood the adult ked feeds. Clearly transported to West Greenland by the Vikings from Iceland, itmust have died out with their sheep-rearing culture. Buckland and Perry (1989) discussed the widespread indoor occurrence in Norse houses in Iceland and Greenland, presuming that these resulted from fleece-processing work.] (Puparia and adult fragments from sites 19; 28; 35; 36; 39; 41)

Family TACHINIDAE (Parasite flies) (Plate 29 fig. 12) [241 British]

This family of flies, whose larvae are parasitic on other insects, was virtually absent from this study. A puparium from Qeqertasussuk probably belongs to the Tachinidae, whilst a fragment of the head of an adult fly from Lindow Man III appears to belong to the genus *Phryxe.* Known Tachinid puparia exhibit a huge range of form in all of the usual taxonomic features, but most remain undescribed.

Tax represented

?Phryxe sp. (Fragment of adult from site 5)

Tachinid sp. (Puparium from site 37)

Family CALLIPHORIDAE (Blowflies etc.) (Plate 29) [32 British]

Puparia Puparia of only two positively identifiable Calliphorid genera have been recovered during this study, namely *Calliphora* and *Phormia.* The most distinctive features of the puparia of these and related genera are the huge size of the posterior spiracles and the diagonal orientation of their parallel respiratory slits (figs. 4,5 and 9). In

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Plate 29 *Calliphoridae* 1-7 *Phormia terrae-novae* puparium, 1 (ventral view); 2 (dorsal view); 3 (lateral view); 4 (posterior view); 5 posterior spiracle; 6 detail of ventral ambulatory welt; 7 section of ventral surface of puparium showing median parts of two ventral ambulatory welts; 8 *Calliphora* sp., puparium (dorsal view); 9 same, posterior spiracle showing *p* peritreme, *b* internal scar (here median in position), *s* respiratory slits; 10 oral sclerites showing *aos* accessory oral sclerite; 11 head and thorax of adult male (dorsal view), *Tachinidae Phryxe* sp., head (dorsal view), (NB, Bristles only indicated on left side in figs, 11 and 12) (Scales 1-3, 8 0.6mm; 4-7,9,10 0.25mm; 11,12 1.0mm) (8,9 after Smith, Rest Orig.)

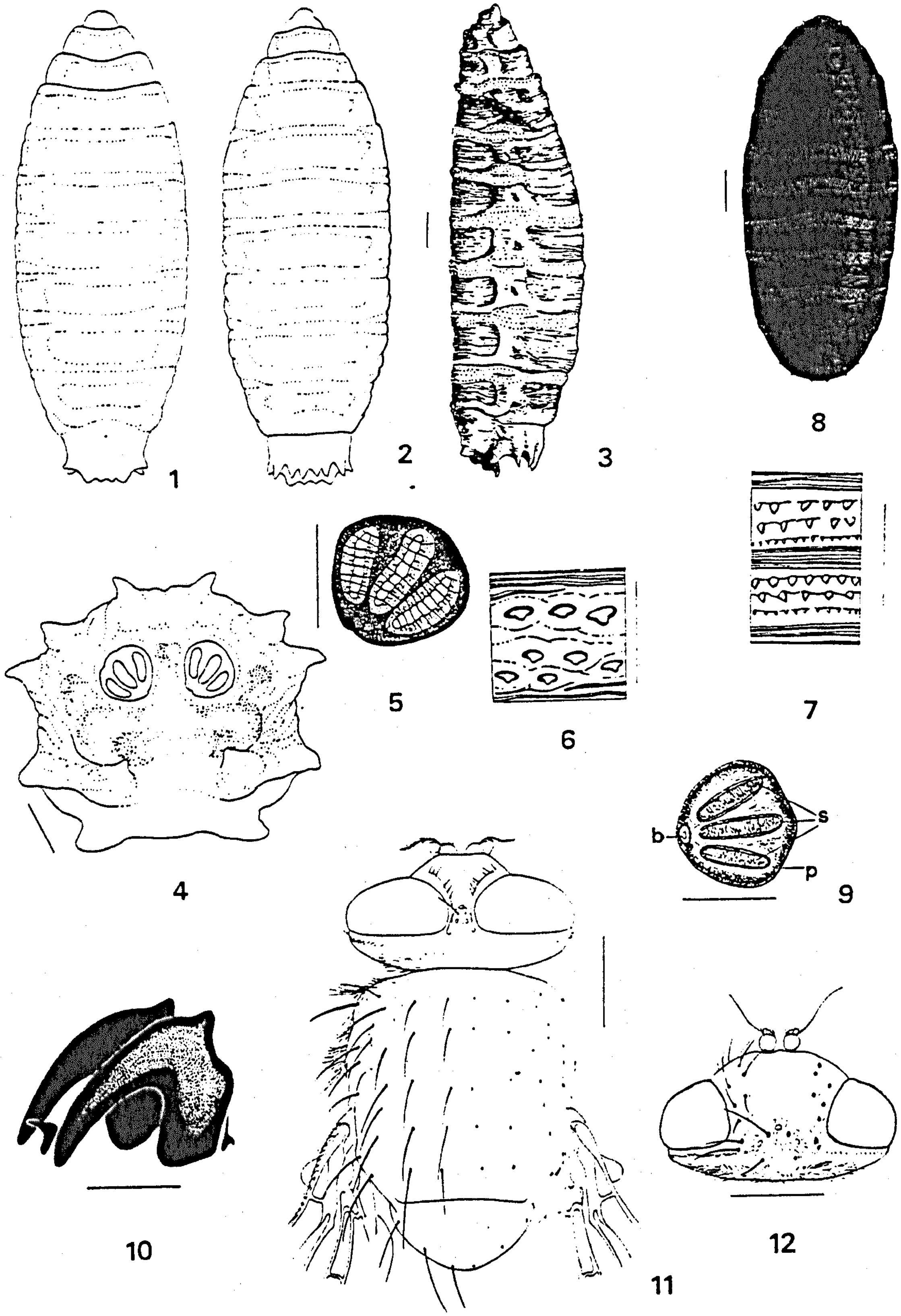


Plate 29

Calliphora there is a single accessory oral sclerite between the apices of the mouth-hooks (fig. 10) and the puparial end-segment differs from that of *Phormia* in the much less rugose appearance and the much less strongly developed perispiracular papillae (fig. 8). In *Phormia* the papillae are very large and the spiracles are in a distinct concavity (figs. 1-3). In *Calliphora* and its close relatives the main taxonomic feature is the shape and relative size of the spicules on the ambulatory welts (fig. 6, 7) (Erzinçlioğlu 1985).

Adults In subfossil Dipterous assemblages the metallic blue or green fragments of Calliphorid adults usually stand out, but it is vital to resort to chaetotactic characters to distinguish these from similarly coloured genera of other Muscoid families.

Biology Whilst a wide variety of larval pabula occur in this family, the genera recovered in this study are exclusively necrophagous. They are amongst the first colonisers of fresh carrion, commonly invading very soon after the death of the animal. *Phormia* is highly heliophilous but species of *Calliphora* have a greater tendency to oviposit in situations of rather lower light intensity. These and related Calliphorid genera have played a major role in Dipterological aspects of forensic work (Erzinçlioğlu 1985; Smith 1986).

Taxa represented

Calliphora uralensis Villeneuve [This, the common bluebottle in Iceland and Greenland, appears to be generally ubiquitous and consequently the extreme scarcity of the species in the Ameragdla material is significant. Smith (1986) states that blowflies are amongst the first wave of invaders into carrion, usually arriving soon after death and ovipositing immediately. But he states that *C. uralensis* is unusual in that, whilst it breeds in a wide range of media, it most commonly utilizes liquid excrement in latrines and cesspools in preference to meat, in stark contrast to *C. vicina.* In view of the extreme abundance of *C. uralensis* throughout Iceland and Greenland, often far from human habitations, such a predilection appears inconceivable as those conditions would not exist. One could only envisage a carrion food-source in such situations. A feature of *Calliphora* species which is rather peculiar in this family, is their slight, but marked, prefence for pabula in shaded locations. This, along with the assertion that they prefer to breed in excrement, renders their extreme scarcity in these middens even more remarkable. Thanks to the detailed researches of Erzinçlioğlu (1985), the biology and larval and puparial morphology of all of the North Atlantic species of *Calliphora*, and certain related genera is now well understood.] (Adult fragments and puparia from sites 25; 39; 40; 41)

C. sp. (Adult fragments and puparia from sites 19; 21; 30; 31; 36)

?Lucilia sp. (Puparium from site 7)

Cynomya mortuorum (Linnaeus.) [Another very common necrophagous fly in the North Atlantic islands today, whose scarcity in the sites discussed here is surprising.] (Adult fragment from site 40)

?Bellardia sp. [A single puparium apparently belonging to this family and doubtfully referred to this genus. It certainly does not belong to any of the necrophagous genera. *Bellardia* larvae are endoparasites of earthworms.] (Puparium from site 27)

Phormia terrae-novae (Robineau-Desvoidy) [The commonest carrion fly throughout much of the Arctic, was represented in the Ameragdla middens by only two puparia from Sandnes. This fact, along with the scarcity of

Piophilids, must infer a virtual absence of exposed carrion. Since it occurs in great abundance into the northernmost parts of the High Arctic, the climate at Sandnes was certainly not unsuitable for it. Furthermore, Böcher & Fredskild (1993) found it to have been the most abundant Dipteron in most horizons of the Palaeoeskimo middens at Qeqertasussuk. *P. atriceps* (Zetterstedt) has the same biology but is restricted to the Arctic, whilst *P. terrae-novae* is cosmopolitan. The puparia of the two species are probably indistinguishable.] (Puparia from sites 17 and 37)

Indet. Calliphorid sp. (Puparium from site 19)

Calyptrate sp. indet. (Puparium from site 21)

5 CASE-STUDIES FROM EXCAVATED SITES

5a Introduction

This section deals with all of the excavation sites from which Dipterous material has been examined during this study. In the interest of brevity a strict format has been adopted in this section:-

a Introduction, giving brief account of site location and period, and an outline of ecological interpretation from other disciplines appearing in the relevant literature.

b Interpretation of site based on the dipterous material examined.

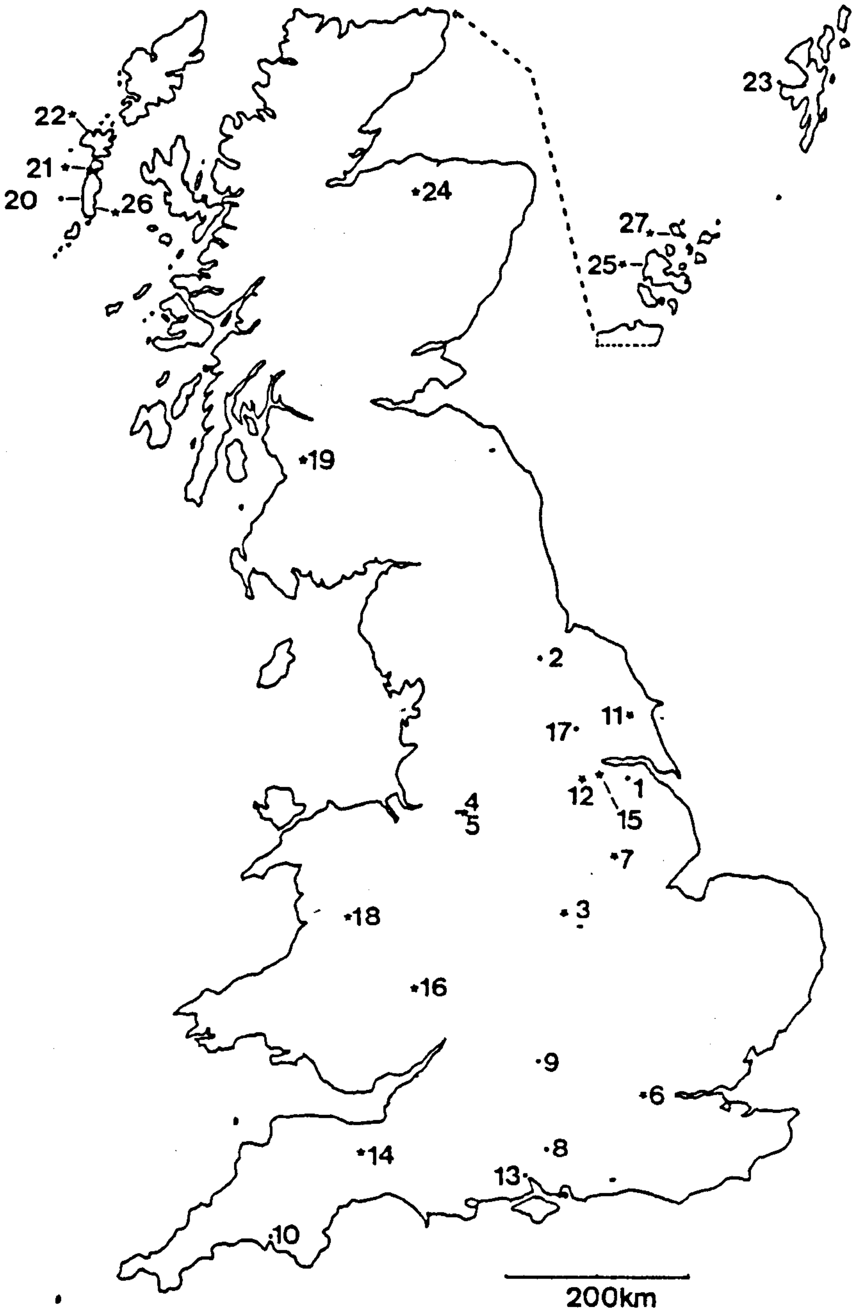
c Tables of taxa present. For each site these provide a complete list of taxa, and numbers of specimens of each, for each sample.

For ease of reference and to avoid unnecessary repetition, biological details of all of the taxa recovered during this study will be found under the respective family in Section 4. Analyses of samples from all of the individual sites appear in Appendix 1. Under the main geographical headings of England, Wales, Scotland, Iceland and Greenland, the individual sites from which dipterous material was examined are listed in Section 3 in the order in which they are discussed in this section. The listing in Section 3 also gives the MNI (minimum number of individuals present) for all Dipterous specimens and for puparia, and the number of taxa for each site and the pages on which the site is discussed.

ENGLAND Map 1, page 147

1 BRIGG RAFT (Lincolnshire)

Introduction. McGrail (1981) provides a detailed account of this Bronze



Map 1 Sites Studied in the United Kingdom

Age boat, sunk in an estuarine reach of the river Ancholme. Buckland, in McGrail (*op. cit.*) deals with the environmental aspects and provides a long list of Coleoptera recovered from beneath the structure. He interprets the environment as an open landscape with very little indication of trees.

Interpretation. The Dipterous material from this excavation was extremely sparse, comprising only three identifiable specimens as given in Table 1. *Bibio marci*, the St. Mark's fly, flies in late April and May and breeds in humus soil. It is mainly an insect of open grassy areas. The northern limit of the fly's range in Britain appears to be across Central Scotland, so the climate was probably not appreciably cooler than today's but could have been warmer. Agromyzids and Chloropids are also most abundant in grassy terrain, Chloropids being almost exclusively graminicolous in their larval stages. Many Agromyzids also develop in grasses.

Conclusions The sparse results from the Diptera would support the general interpretation of Buckland that this was an open grassy habitat with a climate not unlike that of today.

Table 1 Brigg Boat Diptera

Taxon	1069	1070	Total
Bibio marci		1	1
agromyzid sp.		1	1
chloropid sp.		1	1
assorted indet		6	6
Totals		9	9

2 CATTERICK ROMAN CAMP (North Yorkshire)

Introduction Hildyard (1952) published the account of the first survey of this site. Excavations on the site of the Roman fort and town here were carried out by Dr. J. Wacher in advance of the widening of the A1 in 1959 and remain unpublished (*cf.* Wacher 1971). A few specimens from this excavation were sent to me for identification by Dr. M. C. D. Speight, of the Institute of Archaeology, University of London, in February 1969, but no details of the find spot were provided.

Interpretation. Only one sample labelled MP BW 590452 and containing eight puparia of *Musca domestica*, was received from this site. As stated above (pp. 124- 126), this fly is eusynanthropic, requiring pabula in which a high rate of bacterial fermentation maintains high temperatures, such as in cess-pits, garbage dumps etc. It was widespread in England during Roman times.

Conclusions The presence of *Musca domestica* indicates that this was a regular waste disposal site associated with a human settlement, as the fly cannot survive withou human assistance in North Temperate regions.

3 LEICESTER CAUSEWAY (Analysis on pages 332- 346)

Introduction The material upon which this report is based consisted of 112 samples, containing about 1200 specimens (see Table 5 and Appendix 2). The condition throughout was extremely poor, almost all specimens having been mineralised to the point of fossilization. This meant that identification problems were greatly exacerbated. Many specimens were in the form of casts, the organic parts having dissolved so that vital cuticular features such as microsculpture had been erased. Despite the condition however, the material proved interesting in many respects, spanning over a thousand years of human presence on a single site (Dr. A. Monckton, *pers. comm.*). It is unclear whether the apparent faunal changes discussed below were real, or the result of limited data or excavation bias. The mineralised state of the material also raises the question of its origin in this non-calcareous site, and the suggestion is made that it may have resulted from attempts at primitive methods of hygiene by the human inhabitants of the site.

I am indebted to Dr. A. Monckton of the Leicester Archaeological Unit for involving me in this work which is part of an ongoing investigation into the Roman and later horizons under the city centre.

Methods The material was received dry and the condition precluded the normal techniques of examination in spirit and identification by means of microslide preparations. Gross features only were available for study and there was no recourse to dissection of unemerged adults to check specific identity. Submersion of specimens in spirit failed to reveal useful characters so the material was mostly examined dry. As usual, specimens were tentatively referred to taxonomic groups in an initial examination of all of the samples. Then these groups were re-examined and identified to the lowest heirarchical level (usually genus).

Interpretation. This study differed in many respects from others discussed here. The state of the material was incomparably the poorest but the period represented was by far the longest. In interpreting insect assemblages, the absent taxa are often as revealing as those present; and this was certainly the case here.

The species list (Table 5) is notable in the absence of such characteristic synanthropic flies, as *Lucilia* and *Calliphora*, Piophilids and the Muscids *Musca domestica, Stomoxys calcitrans* and *Muscina stabulans.* The absence of these suggests that the environment was in total darkness, and probably in a thermal regime inadequate for *Musca* and *Stomoxys.* These two require temperatures elevated by bacterial activity resulting from continuous addition of decomposing matter (Skidmore 1985), and their absence would infer breaks in that continuity.

Two facts suggest that the poor state of the material may not to have resulted purely from edaphic conditions on site, or from the type of mineralisation referred to by Girling (1979). Firstly it is not situated in a calcareous area, although marls are present and some limestone could have been incorporated into the buildings. But more significantly, it is clear from the Dipterous material that sudden lethal conditions periodically recurred. The bulk of the specimens were virtually fossilized and most of them died before the adults had emerged. Under normal conditions up to 10 percent of the individuals in a fly population may fail to emerge from the puparia (Skidmore 1993). When the majority have failed to emerge, highly abnormal conditions are indicated. In fact it is particularly evident from the specimens of *Eristalis tenax* that death was very sudden. Some of these were at the point in the pre-pupal stage when the larva has contracted and the pupal respiratory horns have appeared as vague protuberances on the dorsal surface of the first abdominal segment before they are extruded to form the familiar shape. The entire prepupal stage lasts only a matter of hours so that death in these specimens must have been almost instantaneous. Also, death occurred during the summer (July to early September), since the overwintering adults oviposit in spring to produce the next generation of adults during this period of summer.

The presence of large numbers of *Eristalis tenax, Thoracochaeta zosterae,* and *Fannia scalaris* strongly infer extremely foul liquid or semi-liquid conditions such as would prevail in cess-pits. The stench, particularly in high summer, could have been such that the human inhabitants were driven to periodic remedial action. The fossilized state of the Dipterous material, together with the evidence of their sudden demise suggest possible applications of lime. If this interpretaion is correct, it should be noted that the practice was in regular use on this site from Roman to late Medieval times.

Of the taxa represented in the Causeway material, eight belong to the cess-pit fauna, and it was upon the presence of one or more of these that samples in Appendix 2 were designated "putrid". The "cess-pit" species recovered in this study were- *Scatopse notata, Eristalis tenax, Heleomyza ?captiosa, Tephrochlamys rufiventris, Telomerina flavipes, Fannia scalaris* and *Hydrotaea dentipes.* According to Lobanov (1964). *Thoracochaeta zosterae,* the most abundant species in this site, also once belonged to this community, having been ubiquitous throughout Britain until late medieval times. Today however it occurs only on the coast, amongst decaying seaweed, and very rare captures in inland localities have always been regarded as representing stray specimens (Pitkin 1988) The remarkable change of habit which has clearly taken place over a few hundred years in this fly remains unexplained but it is undoubtedly related to improved standards of hygiene. A very similar range of habitats is shared by the now rare Urinal fly *Teichomyza fusca* (Smith 1986), although records of this insect from archaeological excavations in Britain have proved to refer to *T. zosterae* (Belshaw

1989, Skidmore 1993).

Telomerina flavipes prefers to breed in dark situations and has a preference for animal protein, either in the form of carrion or in the dung of carnivores or omnivores, including man (Roháček 1982-5). Having entered the system, this fly could probably have bred continuously in total darkness. This would not have been possible however for such heliophilous flies as *Fannia* and *Eristalis*, so there was clearly easy access into the system from outside.

In Table 2 the eight cess-species are listed according to the numbers of samples in which each was found in this study, under the three broad chronological divisions used throughout the archaeological

Table 2 The Occurrence of Cess-pit Diptera in Leicester Causeway Excavations

Taxon	Period	N/S	Total	Taxon	Period	N/S	Total
Scatopse notata	pre-300	1		*Thorac, zosterae*	pre-300	6	
	pre-1100	2			pre-1100	5	
	pre-1400	2	5		pre-1400	11	22
Eristalis tenax	pre-300	2		*Tel, flavipes*	pre-300	2	
	pre-1100	2			pre-1100	6	
	pre-1400	-	4		pre-1400	5	13
Teph, rufiventris	pre-300	1		*Fannia scalaris*	pre-300	6	
	pre-1100	2			pre-1100	16	
	pre-1400	-	3		pre-1400	10	32
Hel, ?captiosa	pre-300	-		*Hydr, dentipes*	pre-300	-	
	pre-1100	-			pre-1100	2	
	pre-1400	1	1		pre-1400	-	2

report (ie. pre-300, pre-1100 and pre-1400. (Monckton, unpubl.)

Table 3 arranges these data so that the percentage frequency of each taxon within each period, and the peak of this fauna during the pre-1100 period, are more easily seen. It will be noted that by far the commonest species in the pre-1100 period was *F. scalaris*, but *T. zosterae* was equally frequent before 300 and marginally more frequent after 1100. *T. flavipes* was the third commonest throughout the sequence. The Heleomyzids were remarkably scarce, whilst *Eristalis tenax* was not recovered from the pre-1400 period. Whether these apparent changes are real is not certain, but fluctuations in frequency could be expected without necessarily inferring marked changes in the type of materials

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Table 3 The Abundance of Eight species of Cess-pit Diptera in Leicester Causeway Excavations

Period	a:	b:	c:	d:	e:	f:	g:	h:	Total
pre-300	1(1)	103(2)	-	-	2(2)	4(1)	23(2)	-	133(8)
	1	*77*	-	-	*2*	*3*	*17*	-	
pre-1100	10(2)	60(1)	24(2)	-	208(2)	17(2)	85(2)	2(2)	406(13)
	2	*15*	*6*	-	*51*	*4*	*21*	*1*	
pre-1400	2(1)	-	-	11(1)	182(4)	12(3)	29(2)	-	236(11)
	1	-	-	*5*	*77*	*5*	*12*	-	
Totals	*13(4)*	*163(3)*	*24(2)*	*11(1)*	*392(8)*	*33(6)*	*137(6)*	*2(2)*	*775(32)*

The species in this table are as follows:- a, *Scatopse notata;* b, *Eristalis tenax;* c, *Tephrochlamys rufiventris;* d, *Heleomyza serrata;* e, *Thoracochaeta zosterae;* f, *Telomerina flavipes;* g, *Fannia scalaris;* h, *Hydrotaea dentipes.* The numbers under each of these refer to the total MNI of that taxon in each period, followed by the number of phases in which each occurred. The italicized figures give the percentage of each taxon for each of the three periods.

deposited.

There appears to be a distinct faunal change on the site through the period represented which Dr. A. Monckton (*pers. comm.*) feels is unlikely to result from a bias in excavation strategy. If correct, this may infer an actual peak of human activity during the pre-1100 period. This apparent faunal change is best seen by considering the relative frequency of uncontaminated and putrid environments through the periods concerned.

Table 4 The occurrence of putrid conditions in the Leicester Causeway Site on Dipterous evidence.

Period	No. Samples.	% Putrid
pre 300 AD.	25	52
pre 1100 AD.	49	90
pre 1400 AD.	36	67

In table 4 the samples indicating putrid conditions are represented as a percentage of the total number of samples for that period. This suggests that the cess-pit element increased from 52 per cent in the pre-300 period to 90 per cent in the pre-1100 period, then decreased before 1400.

Conclusions Despite the poor condition of the Dipterous material from this site, it appears to testify to a series of extremely foul environments persisting over a period of more than 1000 years of human habitation. The fly assemblage suggests accumulations of cess in total darkness though with easy access for a range of coprophagous and saprophagous species. There is some evidence that odours may have become so obnoxious during summer that lime was regularly applied

Table 5 Distribution of Taxa in Leicester Causeway Samples

Taxon	A	B	C	Taxon	A	B	C
Scatopse notata	x	x	x	*?Trachyopella*		x	
Mayetiola sp.			x	*?Drosophila* sp.	x	x	
?Oxycera sp.	x			*Hydrellia* sp.	x		
Chloromya formosa			x	*Scatella* sp.	x	x	x
Megaselia sp.	x	x		Agromyzid sp.	x	x	x
Eristalis tenax	x	x		Chloropid sp.	x	x	
Sepsid sp.	x	?	x	*?Botanophila* sp.		x	
Tephrochlamys rufiventris			x	Anthomyiid sp.			x
Heleomyza captiosa			x	*Fannia ?scalaris*	x	x	x
Ischiolepta sp.			x	*F. ?canicularis*	x		
Thoracochaeta zosterae	x	x	x	*Hydrotaea dentipes*	x	?	
?Telomerina flavipes	x	x	x	*?Spilogona* sp.		x	

Key A, Roman pre-300 AD; B, early medieval (pre-1100) C, late medieval, (pre-1400).

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throughout the period of human occupation of the site. Uncontaminated environments range from deep soil to open water with moss, algae and waterside grasses. The local human population may have peaked in the pre-1100 period.

4,5 LINDOW MAN 2 and 3 (Cheshire) (Analyses on page 346)

Introduction In a study based on a very small amount of non-Coleopterous insect material retrieved from Lindow Man 2 (Skidmore, in Stead et al., 1986), a total absence of any necrophilous Diptera was noted. This fact was seen as entirely supportive of the view that the corpse had been submerged in wholly anaerobic conditions immediately after death. Such conditions could be expected to prevail in the peat pools so typical of lowland raised mires. This report concerns nine samples of insect material collected from the immediate vicinity of Lindow Man 3, and from the body itself. The Dipterous taxa are listed in Table 6. For a published account see Dinnin & Skidmore (in press).

Interpretation The Dipterous material from this site indicates a pure peat-bog community entirely uncontaminated by any elements associated with carrion. Furthermore even such ubiquitous inhabitants of sodden putrifying animal or vegetable matter as Sphaeroceridae and Ephydridae were entirely absent. As with Lindow Man 2, this body lay in a totally anaerobic regime such as would occur deep in a peat pool. Buckland (in press) notes that recent studies have shown that peat pools may survive for centuries on the surfaces of undisturbed lowland bogs and it is therefore possible that the insect fragments from around Lindow Man 3 may have long predated his "burial".

One of the flies which was positively referable to species, namely the tiny Hybotid fly *Stilpon sublunatum* (Pl. 13 figs. 1, 2) is a characteristic inhabitant of lowland peat-bogs where it often abounds in wet *Sphagnum*. By far the most abundant Dipterous fragments were head capsules of larval Tipuloids very closely resembling *Limonia* species as figured by Lindner (1959). These are detritivores, some breeding in wet organic mud. In far smaller numbers were larval head capsules of another Tipuloid, of the genus *Pedicia sg. Tricyphona* (Text-fig. 11). These prey on other Nematocerous larvae, worms etc. Since head capsules of various instars were found, it is not possible to infer the numbers of individual specimens represented. At least two Tipuloids were present as pupal fragments, namely 18 tergal fragments of a *Limnophila*

s. lat. (?*Euphylidorea meigenii* (Verrall)) (Pl. 3 figs. 6-9), and a tergite and respiratory siphon of a Tipulid (almost certainly a *Prionocera*). 14 pupal anal segments may also belong to the same *Limnophila* species. Both *E. meigenii* and the genus *Prionocera* are characteristic members of the peat mud community. The Fever fly *Dilophus febrilis* breeds in humus

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Table 6 List of Dipterous Taxa represented in the Lindow Man 3 Samples.

Taxon	a	b	c	d	e	f	g	h	i	Total
?*Prionocera* sp.				1						1
Tipulid sp. pup.					12				2	14
Limoniine sp. lv.	6	2	1	13	18	1	15	2	84	142
Pedicia sp. lv.	3	1					2		1	7
Limnophila sp. pup.					18					18
Chironomid sp.			1		1					2
Ceratopogonidae	[sample number not recorded, 1 pupa]									1
Dilophus febrilis					1					1
Stilpon sublunatum	1		2					1		4
Dolichopodid sp.							3			3
?*Phryxe* sp.									1	1
	10	3	6	14	50	1	20	4	88	196.

Key to Table 6 a) 0-10cm; b) 100-110cm; c) 110-115cm; d) 115-130cm; e) 140-150cm; f) Frag. 3; g) AE body sample; h) LW/DV 3.1 150; i) LW/BJ. The letters a-e in the above tabulation refer to these samples, and the number given is the total of fragments retrieved under that particular taxon. For reasons explained above it is not possible to assess the actual number of individual Tipulid larvae from the fragments present.

soil and decaying plant matter and abounds in huge mobile swarms. It was clearly a casual intruder into the peat-pool vicinity.

Conclusions The only Dipterous fragments found in association with Lindow Man 2 were single specimens of a Chironomid larval head-capsule and a fragment of an unidentifiable Acalypterate puparium, possibly an Ephydrid. The assemblage from Lindow Man 3 was a Dipterous community characteristic of the peat-pool margins, and it is therefore possible that the actual specimens recovered long predated the submergence of the corpse. The complete absence of necrophagous Diptera from either Lindow Man 2 or 3 suggests that the corpses were neither infested with such flies before, nor after, "burial". Presumably very soon after death the corpses were thrown into the pools, where the anaerobic conditions ensured that no colonisation by necrophagous flies could occur.

6 MINISTRY: LONDON (Analysis on page 348)

Introduction This rather copious quantity of material was received from Dr. M. C. D. Speight, of the Institute of Archaeology, University of London, but unfortunately, no details whatsoever of the provenance were provided.

Interpretation. An interesting but extremely restricted fauna of six species from three samples and numbering 1585 specimens. This was clearly a cess-pit fauna. The spatial and temporal relationships of the three samples studied from this site are not known, but a number of interesting facts arise from the data. This is a classic medieval cess community with the Sphaerocerid, *Thoracochaeta zosterae* accounting for 92 per cent of the total Dipterous fauna. This characteristic member of the littoral wrack-bed fauna was formerly abundant in urea-rich situations around human habitations such as cess-pits and urine-drenched walls, etc. It is interesting to note that in sample 1 it comprised 98 per cent of the fauna whilst in sample 3 it had dropped to 82 per cent; in sample 2 it comprised a conveniently intermediate 84 per cent.

The decrease in *Thoracochaeta* from samples 1 to 3, was accompanied by changes in relative frequency of other taxa making up this very restricted fauna.

a *Heleomyza* crashed from 3 per cent in sample 2 to 0.2 in sample 3 (ie. a ten-fold decrease)

b *Fannia* rocketed from 0.8 in 1 to 16 per cent in 3 (ie. a twenty-fold increase)

c *Stomoxys* shows an increase from 0.2 per cent in 1 to 1.4 per cent in 3 (ie. a seven-fold increase)

Table 7 Diptera from London Ministry samples

Taxon	1	2	3	Total
Heleomyza ?captiosa	6	5	1	12
Themira putris	3			3
Thoracochaeta zosterae	975	140	350	1465
Fannia sp	8	20	68	96
Muscina stabulans		1		1
Stomoxys calcitrans	2		6	8
Totals	994	166	425	1585

Key to table 1, Samples as follows; 1, 86(3998)(355); 2, 86 (3998)(364); 3, 86(3998)(363) d *Themira* occurs only in sample 1

e *Muscina* appears only as a single specimen in sample 2

Of the above taxa, *Thoracochaeta* and *Themira* are capable of breeding in wholly fluid substrates, their larvae having appropriately modified posterior spiracles. The other genera favour less fluid situations. Assuming that the three samples are chronologically arranged, the changes in breeding populations of these flies would appear to suggest a slow progression towards a drier biotope though one still rich in urea. The implication could be a cess-pit which, although in use throughout the sequence, was becoming less liquid in overall consistency. *Stomoxys* is a thermophile in temperate regions, requiring high temperatures generated by bacterial fermentation for successful development. Thus it breeds in situations where artificially high temperatures are maintained by continued addition of decaying matter. Steaming heaps of putrifying material are the classic breeding sites for this fly. The adults suck the blood of mammals, including man, and are of medical significance in situations of poor hygiene.

7 THE NEWARK DITCH (Nottinghamshire) (Analysis on page 349)

Introduction This site was a 17th century Civil War site dug by J. Samuels and a sample labelled (MH 90 (23) 0-10) containing dipterous material from the excavation was sent to me for analysis by M. Dinnin of the Department of Archaeology and Prehistory, Sheffield University.

Interpretation The species recovered from this sample (Table 8) infer a water body containing a very high level of faecal contamination (probably human), perhaps from run-off from a cess-pit or manure heap. The Sphaeroceridae (Small dung-flies) comprise 61 per cent of the total

Table 8 Diptera from Nevark Ditch

Tipula sp	MNI= 1	Ischiolepta ?pusilla	MNI= 94
Ptychoptera albimana	MNI= 1	Copromyza sp.	MNI= 45
P. minuta	MNI= 1	Opalimosina liliputana	MNI= 14
P. albimana/minuta	MNI= 22	Limosinine sp. a	MNI= 9
Psychodid sp.	MNI= 3	Limosinine sp. b	MNI= 1
Chironomus s. lat. sp.	MNI= 1	Agromyzid sp.	MNI= 3
Themira putris	MNI= 4	Calliphora/Lucilia sp.	MNI= 1
Sphaerocera curvipes	MNI= 14	Total taxa 14	Total MNI= 214

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fauna retrieved from the site, and these would suggest the faecal component. Most of these would be more likely to breed above the water table (ie. not in totally fluid locations). Organic mud was close at hand since that is the larval habitat of *Ptychoptera*, only represented here by adults the fragments, including complete genitalic segments of two species. These flies often abound in mires and along land-drains and sluggish streams. The Calliphorid puparium indicates decaying animal protein, either in the form of carrion or meat-derived protein in human faeces (? Smith). The Agromyzid would have developed in one of the ditch-side plants, possibly a grass species.

8 OWSLEBURY (Hampshire)

Introduction The material from this Iron Age and Roman settlement comprised five samples and 33 specimens and was sent to me by M. Speight, Institute of Archaeology, University of London. The excavation was carried out by J. Collis (Collis 1968), but it has not yet been possible to ascertain the precise location from which the samples 1,3,4,6 and 8 were taken;

Taxonomic List.

?Conicera sp. 10 puparia(em)(OW/SW-1(4)), 6 puparia(em)(OW/SW-1(8)) (Length 2.7-2.9mm) MNI= 16

;Diplonevra sp. 12 puparia(em)(OW/PI-1), 3 puparia(em)(OW/SW-1(6) (Length 3.5-4.5mm) MNI= 15

?Metopina sp. 2 puparia(em)(OW/PI-1(1)) (Length 1.4mm) MNI= 2

Total taxa 3 Total MNI= 33

Interpretation An extremely specialised fauna comprising perhaps three Phorid taxa as listed below. Whilst their identity is unknown, it is most likely that the habitat was one of organic putrefaction in an enclosed situation remote from outside contact. The genus *Conicera* includes the well-known "coffin flies", whilst members of the genus *Diplonevra* and *Metopina* have also been reared from buried carrion.

9 ST.BUDOC'S CHURCH, OXFORD: MONK'S SHROUD (Oxfordshire)

Introduction The material consisted of three small samples of puparia from the shroud of a Saxon Monk from the crypt of St.Budoc's Church, Oxford. It was sent to me for analysis by Dr.M.C.D.Speight, of the Institute of Archaeology, University of London, in February 1969.

Interpretation This sample is a curious assemblage, larvae of two of of the three genera present (ie. *Muscina* and *Hydrotaea*) being facultative carnivores which usually colonise media infested by maggots of House-flies, Blow-flies etc., upon which they prey. Here however the only other species present, *Megaselia*, would be below the normally acceptable size-range for these predators. The inferred habitat is putrifying organic matter exposed to daylight since *Muscina* and

Hydrotaea are heliophiles, but the absence of other exophilic flies is inexplicable. In carrion, *Muscina, Hydrotaea dentipes* and *ignava* are amongst the early colonisers, usually following the exophilic Calliphorids. Oviposition must have occurred during the warmer months when likely prey-species would also have been active. *Megaselia* are active throughout the year and will colonise carrion in total darkness at a much later stage of decay. Here possibly *Megaselia* invaded after the muscids had vacated the corpse, perhaps after burial.

Taxonomic List

Megaselia ?rufipes 17 puparia(em) MNI= 17 *Hydrotaea dentipes* 7 puparia(em) MNI= 7

Muscina stabulans 10 puparia(em) MNI= 10 *H. ignava* 7 puparia(em) MNI= 7

Total taxa 4 Total MNI= 41

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10 PLYMOUTH DRAIN (Devon)

Introduction Only a single sample, containing 13 puparia, was received from this site, a town drain dating from the thirteenth century. The material, which was sent to me by Dr. M. C. D. Speight, Institute of Archaeology, University of London, was insufficient for detailed interpretation, but Dennell (1985) discusses the vertebrate remains from the drain (Drain D 1). It is likely that the Dipterous material came from the uppermost layer in the drain (ie. category three in Dennell, *op. cit.*)

Interpretation As suggested by Dennell (*op. cit.*) this drain evidently had some human faecal input, inferred mainly by the dominant Dipterous species, *Thoracochaeta zosterae*. The presence of *Muscina* is a little more problematical and would infer some solid decomposing organic matter inhabited by other, more heliophilous Diptera. Larvae of *Muscina* are well-known predators of maggots of such common synanthropes as *Musca, Stomoxys, Phormia, Lucilia, Calliphora* etc. and this may have been a contaminant from an underlying horizon in the drain which contained carrion (Dennell *op. cit.*)

Conclusion The limited material available indicates a drain containing cess and possibly decaying organic matter from other sources.

Taxonomic list.

Sepsid sp. 4 puparia(em)	MNI= 4
Thoracochaeta zosterae 6 puparia(em)	MNI= 6
Muscina stabulans 3 puparia(em)	MNI= 3
Total taxa 3	Total MNI= 13

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11 RUDSTON ROMAN VILLA WELL (East Yorkshire) (Analysis on page 347)

Introduction Two samples only were studied from the Well, in the Villa complex which is fully discussed by Stead (1980). Buckland, in Stead (*op. cit.*) deals with the subfossil Coleopterous fauna, from the Rudston Well, noting also the presence of about 50 Psychodid pupae.

Interpretation This was another curious assortment of species in which a Psychodid was dominant in sample *b*, inferring a wet regime. The overall inferrence from the species in this sample was of decaying organic matter, including cess (*Sylvicola, Scatopse* and *Thoracochaeta zosterae*). Sample *a* contained far fewer Diptera, only one of which, queried as belonging to the genus *Anthomyza* was found also in sample *b*.

Table 9 Diptera from Rudston Well

Taxon	a	b	Taxon	a	b
Tipula sp.		1	*?Spelobia* sp.	1	
Psychodid sp.		50	Limosinine spp.	7	
Sylvicola cincta/fenestralis		1	Piophilid sp.	1	
Bibionid sp.	1		*?Anthomyza* sp.	2	6
Scatopse notata		1	*Delia* sp.		1
Megaselia "rufipes" type		1	Coenosiine sp.		1
Themira sp.		1	indet. puparia		20
Thoracochaeta zosterae		2	Total MNI=	12	85

Total taxa c.18 Total MNI= 97

Key to samples a RW/QO 660118; b 660112

Anthomyzids are mostly associated with sickly grasses, reeds and sedges. Sample *a* was probably drier than *b* and showed a trace of carrion (Piophilids). Humicolous (Bibionids and Coenosiine) and phytophagous elements (ie. Anthomyzids and *Delia*) were also present.

12 SHIRLEY POOL (South Yorkshire) (Analysis on page 350)

Introduction Only two samples containing Diptera were received from this study, namely one from 0-20cm., the modern surface of the peat, and another from the bottom of the sequence, perhaps late medieval (Dinnin 1992). Together these provided only 7 taxa and a total MNI of 34 Dipterous specimens (see Table 10).

Interpretation This is a typical wetland environment, showing no evidence of human influence. The upper sample contains no evidence of an aquatic fauna, whilst the much richer assemblage from the bottom of

Table 10 Diptera from Shirley Pool

Taxon	a	b	Taxon	a	b
Tipulid sp.	1		*Tetanocera* sp.		1
Psychodid sp.		22	Chloropid sp.		1
Chironomid sp.(a)		5			
Chironomid sp.(b)		2	Total MNI=	1	33
Chironomid sp.(c)		2	Total taxa 7 Total MNI=		34

Key to samples a 0-20cm; b bottom

the core is wholly aquatic, suggesting that the he site had silted up over the period represented by the core. Of the six Dipterous taxa recovered from the bottom sample, by far the most numerous was a Psychodid, pupae of which accounted for 65 per cent of the total Dipterous MNI. Twelve of the remaining specimens from the "bottom" sample were fragments of adult Diptera. One of these, *Tetanocera* is parasitic on various snails in the larval stage. Chloropids mainly mine in grasses, several being host-specific.

Conclusions Open water and marginal marsh vegetation with carrland is indicated by the insect community as a whole, but the precise location represented by the sample was probably a marginal area of water which was slowly silting up.

13 SOUTHAMPTON PIT (Hampshire)

Introduction Buckland et al.(1976) discuss this site in the Saxon settlement of Hamwich, and incline towards the view that this pit (SAR XI F47) may have been filled with waste from a butcher's yard. The specimens from this site were sent to me by Dr.M.C.D.Speight of the

Institute of Archaeology, University of London, in February 1969.

Interpretation The presence of six puparia of the Muscid *Eudasyphora cyanella* would support the view that ungulate dung comprised much of the matrix in this pit. However, *Thoracochaeta zosterae*, accounting for 68 per cent of the total Dipterous fauna recovered, sits rather uncomfortably in this interpretation, suggesting a presence of urea-rich fluids such as urine, or decaying seaweed.

Taxonomic List.

Thoracochaeta zosterae	13 puparia (6 em.)	MNI= 13
Eudasyphora cyanella	6 puparia(em) (Buckland et al., *lc.*)	MNI= 6
	Total Taxa 2	Total MNI= 19

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14 TAUNTON MEDIEVAL CITY SITE (Somerset) (Analysis on page 349)

Introduction Ten samples from the excavation were sent to me for analysis by J.Greig of the Department of Plant Biology, University of Birmingham. The species recovered are listed below (Table 10). Nine of the samples were from the Pig Market (93 and 120) and one from the Priory Barn (40). Unfortunately, total numbers of specimens were not noted in some of the samples, which were returned to Mr. Greig in 1982, so it has not been possibe to adequately revise the analysis of the material.

Interpretation These appear to be typical medieval cess-pit assemblages with the dominant species, *Thoracochaeta zosterae*, comprising over half of the fauna recovered. The presence of *Musca* domestica and *Stomoxys calcitrans* indicate that deposition was probably

Table 11 Diptera of the Taunton Excavations

Taxon	1	2	3	4	5	6	7	8	9	10	MNI
Sciarid sp.				1							1
Scatopse notata	1		13	1							15
Psychodid sp.	1										1
?*Megaselia* sp.							9				9
?*Themira putris*		3		2			3				8
?*Sepsis* sp.				1							1
?*Tephr. rufiventris*						3	2	x			c.30
Copromyza sp.	1					1				x	c.30
Sphaeroc. curvipes				3							3
Ischiolepta sp.	7										7
Thorac. zosterae	10			275	5		X	X	X	?2	c.600
Spelobia sp. a	26										26
Spelobia sp. b	1										1
?*Tel. flavipes*	44						x				c.100
Limosinine spp. a-d	2a		1b	8c	6d		2e	8e			27
?*Madiza* sp.	1										1
Scathophaga sp.						1	1				2
Anthomyiid sp.					1		6				7
Fannia sp.								12	2		14
Muscina stabulans							2			2	4
Hydrotaea dentipes					1		1		2		4
?*Hydrotaea* sp.						1					1
Musca domestica					1		2	x	5	25	c.50
Stomoxys calcitrans					5		3	x	5	50	c.100
Total about 28 taxa MNI=	94	3	14	291	19	6	170	270	110	130	c1100

Key to samples 1- 9 Pig Market (sample 120, except 8 which is sample 93);

10 Priory Barn (sample (R20S; 40) X indicates presence of taxon, but numbers unrecorded

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on a continual basis so that high temperatures were maintained by bacterial fermentation. The fact that these two flies are markedly heliophilous suggests that the deposition sites were at least partially sunlit. *Hydrotaea dentipes* adults are also sun-lovers whose larvae are well-known facultative carnivores which prey especially upon maggots of *Musca* and *Stomoxys*. *Thoracochaeta* is not known to have preferences insofar as insolation is concerned, but the necrophilic *Telomerina flavipes* favours dark places. Here it probably derived the requisite protein from meat in human diet.

Conclusions These two sites appear to have been traditional medieval cess-pits in which the fly *Thoracochaeta zosterae* predominated with other exophilic eusynanthropes which, unlike *zosterae* today, are still common associates of man.

15 THORNE MOOR BRONZE AGE TRACKWAY (Analysis on page 352)

Introduction This site formed the subject of an extensive study by Buckland (1979), prompted by the exposure of the timbers of a Bronze Age trackway by peat-workers on Thorne Moor. A massive quantity of Coleopterous fragments was recovered and the most detailed study ever undertaken into the Coleopterous fauna of the Urwald as it was in Britain over 3000 years ago, was produced. The limited Dipterous material from this study provided the basis for the present note. Five samples provided a mere 15 taxa and 58 specimens, of which 34 belonged to a single species of hygrophilous cranefly, *Pedicia rivosa*.

Interpretation. By far the most abundant Dipteron recovered from this site was the cranefly *Pedicia rivosa*, of which a total of 34 larval head-capsules were found. Since these were all of final instar specimens they clearly belonged to different individuals. *P. rivosa* is one of our largest craneflies, and is unmistakeable on the morphology and size of the final instar larval head-capsule. In general, this very closely resembles that of *P. (Tricyphona) immaculata* (text-figure 11) but is very much larger. *P. rivosa* breeds in shallow water, showing a marked preference for fast-flowing streams, although it can be found in almost stagnant forest rivulets. The larvae are voracious carnivores, preying on other aquatic invertebrates.

The other Diptera recovered from the trackway were mostly

Table 12 Diptera of the Thorne Trackway site.

Taxon	1	2	3	4	5	MNI	Taxon	1	2	3	4	5	MNI
Pedicia rivosa	17		11	4	2	34	*?Anthomyza* sp.		4				4
small Tipulid sp.		3				3	*?Cordilura/Pogonota*		1				1
Psychodid sp.		1				1	Anthomyiid sp.				1		1
Chironomid sp.		2				2	*?Spilogona* sp.			1	1		2
Ceratopoginid sp.		4				4	*Phaonia ?errans*	-		1			1
Mayetiola sp.		1				1	?*P.* s.str. sp.			1			1
?Empis sp.		1				1							
Brachyopa sp.		1				1	Total taxa 15						
Leptocerine sp.		1				1	Total MNI=	17	20	13	6	2	=58

Key to samples 1 Thorne Moor Tree 1 (Bottom); 2 Thorne Moor Tree 1 (Top); 3 Thorne Moor Trackway (Cranberry horizon); 4 Thorne Moor Trackway over top of Fen peat; 5 Thorne Platform C 14 Birch bark.

represented by single specimens. The inferred habitat agrees perfectly with that indicated in much greater detail, by the Coleopterous fauna; namely a woodland with a high water-table, developing bog and decaying trees. Sickly foliferous trees were inferred by the hoverfly *Brachyopa*. The single "false puparium" of *Mayetiola* possibly indicates the grass *Phalaris arundinacea*.

16 THE WORCESTER BARREL LATRINE (Analysis on page 353)

Introduction A report on this 15th century structure is provided by Greig (1981) who lists 38 Coleopterous species, consisting mainly of taxa which are predatory on Dipterous larvae. He interpreted the assemblage as a typical cess-pit fauna.

Interpretation The Dipterous fauna wholly supports Greig's interpretation. This is a typical medieval cess-pit community characterised especially by the fly *Thoracochaeta zosterae*, although today this is only found commonly amongst decaying seaweed on the coast. The presence of a single *Muscina* is a little unusual as this usually breeds in profusion in situations supporting large populations of Housefly and related larvae upon which the *Muscina* larvae prey. They

Taxonomic List

Scatops notata	MNI= 1	Limosinine sp.a	MNI= 7
Heleomyzid sp.	MNI= 1	Limosinine sp.b	MNI= 2
Sepsid sp.	MNI= ?	*Muscina stabulans*	MNI= 1
Leptocera sp.	MNI= 7		
Thoracochaeta zosterae	MNI= 19	Total taxa 8	Total MNI= 40+

are however facultative carnivores quite capable of attaining maturity on a purely saprophagous diet.

17a CHURCH STREET ROMAN SEWER, YORK

A detailed report on this site, including a list of taxa present, was produced by Buckland (1976). This note discusses various aspects of the Dipterous material recovered from the site and referred to in that paper.

Whilst it is clear that at least two different Psychodid taxa were represented, and that the general environmental interpretation given stands, the taxonomy of the family has changed markedly in recent years (Withers 1989). Whether the species present in the Church Street Sewer would now be referable to the genera stated is uncertain. The massive dominance of Psychodids typify an effectively closed, aquatic environment rich in organic nutrients such as a sewer. *Leptocera fontinalis* would certainly breed in the less fluid places in such a situation, but this species was in very small numbers. Unfortunately the identity of the most numerous Sphaerocerid was not ascertained, but the most likely contender would probably have been *Thoracochaeta zosterae*, formerly a characteristic inhabitant of cess-rich humn environments. The single Calliphorid and Muscid puparia had evidently been "flushed" into the system from outside, as neither could have bred in the type of environment inferred.

17b "PILCHER GATE", YORK

Introduction A single sample was received containing the above label but it has not yet been possible ascertain the source. The site name is unknown in York and none can be suggested, even allowing for the most imaginative error of transcription. The reverse side of the label states "York Cess-pit 1830", but the numerals are believed to refer to sample number rather than date.

Interpretation Whilst the location of the site from which the sample was collected is unknown, there is no doubt regarding the nature of the matrix. This was unquestionably a cess-pit or similar structure. The analysis appears below, where it will be seen that the most abundant taxon, *Thoracochaeta zosterae*, accounted for 85 per cent of the sample. This would suggest a sodden environment rich in urea, such as would prevail in a cess pit or unmanaged urinal. The Black-bottle, *Phormia terrae-novae* on the other hand, which accounted for 14 per cent of the fauna, breeds in carrion in sunlit situations. The Room-fly *Muscina stabulans*, another heliophile, is predaceous in the larval stage, preying on other maggots, including *Phormia*, but not *Thoracochaeta*, which would be too small. The habitat therefore could have been a sunlit cess pit into which carrion had been thrown. If the cess-pit were dark, it is more likely that the carrion was infested by the Calliphorid and its predator before being thrown into the cess accumulation inhabited by *Thoracochaeta*. It is most unlikely that

Taxonomic list

Thoracochaeta zosterae 80 puparia,	MNI= 80
?Phormia terrae-novae 13 puparia	MNI= 13
Muscina ?stabulans 1 puparium	MNI= 1
Total taxa 3	Total MNI= 94

either *Phormia* or *Muscina* would breed in a liquid faeces-rich environment in total darkness which could sustain populations of *Thoracochaeta*. Conversely, the latter would not breed in pure carrion in a sunlit situation which would best suit *Phormia*.

Conclusion This site appears to have been a traditional cess-pit into which some decomposing carrion had been thrown. It is not clear whether this was an open or closed pit or channel. If closed, the carrion was probably "fly-blown" when it was deposited.

WALES Map 1, page 147

18 HEN DOMEN, MONTGOMERY (Powys) (Analysis on page 353)

Introduction A report on this timber castle on the borders of England and Wales was produced by Barker & Higham (1982). They state that nine horizons were sampled and numbered 10, at the top of the sequence down to 19, and that Dipterous puparia were present only in 10 and 12b. In Table 3 of their report however they list undetermined Dipterous fragments in Layer 11 (21), Layer 12e (8) and Layer 13s (19). The richest Coleopterous fauna was found in 12c and the data shows that 12e was less foul than 13s. Skidmore however, in the same report, gives 12e and 13s as the only samples from which Dipterous material was examined. A re-examination of this material has been made which warrants some additional comment. This note serves as a revision of this material.

Interpretation Skidmore (1982) stated that the Dipterous remains consisted of a collection of puparia from two horizons, namely 12E and 13S and belonged to at least four families:- Sphaeroceridae, Heleomyzidae, Anthomyiidae and Muscidae. Three species of Muscid were present namely several puparia of the House-fly *Musca domestica* and one of the Biting House-fly *Stomoxys calcitrans* from 13S, and two puparia of *Hydrotaea dentipes* from 12E. He noted that the predatory larvae of *H. dentipes* were well-known enemies of *Musca* and *Stomoxys*, both of which in Britain owe their presence to man. Further study has shown that the Sphaerocerids consisted of at least four genera and it is likely that they were breeding in some faecal material. The two layers 12E and 13S are very different in their Dipterous fauna, sharing only one species, namely *Ceroxys urticae*, a wetland fly associated with rotting vegetation but also known from cess-pits and manure heaps (Lobanov 1964). The dominant taxon in 12E, *Discocerina*, breeds in organic mud.

Table 13 Diptera of Hen Domen

Taxon	12E	13S	MNI	Taxon	12E	13S	MNI
Ceroxys urticae	1	1	2	*Discocerina* sp.	9		9
?Heleomyza captiosa		1	1	*?Scaptomyza* sp.	1		1
Themira sp.		1	1	*Scathophaga* sp.	1		1
Sphaerocera curvipes		6	6	Anthomyiid sp.	1		1
Ischiolepta pusilla		1	1	*Hydrotaea dentipes*	1		1
Copromyza sp.		36	36	*Musca domestica*		5	5
?Leptocera sp.	2		2	*Stomoxys calcitrans*		1	1
Spelobia sp		4	4	Coenosiine sp.	5		5
Telomerina flavipes		1	1				
Trachyopella ?lineafrons		1	1	Total taxa 17			
Piophilid sp.	6		6	Total MNI=	27	58	85

SCOTLAND Map 1, page 147

19 BUISTON CRANNOG (Strathclyde) (Analysis on pages 353- 367)

Introduction I am indebted to AOC (Scotland) Ltd., for the opportunity of involvement in this study, the provision of the non-Coleopterous material from their Provisional Report on the Buiston excavation and the supporting information, especially the Report on the Coleoptera and other Invertebrates by Kenward et al. (1994). This account is solely concerned with the Diptera from the Buiston Crannog excavations, which were contained in 33 samples from six of the Phases recognised in Kenward et al. (*op. cit.*). The Dipterous material consisted of 1978 specimens (MNI= 1933) and over 60 taxa, making this the most diverse assemblage in this programme of work. In the supporting information sent to me by AOC (Scotland) Ltd., there is a considerable discrepancy in the Phase and Group allocations of the samples. In this Report, I have followed the system used by Kenward et al. (*op. cit.*). In general, the interpretations for all of the samples discussed by Kenward et al. (*op. cit.*) are wholly supported by Dipterous evidence, the few points which differ marginally are noted in the Analyses in Appendix 2.

The present account is an extended version of that which I submitted to AOC (Scotland) Ltd. for inclusion in their Site Report (Skidmore, *in press*). For their purposes they requested results from only 12 of the 33 samples examined. Also, subsequent alterations to the Phase and Group numbers mentioned above, and some of the findings of Kenward et al. (*op. cit.*), have necessitated some changes.

Table 14a gives a summary of the number of fragments per sample, highlighting the totals for the House-fly *Musca domestica*. Table 14b lists all Dipterous taxa recovered, under the respective Phase categories.

Interpretation The overriding impression, based upon the samples studied here, is in keeping with the known characteristics of the site. Several species attest to the general picture of open water margined by beds of rushes (*Juncus* species), emergent grasses and carrlands. Peat-bog, with some ericaceous plants, had probably developed over part of the marshes as a natural hydroseral progression

In warm weather farmstock and humans were evidently pestered by bloodsucking Tabanid flies, whilst Chironomid midges and mayflies swarmed over the marshes. In the midst of this watery scene stood Buiston Crannog. The occupants clearly kept herds of sheep and cows, and utilised the peat, grass and rush beds, and carr-woodland for floor litter, fuel, construction work etc.

Two samples only were examined from Phase I (ie F115, F119). Apart from a single Drosophilid puparium, the other taxa (ie. *Prionocera/Tipula, Chironomus* sp., and *Hilara*), are aquatic, non-synanthropes. Kenward et al. (1994), who also interpreted this phase as an aquatic sediment, noted some "100 Nematocerous fly larvae", presumably head-capsules, in the material which they examined from this phase. They did not however indicate to which family these Nematocerous larvae belonged. There was therefore no Dipterous evidence of human presence in Phase I. No samples were seen from Phase II.

Phase III probably marked the establishment of the early settlement before increasing human activity reduced the site to a virtual cess-pit. Living conditions in the Crannog during much of Phase III and Phase IV became extremely squalid with humans and houseflies living together, the latter periodically reaching major "plaguepopulations", which perhaps prompted occasional changes of floor litter by the human occupants. With a lack of hygiene, the human inhabitants must have suffered a high incidence of Myiasis and fly-borne diseases (see for example Greenberg 1971-73, and Hewitt 1914). The biology of this fly on a site like Buiston Crannog is of pivotal significance, in Dipterous terms, in understanding the origins of the deposits in which the species is found. A eusynanthropic fly, it is extremely unlikely that it would have bred outside man's immediate environment.

The two large accumulations of House-fly puparia in F227 (Phase III; 9) and F312 (Phase IV; 16) warrant special consideration. Of the 1196 House-fly puparia present in these samples only eight had not hatched; this represents a success rate of 99.3 per cent. These were two separate populations in terms of location and time. The length of the puparia ranged from 8.0- 9.1 mm (n= 1196), compared with an average of 6.3 mm in Hewitt (1914) and a range of 3.00-6.85 mm (n= 116) in Skidmore (1985). It is pertinent to mention that a re-examination of some of the specimens upon which the latter size-range was based suggests that the last dimension should probably have read 8.65 mm, not 6.85. No Hymenopterous parasites or Dipterous predators of House-flies were found in either sample. Clearly these were extremely successful and healthy populations enjoying optimum conditions in terms of pabulum, humidity and temperature.

The deposits supporting the *Musca domestica* populations probably consisted of human faeces and domestic garbage including fouled floor-litter and food-waste. The larvae require high temperatures maintained by bacterial fermentation resulting from continuous accumulation of the food-source, and this presumably infers a crowded and active human colony. Deposition was almost certainly indoors, as in lighter situations Muscid predators of House-fly larvae, like *Hydrotaea dentipes, Myospila meditabunda* and *Muscina stabulans* should have been present. These flies are more heliophilous than *Musca domestica* and hence usually avoid darker places. Since many such predatory muscid larvae are cannibalistic in the absence of alternative prey, they can eradicate House-fly populations locally before attacking each other as noted by Portchinsky (1911) and Skidmore (1985).

If the sample numbers have any chronological significance, there may have been a lull in *Musca* populations between these peaks. Percentages of total Dipterous material made up by *Musca* in the peak samples (see Table 14a) were 99 % and 97 % respectively; in the intervening ones, in F327 (Phase IV 14) and F12 (Phase IV 15), they were 11 and 69 per cent respectively. Thus, between Phases III 9 and VI 16, *Musca* populations may have partially collapsed, supporting the view that the Crannog saw a drop in human activity. That humans were there is clearly shown by the continued presence, albeit in reduced numbers, of *Musca domestica*.

After the second House-fly population peak in Phase IV 16, the species almost disappears from the record -(see Table 14a). Does this suggest a better level of hygiene or a lower level of human activity ?

The House-fly populations in Phase III and IV at Buiston Crannog constitute the earliest positive records of the species in Scotland, though it appears to have been common throughout Roman England north to Carlisle. The known dispersal powers of this fly (Skidmore 1985) strongly infer that its presence at Buiston could not have represented an isolated colony, and one must assume that it bred widely in human settlements between Carlisle and Buiston and probably more widely throughout the Scottish Lowlands.

A feature of the Buiston material was the inexplicable absence of three ubiquitous endophilous eusynanthropes of rural England today, the Stable-fly *Stomoxys calcitrans*, the Latrine-fly *Fannia scalaris* and the Lesser House-fly *F. canicularis*. The absence of the House-fly predators, as suggested above, and the extreme scarcity of the sun-loving *Scathophaga*, probably indicate dark depositional situations. Likewise with the carrion-feeders; the lack of Piophilids, Sarcophagids and necrophagous Calliphorids infer an absence of exposed carrion as these flies normally oviposit in sunlit situations. Species like *Telomerina*

Table 14a Summary of numbers of fragments per sample

Phase/Gp.	Sample	MNI	M,dom.	Phase/Gp.	Sample	MNI	M,dom.	Phase/Gp.	Sample	MNI	M,dom.
Ph.,I/2	F115	7		Ph,III/9	F207	11	5	Ph,V/21	F310	7	
"	F119	2		Ph,III/8	F209	14	14	"	F39	1	1
Ph,III/5	F108	4		Ph,III/9	F213	1		"	F41	4	
Ph,III/7	F59	7		"	F215	11	11	"	F45	11	
Ph,III/8	F50	3	3	"	F223	1	1	"	F308	5	
"	F55	7	1	"	F224	2	1	"	F402	84	
"	F56	13	3	"	F227	649	643	Ph,VIII	F2	307	
"	F233	35	24	Ph,IV/14	F327	47	5	Ph, ?	F005	2	
"	F234	3		Ph,IV/15	F12	15	11	Ph, ?	POA	27	
"	F235	14		Ph,IV/16	F312	569	553	Total phases	?6		
Ph,III/9	F48	15	3	"	F316	23	2	Total samples	33		
"	F71	4		"	F341	74	8	Total=		1979	1392

Table 14b Diptera of Buiston Crannog

Taxon	Phases 1	 3	 4	 5	 8	 X	 MNI
Prionocera turcica		5					5
Tipula ?vernalis		2					2
Prionocera/Tipula	1			5	6		12
Limonia adult				1			1
Limoniid larvae						13	13
Pilaria discicollis		1					1
Erioptera lutea v. taenionota		2					2
Chironomus ?plumosus	5	2					7
Ceratopogonid sp.				1			1
Dilophus sp.		1	1	3		2	7
Scatopse notata		3	25	12	2		42
Rhegmoclema cooki				1			1
?Mayetiola sp.		1	15	1			17
Chloromyia formosa		1		1			2
Haematopota/Chrysops		2		1			3
Empid sp.		1		1			2
Hilara chorica	1						1
Dolichopodid sp.						1	1
Eristalis abusivus/arbustorum				1			1
Ceroxys urticae					7		7
Loxocera sp.		1				2	3
Psila sg. *Chamaepsila* sp.			1		62		63
Heleomyza borealis				3			3
H. captiosa/serrata					19		19

Taxon	Phases						
	1	3	4	5	8	X	Tot.
Heleomyzid spp.			1				1
Sepsid sp.		2		1		1	4
Ischiolepta pusilla		1	12				13
Copromyza sp.		1		1		1	3
?Leptocera sp.			1		42		43
Limosina silvatica				63			63
Herniosina bequaerti			6		13	-	19
Spelobia sp.		1	7				8
Telomerina flavipes			5		88		93
Trachyopella sp.			34	1			35
Sphaerocerid sp.		2	13	7			22
Limosinine spp.(several spp.)		5	3	1			9
Piophilid sp.					1		1
?Anthomyza sp.		3					3
Drosophila ?subobscura				1			1
D. sp.	1				1		2
Hydrellia sp.		3					3
Limnellia sp.		1					1
Ephydrid sp.		1		1	60		62
?Phytomyza sp.		1					1
Meromyza sp.		3					3
Acalypterate indet. spp.		16	1	5			22
Scathophaga/Botanophila sp.		2		1			3
Anthomyiid spp.		1		3	1		5
Hydrotaea ?albipuncta				3			3

Taxon	Phases						
	1	3	4	5	8	X	Tot.
Eudasyphora cyanella			1				1
Neomyia cornicina			1				1
Musca domestica		703	23	553			1279
Mydaea/Myospila sp.				1			1
?Spilogona sp.		6		2		8	16
Helina evecta		2		1			3
Phaonia ?angelicae		1			2		3
P. ?errans				1			1
Melophagus ovinus			1	2	1		4
Calliphora sp.				2	1		3
Calypterate indet. spp		2		2			4
Total taxa 60+	8	779	151	681	307	28	1935

Key to Phases; 1 Phase I; 3 Phase III; 4 Phase IV; 5 Phase V; 8 Phase VIII; X Phase ?

(for samples included under Phases see Table 13)

flavipes and the two Heleomyzids, which require animal protein, may have obtained it through human faeces or rotting meat products indoors as they favour dark places.

The only sample seen from Phase VIII, namely F2, is particularly interesting. Containing 307 specimens, it was the third richest in total Dipterous material, yet *Musca domestica* was totally absent. This sample nevertheless contained a substantial indoor assemblage (ie. *Telomerina*, *Herniosina* and *Heleomyza*) accounting for 39 per cent of the total MNI. Clearly some refuse containing carrion or human faeces which had accumulated indoors had been ejected and provided a substrate for colonisation by exophiles. The endophilous fauna suggests that the pabulum should have been eminently suitable for *Musca*, and its absence is inexplicable, unless the species had died out in the region.

The Analyses in Appendix 2 include some interpretive comments on each sample. In that section, samples are arranged numerically under their respective Phase and Group numbers and under each sample number dipterous taxa are listed. A brief description of the deposit, from information provided by AOC (Scotland) follows next, and finally an interpretation of the depositional habitat based on the dipterous taxa present. Reference to fermenting organic material indicates human occupation.

20 DUN VULAN (South Uist)

Introduction Only two Dipterous taxa were recovered from a single sample from this site, which is situated on the beach at Loch Ardvule (Grid Ref. NF713297). The specimens were passed to me by Miss T. Roper of the Department of Archaeology and Prehistory, the University of Sheffield, who is involved in a study of the site.

Interpretation Single puparia of the Sphaerocerids *Thoracochaeta zosterae* and *?Trachyopella* were the only Dipterous specimens present. Both occur today in moist heaps of rotting seaweed on the coasts of Scotland and they presumably infer a similar habitat in this site.

21 LOCH DRUIDIBEG (South Uist) (Analysis on pages 368- 371)

Introduction. This report is based on seven samples, each 3 to 4cm thick, from a monolith of organic silts, 0.24m in length. These had accumulated in a shallow depression in the bedrock on an islet in Loch

Druidibeg (Grid Ref. NF943383). The sequence formed part of a study into the origins of the entomofauna of the Outer Hebrides (Dinnin 1993; Dinnin, *in press*). After extracting the Coleoptera for study, Dr. Dinnin passed the remaining specimens to me. The age of the lowest horizon was

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Table 15 Taxonomic List

Taxon	a	b	c	d	e	f	g	MNI
Tipula ?oleracea/paludosa	2		1	6				11
Limonia s. str. ? *trivittata*	1	2	4					7
?Dicranomya modesta	4	1						5
Limnophila ?meigeni	x	x	x	10	x	x	x	*70*
?Molophilus sp.		1						1
Psychodid sp. 1	1							1
Psychodid sp. 2					x	1		10
Chironomid spp.	4	1	x	x	1	1		20
Simuliid sp.		1						1
Bibio ?johannis/nigriventris	1n	1j	1	1n	1	1		6
Sciarid sp.	1							1
Empid sp. 1 (*?Trichina*)	3	2	1	1	4	1		12
Empid sp. 2 (Hemerodromiine)	3	1	1	1	1			7
Empid sp. 3 (*?Hilara*)		1						1
Trichina clavipes	*1*							*1*
Hilara chorica	1							1
Dolichopodid sp. 2 (*Rhaphium* sp.)	2	1	1		1			5
Dolichopodid sp. 1	1			1	1			3
Campsicnemus loripes	1							1
Lonchoptera lutea	1							1

Taxon	a	b	c	d	e	f	g	
Megaselia sp.	2		2	1	1			6
Platycheirus clypeata s.lat.			1					1
Sepsid sp.							1	1
Themira ?leachi				1	1			2
Coelopa frigida	1	2						3
Copromyza sp.				1				1
Geomyza balachowskii		1						1
Hydrellia sp.	8	3		1		1	1	14
Hyadina guttata		1						1
Scatella ?subguttata	1		1		1			3
?Philhygra sp.					1			1
Cetema sp.			1					1
Acalypterate sp.(2 spp.)			1					1
Calliphora sp.		1						1
Zaphne caudata		1						1
Anthomyiid sp.1		1						1
Anthomyiid sp.2			1					1
Anthomyiid sp.3		1						1
Neomyia cornicina					1			1
Phaonia ?incana			1		1			1
Muscid sp.(eggs)			1		1			2
Calyptrate sp.		1						1
Total Taxa 41 Total MNI =	46	34	38	34	36	15	12	215

Key to Samples a 0-2cm; b 2-6cm; c 6-10cm; d 10-14cm; e 14-17cm; f 17-20cm; g 20-24cm.

An X in place of a numeral indicates an estimated MNI of about 10.

not ascertained, but it was thought to be several centuries old. The Coleopterous fauna indicated a woodland element in samples c to f (6 to 17cm), but predictably this was not apparent from the dipterous material, the condition of preservation of which was extremely good.

Interpretation The seven samples from this site, possibly spanning a period of several centuries, are all very alike, suggesting little change of environment during this period. The inferred habitat is an organic silty or muddy lake-margin which was at least periodically submerged. The most abundant Dipteron was a species of *Limnophila* s. lato, probably either *Euphylidorea meigeni*, a peat-pool species, or *E. fulvonervosa*, a more eurytopic lacustrine one. Both breed in saturated muddy conditions. Proximity to drier humus, probably pasture soil, was indicated by adult Bibionids, *Lonchoptera*, Opomyzids, Chloropids, *Phaonia incana* etc. That some animal farming was practised nearby was inferred by adult *Neomyia cornicina*, which is only known to breed in cow-dung, and by several Scarabaeoid beetles noted by Dinnin (*in press*). Adult *Coelopa* testify to the proximity of coastal wrack-beds, the nearest of which are some 2km to the east of the site. The condition of the material was remarkably good, a *Zaphne caudata* puparium containing the complete male hypopygium in perfect condition. An interesting feature of this assemblage was the presence of several Empidoid pupae; these are described on page 70- 76.

22 LOCH OLABHAT (North Uist) (Analysis on page 372)

Introduction. Mr. C. Warsop of the Department of Archaeology and Prehistory at Sheffield University asked if I would examine two small samples of Dipterous material from the excavations at Loch Olabhat on

North Uist. The site was the Neolithic Island Settlement on Eilean Domhnuill a Spionnnaidh, North Uist, Outer Hebrides (Grid Ref. 746753).

Interpretation. The two samples differed in most respects including the state of preservation, sample "a" being in a much poorer condition than "b". Table 16 shows that no species was common to both samples, and that whilst there were no dominant species in *a*, in *b*, *T. zosterae* and *L. silvatica* accounted for 74 per cent of the total MNI.

Sample a. Mr. Warsop describes the deposit thus- "Context 563- when excavated this was a waterlogged deposit with high organic content in black-brown loam matrix. One of the evident phases so far excavated on the islet above present water level, this may have undergone intermittent drying and wetting. It appears to represent organic materal *in situ*, forming the structure and matrix of a timber entrance-way sealed under a later, more substantial stone entrance, and itself seals the earliest entrance features- possible supports for the timber context". The only positive habitat indicators were *E. cyanella* and *N. cornicina*, well-known members of the cow- dung community, of which the latter is not known to breed in any other medium. *E. cyanella* has been reared from sheep-dung and decaying vegetation, though this could perhaps have been contaminated by, or adjacent to, cow-dung (Skidmore, 1985). Neither species is known to breed in manure, only in fresh dung lying in the pastures. *Scathophaga* is mainly associated with the dung of ungulates, but at least two species (*S. calida* and *litorea*), which abound in the Western Isles of Scotland, breed in rotting plant and animal matter on coasts (see page 110). It was impossible to identify the species present in this sample, but the fragments were indistinguishable from the dung-frequenting species *S. stercoraria* and *furcata*. *Scatopse notata* breeds in a wide range of decaying materials and faeces, etc. In archaeological sites in the North Atlantic area studied here it proved to be one of the most ubiquitous synanthropes, but it does occur in places remote from human settlements.

Sample b. Mr. Warsop gives following details of the deposit 'Context 1008- Straw-like deposit containing wood and other organic materials. Sample 8- Organic material round straw layers. These levels are interpreted as living floors or other activity areas. The context has not been related to the main phases of occupation excavated from the islet, but may represent the earliest occupation discovered so far'.

Two species in sample b (*Orygma luctuosum* and *Thoracochaeta zosterae*) are typical "Wrack-bed" flies. The latter was the second most abundant species in the sample, and, whilst it is probably a seaweed indicator in this site, being associated with *Orygma*, in medieval times it was a ubiquitous cess-pit fly. The most abundant species in the sample was *Limosina silvatica* of which 17 puparia were present, out of a total of 50). This fly is usually associated with decaying vegetation in woods, but it has also been reared from manure and old cow-dung,

Table 16 Dipterous Taxa from Loch Olabhat

Taxon	a	b	Total	Taxon	a	b	Total
Tipulid sp.	2		2	*?Trachyopella* sp.		3	3
Psychodid sp.		1	1	Limosinine spp. a-c	3		3
Scatopse notata	2		2	*Scathophaga* sp.	2		2
Orygma luctuosum		1	1	*Nupedia/Paregle* sp	1		1
Leptocera ?fontinalis		2	2	*Hydrotaea dentipes*		2	2
Thoracochaeta zosterae		11	11	*Eudasyphora cyanela*	1		1
Limosina silvatica		17	17	*Neomyia cornicina*	1		1
?Telomerina flavipes		1	1	Totals	12	38	50

both indoors and in the field, also from decaying organic matter in caves, mammal-burrows, etc; it is said to prefer at least partially shaded places. *Telomerina flavipes* was one of the most ubiquitous synanthropes in the North Atlantic medieval settlements (Skidmore 1992). Primarily a necrophagous troglodyte, it also breeds in dung of omnivores and carnivores, decaying fungi, etc. The single incomplete puparium tentatively referred to this species could perhaps belong to extremely similar *Opalimosina liliputana* (Skidmore, *op. cit.*), a poly-saprophage occurring in decaying vegetable matter, compost heaps, dung of many mammals, mammal-burrows, etc. *Hydrotaea dentipes* larvae are highly predatory on the maggots of other flies and the species is strongly synanthropic in more northerly areas.

Conclusions It appears from the sparse Dipterous material from Loch Olabhat that at site "a" there was some ungulate (probably cow-) dung, and decaying plant matter, but there is no indication that it was an enclosed site. Site "b" appears very different; there was a strong inference of decaying seaweed and domestic refuse, comprising possibly human faeces and (or) decaying animal matter in addition to rotting plant matter. Site "b" was perhaps inside a dwelling or other building, but conditions were decidedly foetid.

23 PAPA STOUR (Shetland)

Introduction Only one sample, labelled PL50 084, containing two Dipterous fragments, was received from this site.

Interpretation The Dipterous material comprised an incomplete puparium of a *Spilogona* species and a tipulid pupal fragment. These would give no indication of human presence, but of soil or sand, probably with some humus content.

24 PLUSCARDEN PRIORY (Moray) (Analysis on page 371)

Introduction. An interesting and highly specialised assemblage comprising 439 identifiable Dipterous specimens from the pit at Pluscarden (Site no. 147; F23). I am again indebted to AOC (Scotland) for involvement in this site study. I am informed by them that the assemblage discussed here came from a pit close to the West front of the Priory building.

Interpretation By far the most abundant Dipteron present was the troglophilous Sphaerocerid, *Terrilimosina racovitzai* (Bezzi). The Sphaerocerid puparia present all appeared to be identical, but other species were perhaps present since the puparia of most species remain undescribed, and many will probably prove to be indistinguishable on external characters. The identification of the Pluscarden material rests primarily upon just 2 unemerged males amongst 5 unhatched examples from a total of 403 puparia. The spermathecae of the 3 females agreed with *T. racovitzai*, but these are of less diagnostic significance since several species possess very similar structures. Three Sphaerocerid wings and 18 adult head capsules also agree well with descriptions and figures for *T. racovitzai* in Roháček (1983). The wing size and venation, notably the slight prolongation of the costal vein, agree very closely with Roháček's figure.

T. racovitzai is a specialised species having the reduced eyes typical of so many troglophilous Acalypterates. The male is unique amongst described European Leptocerine Sphaerocerids in the remarkable bifurcate median process and lateral curved teeth of sternite 6, features clearly visible on the male puparia from Pluscarden. Recorded originally from caves, *T. racovitzai* has also been found in mole burrows, but according to Roháček (*op. cit.*.) the largest populations occur in cellars containing large amounts of decaying vegetable material. Although it will breed in carrion, it possibly favours decaying vegetable matter.

Two Heleomyzids species were present in modest numbers (19 empty puparia), both very close to *Heleomyza serrata* but four were larger and had a densely spiculate "end-segment", somewhat as in *Scathophaga*, but lacking the perispiracular papillae. Several Heleomyzines are of subterranean habit (eg. *Scoliocentra*, *Eccoptomera* etc.) and even the more eurytopic *Heleomyza serrata* often abounds in caves or large mammal burrows. Like *T. racovitzai*, Heleomyzines are not predominantly associated with carrion but exceptions are known (ie. *Neoleria* and possibly *Scoliocentra* species).

Taxonomic List

Taxon	MNI	Taxon	MNI
Psychodid sp.	1	*?Scoliocentra* sp.	5
Trichocera sp.	1	*Fannia ?scalaris*	8
?Megaselia sp.	1	*Helina ?reversio*	3
Terrilimosina racovitzai	403		
?Heleomyza captiosa/serrata	14	Total taxa 8 Total MNI= 436	

Fragments of eight *Fannia* puparia all appeared to belong to the same species, probably the Latrine-fly, *F. scalaris*, a polysaprophage omnivores. It formerly abounded in privvies before the advent of the "flush toilet". Whilst adults of *T. racovitzai*, and probably also the Heleomyzid, could survive and breed in total darkness, *Fannia* species, as far as is known, require access to sunlight, the males having a highly developed nuptial swarming habit.

The Psychodid pupa infers at least a partially wet organic biotope, whilst the three puparia of predatory Muscids, which are tentatively referred to the genus *Helina*, breed in rich humus soil. It is noteworthy that, apart from the *Fannia*, there is a total absence of any heliophilous polysaprophagous element in the fauna such as for instance Piophilids, *Madiza*, *Drosophila*, *Calliphora*, *Sarcophaga*, *Muscina*, *or Hydrotaea*. The inferred habitat therefore is one of a mass of faecal or decaying plant material lying in permanent darkness. None of the taxa present unequivocally point to the presence of carrion and it is possible that any which may have been present may have been uncontaminated by flies when it was cast into the pit.

25 SKARA BRAE (Mainland, Orkney) (Analysis on page 372)

Introduction The only subfossil Diptera received from this site were contained in a single tube from a soil sample from Childe's Black Midden. The material, which was passed to me by Dr. P. C. Buckland, was very limited in quantity and badly fragmented and crushed. Identification to species level was therefore generally impossible and any interpretations must be considered tentative. There are however indications that a thermal regime with values at most comparable to today's prevailed there during the time of deposition.

Interpretation As stated any comments regarding the nature of the site are perhaps hazardous on the basis of such a small quantity of material and it is probable that the specimens extracted were not all alive at the same time. However a number of observations can be made which may corroborate inferences derived from other disciplines.

Humus soil is indicated by the Muscid and probably the Tipulids. Larvae of the subgenus *Phaonia* s. str. are predatory humicoles (Skidmore 1985) and probably the *Tipula* larvae also belong to one of the very many soil-frequenting species. Bibionid larvae also develop primarily in rich organic soils, but, since only adult females were present in the sample, their presence is perhaps inconclusive in this regard (see below under b)).

It was not possible to ascertain the Bibionid species concerned, apart from the fact that it was one of the small species of *Bibio* or a *Dilophus*. Bibionid adults swarm at various times from April to September, depending on the species. Clearly, the depositional area therefore was exposed to the elements during this period. It is somewhat odd that females only were present as males are usually more obtrusive due to their swarming habits and are commonly seen on the ground. Perhaps the females were penetrating deeper into the substrate for the purpose of oviposition after the mating flight. This being so, the Bibionid females would also suggest humus soil.

In the depositional site there was clearly some decaying animal matter, indicated by the Piophilid and *Calliphora* puparia. Carrion is perhaps inferred, rather than animal protein in the form of human faeces or the dung of carnivores for, whilst *Heleomyza borealis* is more often found in the latter type of materials, it can develop in carrion. Conversely, Piophilids and *Calliphora* can utilize dung of omnivores and carnivores, but they are far more frequent in carrion. The Sphaerocerids and Drosophilids were unidentifiable to species but the groups include species having preferences for decaying animal and plant matter, and some which are truly polysaprophages.

The presence of dung cannot be categorically verified since the specific identity of the *Scathophaga* was not known. The genus includes the "Yellow dung-flies" which breed primarily in the dung of ungulates, but two species are only known to develop in littoral débris. However, the absence of other seaweed species on this site, which is adjacent to the cvoast, perhaps suggests that the *Scathophaga* was in fact one of the stercoricolous species. *Heleomyza borealis* and *serrata* were the ubiquitous "House-flies" of the Viking settlements of the North Atlantic, where they bred in profusion in the cess-pits and middens, *H. borealis* replacing *serrata* in the colder, more northerly regions and extending into the High Arctic. However, as stated above, these flies can develop in decomposed carrion.

Taxonomic List

Taxon	MNI	Taxon	MNI
Tipula sp.	4	*Scathophaga* sp.	1
Bibionid sp.	7	Anthomyiid sp.	1
Heleomyza borealis	1	*Phaonia ?incana*	1
?Spelobia sp.	6	*Calliphora uralensis*	1
?Allopiophila vulgaris	5		
Drosophilid sp.	1	Total taxa 10	Total MNI= 28

The climate was most unlikely to have been warmer than today but could have been colder. As a climatic indicator the most significant species present in the Skara Brae material was the blowfly *Calliphora uralensis*. Laurence (1991) reviews the status, range and ecological preferences of this alpine to arctic fly in Britain, showing it to be the dominant Blowfly in the most exposed and windswept areas of the Outer Hebrides, Orkney and Shetland. Its presence in the Skara Brae deposits clearly infers a climate no warmer than today's. Abroad the species occurs in the Alpine region then in the colder parts of Scandinavia westwards to West Greenland (north to about 71°N). It abounds in the southern half of Greenland and is by far the commonest bluebottle in Iceland (Nielsen *et al.* 1954).

Conclusions As far as the synanthropic species are concerned this fauna is very similar to that revealed in many medieval sites in Iceland and Greenland. But the extreme paucity of the synanthropic material and the dominance of the humicolous fauna perhaps infers that the site was on the periphery of the main depositional area for the settlement. The climate was at best no warmer than today

26 SOUTH LOCH BOISDALE (South Uist) (Analysis on page 372)

Introduction Five samples containing Dipterous material were received from this site, which was researched by M. Dinnin of the Department of Archaeology and Prehistory, Sheffield University, as part of his study into the origins of the entomofauna of the Outer Hebrides (Dinnin 1992; Dinnin, *in press*). In contrast to the Loch Druidibeg series, Dinnin found a strong saproxylic element was found in all horizons at the present site, which was a profile in a new peat-cutting which contained protruding tree trunks and branches. A series of samples were taken from depths, in the exposed face, from 80 to 155cm. The results of the Coleopterous analysis are discussed by Dinnin (*op. cit.*). Thirteen Dipterous taxa were recovered, indicating riparian, aquatic and grassland habitats. The date was not ascertained.

Interpretation Though very much smaller, the fauna closely resembled that from Loch Druidibeg in that the most abundant taxon was a *Limnophila*, most likely the same species, but *Pedicia rivosa*, which was not recovered from Loch Druidibeg was a prominent feature in the

Table 17 Diptera of South Loch Boisdale

Taxon	a	b	c	d	e	MNI
Tipula/Prionocera sp.	1		1	3	1	5
Dicranomya ?modesta			30		1	31
Pedicia rivosa	3		4	3	5	15
Limnophila sp.	3	3	40	14	23	83
Psychodid sp.					2	2
Ceratopogonid sp.			2	2		4
Dilophus sp.			4			4
Opomyza germinationis/petrei			1			1
?Ephydrid sp.			1			1
?Scaptomyza sp.			1			1
Cordilura sp.	1			1		2
?Coenosiine sp.			2			2
Calyptrate sp.		1				1
Total taxa 13 Total MNI=	8	4	86	23	32	153

Key to Samples *a* 90-95cm; *b* 110-115cm; *c* 140-145cm; *d* 145-150cm; *e* 150-155cm.

present samples. *P. rivosa* larvae require at least slowly moving water bodies, preferably surrounded by marsh vegetation. An assemblage comprising these two taxa, along with two other hygrophilous Tipuloids, occurred in all of the samples. This infers that the habitat throughout the sequence was remarkably uniform in comprising a silty or muddy substrate, which was, at least periodically, submerged by fresh running water, presumably from a watercourse which must have traversed the site. Apart from saturated mud and clean running water inferred by the Tipuloids, there was some grassland and *Caricetum* , as indicated by *Opomyza* and *Cordilura* respectively. There was no Dipterous indication whatever of any human influence, or of a woodland element, although the presence of the latter was clearly evident from the subfossil Coleopteous fauna and from the exposed section. The richest and most diverse subfossil Dipterous fauna occurred in the lower woody layer of the series, at a depth of 140 to 145cm.

27 TUQUOY (Westray, Orkney) (Analysis on pages 373- 377)

Introduction. 11,101 specimens were examined in this study, from 12 horizons from the pitfill site in section I to J at Tuquoy (Owen 1988). The material was obtained from the site by J. Sadler of the Department of Archaeology and Prehistory, Sheffield University (Sadler 1992), on behalf of AOC (Scotland), who were involved in major excavation work there. About 60 Dipterous taxa were recovered, as listed in Table 20.

Interpretation When dealing with such a large assemblage it is desirable, for the purposes of interpretation, to divide the taxa into trophic groups. The immature stages in the material are most likely to have been actually breeding on site, whereas fragments of adults may have immigrated from adjacent biotopes. The total number of specimens of the immatures present therefore, and a system of broad larval habitat requirements of the taxa present, are given in Table 18 below.

Table 18 Analysis of Dipterous taxa from Tuquoy in terms of habitat requirements

Trophic group	Taxa	MNI	% of Total MNI
Coprophiles	13	10,727	98,18 %
Hygrophiles	13	63	0,58 %
Fucicoles	6	28	0,26 %
Humicoles	9	8	0,07 %
Unspecified	c,13	100	0,91 %
Total number immatures		10,926	100 %.

Table 18 allows for the following tentative interpretations to be made.

a) Although so close to the seashore, very small populations of fucicolous flies were actually breeding on the site, suggesting there was very little seaweed accumulating in the feature. On the other hand a rich fauna of these species occurred nearby since adults of *Orygma luctuosum, Coelopa, Heterocheila buccata, Thoracochaeta zosterae, Fucellia* and possibly *Malacomya*, all of which breed in rotting seaweed, were present in the samples. A presence of fucicolous species breeding on the site was apparent in horizons a, c, d, e and g, but it accounted for only 0.26 % of the total sample of immatures.

b) There was clear evidence of a wet substrate at 806, 808, 810, 814, 816 and 817, suggesting marshy conditions, possibly muddy banks of a stream or flush. The richest wetland stratum was 810 where four species of hygrophilous Tipuloids were breeding (ie. *Limonia*, *Pedicia*, *Limnophila* and *Erioptera*) as well as *Scatophila*. But the total hygrophilous component represented a mere 0.58 per cent.

Table 19 The Coprophilous Sphaeroceridae of Tuquoy

Taxon	MNI	Percent.
Trachyopella coprina	9313	86.82 %
Spelobia/Opalimosina	983	9.16 %
Copromyza equina/similis	299	2.79 %
Pullimosina heteroneura	75	0.70 %
Sphaerocera curvipes	10	0.09 %
Other species	47	0.44 %
Total taxa 11+ Total MNI=	10,727	100 %

c) The presence of breeding Sphaeroceridae throughout the series indicate continued presence of decaying organic matter, most probably including dung of herbivorous farm animals (cattle, horses or sheep). Of the 10,926 immature specimens from the Tuquoy excavation in this study, 10,727 belonged to the Sphaeroceridae. The numbers of sphaerocerid puparia and their percentage of the total coprophilous fauna is given in Table 19 above. Clearly conditions were optimum for the thermophilous synanthrope *Trachyopella coprina* which vastly outnumbered all other Diptera combined. This very strongly suggests that this was a manure heap, where high temperatures resulting from bacterial fermentation were being maintained throughout the sequence.

d) *Scatopse notata* is strongly synanthropic in northern parts of its range and may be so on Orkney. Its regular occurrence throughout the sequence further confirms a presence of decaying organic matter such as would be unusual in entirely natural environments, and wholly supports the hypothesis that this was a manure heap. The species was however in very modest numbers, accounting for only 0.29 % of the coprophilous fauna breeding on site.

e) No species were found which are exclusively associated with the dung of any one species of domestic animal; all will breed in a wide range of dung or manure types.

f) Noteworthy was the total absence of bucoprophilous Muscids which usually breed in fresh dung (see Skidmore 1991), and even species of *Scathophaga*, which also utilise this medium, were almost absent (ie. two puparia only, or 0.02 % of coprophilous fauna). These results substantiate the view that the site was used for tipping old dung.

g) The absence of *Stomoxys calcitrans* and *Musca domestica* is noteworthy in view of the quantity of material examined, and it is probable that they had not yet arrived at these latitudes. The dominance of *Trachyopella coprina* strongly infers that thermal values on the site were adequate for *Stomoxys* and *Musca domestica*.

h) Surprisingly few humicoles were found, suggesting that the deposits may not have been allowed time to humify properly before the next material was added. Only 0.7 % of the immatures present could be regarded as being essentially humicolous.

i) No clear evidence of any carnivore or human faecal presence, nor any carrion-feeders, was found in the sequence. *Heleomyza* species, which occur in vast profusion in many Viking sites, where they indicate accumulations of human faeces, were totally absent from Tuquoy. Also Piophilids and necrophagous Calliphorids were absent, so that, although bones were found at several horizons, there must have been no flesh attached to them.

Conclusions This study conveys an overall picture of a marshy area into which dung of farm animals was being regularly dumped. There is no evidence of fresh dung being deposited on the site, which was probably a manure heap. This wholly supports the view expressed in Owen (1988) that the site was used for depositing litter from the byres. The rather curious admixture of species and their relative populations, together with an absence of bucoprophiles, suggest that sheep or horses, rather than cattle, were involved. Although this was clearly a human settlement, there is no evidence of human faeces.

The superabundance of *Trachyopella coprina* is interesting so far north but it may still occur on Orkney. One could have expected that a species in such abundance on Orkney during the colonisation of Iceland would have been transported thence, but in Iceland, as elsewhere in Scandinavia, it appears to be replaced by the closely related *T. bovilla*. In that species however the surstyli of the male adult are very different from *T. coprina* (Roháček & Marshall 1985).

There is no clear evidence of climatic conditions different from the present during the time the Tuquoy deposits were being laid down.

This study was valuable in highlighting the need, noted by Pitkin (1988), for re-describing many Sphaerocerid puparia, as many existing descriptions were probably based on misidentifications. This underlined the wisdom of identifying puparia by a study of unhatched adults, and resulted in the revision of British Sphaerocerid by Skidmore (1993, in Appendix 1).

Table 20 Diptera of Tuquoy

Taxon	a	b	c	d	e	f	g	h	i	j	k	l	MNI
Tipula sp.					1			1			2	16	20
T. oleracea/paludosa						1							1
Pedicia immaculata					2		4		3			3	12
Limonia sp.							2		5				7
Limnophila sp.							2						2
Erioptera lutea taenionota							2		5		2		9
Psychodid sp.						1							1
Ceratopogonid sp.							1					1	2
Chironomids						5			3	8		4	20
Bibio nigriventris							1		1			1	3
Dilophus febrilis/femoratus									5				5
Bibionid sp.			2		1								3
Scatopse notata		1	6		15	3	1			1	2	1	30
?Scatopsciara vivida			1		1							1	3
Lycoriella/Bradysia sp.							1					1	2
Nematoceran sp. indet.						1							1
Haematopota/Chrysops sp.				1									1
Sympycnus desoutterri					1								1
Lonchoptera lutea					1								1
?Syrphid sp.							1						1
Calobata petronella	1				1								2
Orygma luctuosum	1												1
Coelopa frigida					1								1
Heterocheila buccata					2								2
?Malacomya sciomyzina		2											2

Taxon	a	b	c	d	e	f	g	h	i	j	k	l	MNI
Sphaerocera curvipes					10								10
Copromyza equina						1							1
C. similis							2						2
C. equina/similis		2	64	14	137	58	5	1	1	1		11	279
Leptocera fontinalis							3		1			1	5
Limosina silvatica						4	5		1				10
Opacifrons humida					1								1
Thoracochaeta zosterae			13	6	7		1						27
Opalimosina liliputana		1	9		38	1							49
Minilimosina ?fungicola					3								3
Pullimosina heteroneura			14		45	5	4		2			5	75
Spelobia clunipes						2							2
S. ?rufilabris	1	8	332	15	304	193	9	5	2		13	63	945
Trachyopella coprina		3	201	5	8351	588	15		17	1		132	9313
Sphaerocerid sp.					6		6		1				13
Limosinine sp.			6			3	5	2	3	1			20
Agromyzid sp.								8					8
Hydrellia ?modesta	2											2	4
Scatella sp.					2								2
Scatophila sp.						1	13						14
Limnellia quadrata					1								1
Ephydrid sp.										1			1
Scaptomyza graminum					1		2			1		2	6
Acalypterate indet.					1								1
Scathophaga ?furcata					2				1	1		1	4

Taxon	a	b	c	d	e	f	g	h	i	j	k	l	MNI
Fucellia ?fucorum									2				2
Anthomyiid sp.					2								2
?Thricops sp.							1						1
Coenosia mollicula					1			1					2
C. sp.												3	3
Helina evecta					1							1	2
H. sp.							2					1	3
?Bellardia sp.	1												1
indet.	1		1		3	2	6			1			14
	7	17	649	41	8993	901	105	18	62	17	22	260	11,101

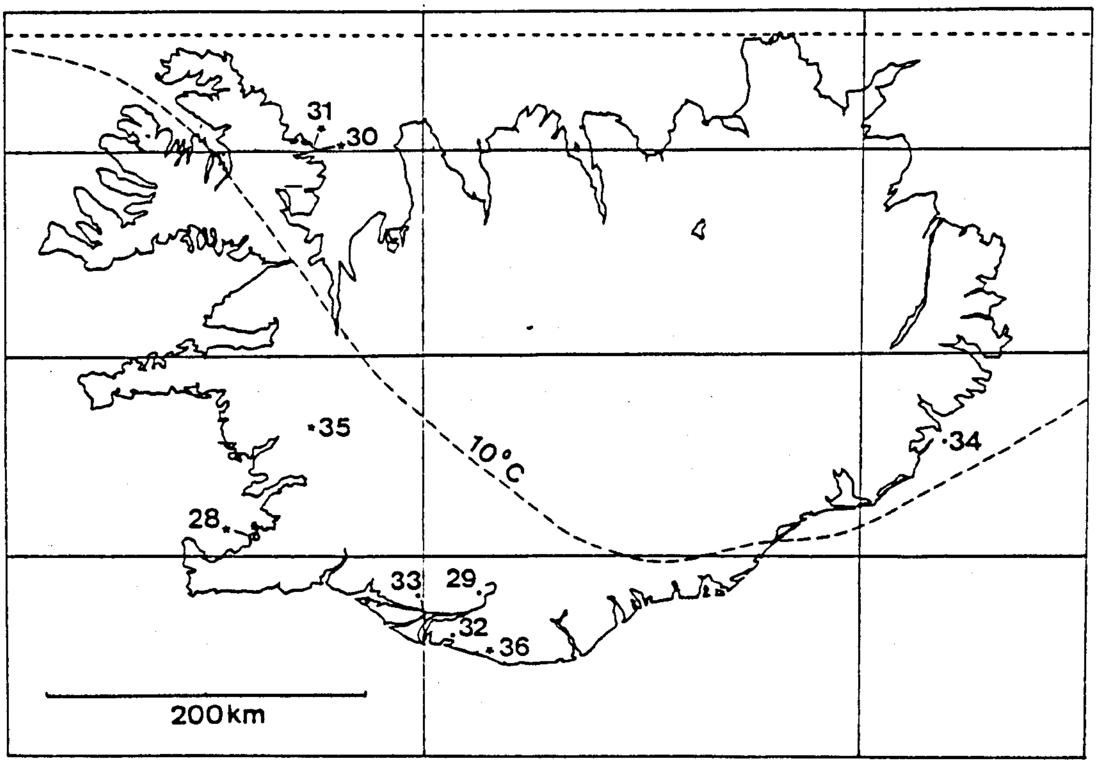
Sample numbers in above table as follows;- a TQ801J; b TQ803J; c TQ803- 88 Pitf; d TQ804; e TQ806; f TQ808; g TQ810; h TQ813; i TQ814; j TQ815; k TQ816; l TQ817.

ICELAND Map 2, page 207

28 BESSASTAÐIR (Gullbringusýsla) (Analysis on page 377)

Introduction The material from this site was collected during the excavation referred to in Amorosi et al (1992), in which a detailed discussion and interpretation is given. This account deals with the Diptera from samples 10, 11, 14, 15, 17, 18 and 19 mentioned in that paper.

The samples span a period of several centuries, the oldest horizon (sample 10) having been laid down before 1226 as it underlies a volcanic ash from an eruption that year off Reykjanes. Horizon 11 lies between that ash deposit and tephra from the Katla eruption of 1485. In



Map 2. Sites in Iceland

terms of the Dipterous assemblages, these two horizons are the only ones from which a large amount of material was recovered. Samples 15 to 19 are from a structure and are thought to represent floor levels.

Always an important farm, from later medieval times, Bessastaðir became the official home of the Danish governor,, and was hence a high status site. There is in consequence, considerable interest in any data touching upon the living conditions in this most prestigious of Icelandic households. The Dipterous evidence suggests that great changes occurred at the site after the 1226 eruption near Reykjanes, but whether these took place during the occupancy of the farm by Snorri Sturlason, or subsequently under the Danish Governor, is not clear. The period of change however predated the Katla eruption of 1485 and may have had some economic or political cause.

The Dipterous material from Bessastaðir consisted of 18 taxa and 934 specimens, as shown in Table 21.

Interpretation A number of notable features of the dipterous fauna from the Bessastadir excavations have come to light and these are discussed below.

a) Whilst the number of Dipterous specimens recovered greatly exceeded that of the Coleopterous (934:642), the number of Dipterous species was very much smaller (18:64), hence showing a very much lower diversity. This apparent anomaly appears to be the rule where the Coleopterous and Dipterous fauna have been studied. In that the total modern Icelandic Dipterous fauna is more than twice that of the Coleoptera (c.350: c.160), the Bessastaðir results appear to be at variance with reality. It is most improbable that the Icelandic Dipterous fauna at the time was smaller than the Coleopterous, and it is more likely that these results partially reflect the relative durability of the exoskeletons of Coleoptera and Diptera.

b) Only in samples 10 and 11 were Diptera recovered in any meaningful numbers; indeed none at all were received from 12, only one from 14, and extremely few from the remainder. However a comparison between the two oldest midden samples (ie. 10 and 11) shows that great changes occurred during the periods separated by the Reykjanes eruption of 1226, which may have had a devastating effect on the farm at Bessastaðir. These changes are itemised below.

i) Species diversity almost doubles (10: 18 species)

ii) A great decrease in *Heleomyza serrata* (39%: 22% of total). Whilst this could infer a reduction in deposition rate of the most likely pabulum (ie. human faeces), this appears unlikely since *Telomerina flavipes* maintained high populations.

iii) Though still not a major faunal component, a massive increase in numbers of *Scatopse notata* (1%-14%). This presumably resulted from increased deposition rates of some suitable decaying organic matter, possibly either rotting plant material, dung of herbivores, or manure.

iv) Marked increase in *Scathophaga* and *Copromyza*, probably indicating that more herbivore dung (sheep?) was being dumped on the site. (See comment under *f* below).

v) Three-fold increase in *Melophagus ovinus* may infer increase in fleeces on the farm.

c) *Telomerina flavipes* maintained a high population in horizons 10 (56), 11 (54), 17 (60) and 19 (62.5 per cent), and it was the only dipteron in sample 18. Almost all puparia had hatched, indicating that ideal breeding conditions prevailed. As in West Greenland, the species evidently bred mainly indoors in Iceland in fouled floor-material, and indicated a warm thermal regime. *Herniosina bequaerti*, a closely related species of very similar, troglodytic habits was present in much smaller numbers. It is thought originally to have been purely a cave-frequenting species which may have accompanied man from earliest times into his dwellings (Roháček 1983). Some wings found in the same horizons appear to more nearly resemble *H. bequaerti* than any other Sphaerocerid known today from Iceland, but confirmation is desirable, and a healthy scepticism is in order regarding the identity of these wings with *H. bequaerti*. Two puparia, almost certainly of this species were found in samples 11 and 19. There were also a very few empty puparia of *Leptocera ?fontinalis* and *Limosina silvatica*. The former breeds in foul slurry and organic mud, and often occurs in profusion in blocked drains. Roháček (*op. cit.*) states that *L. silvatica* is an obligative polysaprophage which usually breeds in decaying leaf litter but will utilise manure heaps and wet straw, etc., mainly in shaded situations.

d) *Aleochara sparsa*, a parasite of Dipterous puparia, may have been mainly attacking the dominant Sphaerocerid, or perhaps the *Scathophaga*. Had it been preying upon *Heleomyza*, it should have been in larger numbers in horizon 10. No puparia were found which had clearly been attacked by *Aleochara*.

e) Despite the coastal location of Bessastaðir, there was no unequivocal evidence of seaweed having accumulated on the site. No puparia of such common seaweed flies as *Coelopa* or *Fucellia* were found, and only three unconfirmed *Thoracochaeta zosterae*. Fragments of adult *Scathophaga calida/litorea* attested to the proximity of the littoral zone.

f) Carrion, or excrement resulting from a diet including animal protein, was strongly inferred by the abundance of *T. flavipes*, but the only exophilic necrophage, *?Allopiophila vulgaris*, was represented by just two puparia, one of which contained the ovipositor of the female. The abundance of bones on the middens (see Amorosi et al, 1992), and of *Telomerina flavipes*, shows that meat products were of great importance, but the absence of the exophilic necrophages suggests that neither meat nor marrow was thrown out- not even by the Governor of Iceland ! Precisely the same degree of utilisation of animal products was evident on the middens of most other Norse farmsteads in Iceland and West Greenland, and was perhaps a cultural feature.

g) That dry vegetable matter is generally most unattractive to Diptera was reflected by their virtual absence from several Bessastadir samples.

h) Phytophagous and wholly humicolous Diptera were totally absent from the Bessastaðir material examined. Indeed the only non-synanthropic species present were single specimens of *Dolichopus plumipes*, and *?Nupedia*.

i) Amongst the noteworthy absentees from the Bessastaðir middens were those modern eusynanthropes *par excellence*, *Musca domestica* and *Fannia canicularis*. The conditions in horizons 10 and 11 should have been eminently suitable for them and one must assume that neither had yet arrived in Iceland. The overlying horizons apparently lacked the requisite conditions of high bacterial fermentation.

j) *Heleomyza* species were evidently the "houseflies" of the Norse colonies, breeding presumably in accumulations of human faeces about the settlements. The biological and ecological requirements are discussed elsewhere, but it needs to be reiterated that where they are found without any trace of exophilic necrophages, dark conditions are inferred. *H. borealis* may have been present at Bessastaðir, but all unhatched puparia with surstyli were *H. serrata*, which is evidently less tolerant of very low temperatures than *H. borealis*. (At Reykholt and Finnbógastaðir the latter species only has been positively confirmed.)

The precise nature of the changes which occurred at Bessastadir after the Reykjanes eruption are difficult to interpret in terms of the life of the farm. They may merely reflect changing patterns of refuse disposal, or perhaps there was greater emphasis on sheep-farming. Squalid, but relatively warm living conditions continued much as before the Reykjanes eruption, as shown by *Telomerina* populations. The factor which resulted in the population crash in *Heleomyza serrata* in the farmstead remains a mystery, but a similar collapse with *H. borealis* was noted at Nipáatsoq. At Bessastaðir, a change occurred also which led to a great population explosion in *Scatopse notata* and it is possible that the two changes were related. *S. notata*, as stated above, is a typical inhabitant of manure heaps of herbivore or omnivore origin, and it may be that the crash in *serrata* and explosion in *notata* reflect a change in emphasis on the farm. A problem however remains to be explained. Why did *serrata* suffer decline whilst *Telomerina* continued to thrive, since they often breed in darkness together? The upper level of thermal tolerance is not known for *H. serrata*, but it is perhaps possible that indoor temperatures became too warm for *it*. *H. serrata*, as distinct from the very similar *H. captiosa*, is intermediate in thermal preferences between *H. borealis* and *captiosa*. Today, *serrata* is replaced across much of Europe, except Scandinavia, by *captiosa*. Martinek (1969) suggests that in Central Europe, *serrata* may be a high-boreal relict, occurring in mountainous areas only. These two species are only

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Table 21 Diptera of Bessastaðir

Taxon	10;	11;	14;	15;	17;	18;	19;	MNI.
Trichocera sp.		4;					1;	5
Psychodid sp.		1;						1
Sciarid sp.		1;						1
Scatopse notata	5;	56;		1;			1;	63
Dolichopus plumipes		1;						1
Megaselia sp. (nr. *rufipes*)		1;						1
Heleomyza serrata	190;	94;			1;		1;	286
Copromyza equina/similis	1;	5;			1;			7
Leptocera ?fontinalis	6;	2;						8
?Thoracochaeta zosterae	2;	1;						3
Limosina silvatica	2;	3;						5
?Herniosina bequaerti		2;					2;	4
Telomerina flavipes	269;	229;			3;	1;	10;	512
?Allopiophila vulgaris	1;	1;						2
Scathophaga sp.	3;	13;					1;	17
S. calida/litorea		2;		1;				3
?Nupedia sp.		1;						1
Melophagus ovinus	3;	9;	1;	1;				14
Total MNI per sample	482;	426;	1;	3;	5;	1;	16;	934
Total taxa per sample	10	18	1	3	3	1	6	18

distinguishable only on the form of the male surstyli, those of *H. captiosa* being more slender than in *serrata* (see Plate 19, figs. 12 and 14).

Conclusions The Dipterous fauna of the Bessastadir farm deposits was very restricted, consisting almost entirely of synanthropic species. By far the most abundant species (ie. *Heleomyza* and *Telomerina*, accounted for 85 per cent of the total (31 and 55 per cent respectively). This species combination strongly suggests that these horizons were fouled floor-coverings. Bones which had been thrown onto the midden had been cleared of flesh and marrow, and there appears to have been little or no further Dipterous colonisation after the refuse was tipped onto the midden. This infers that the middens either dried out very quickly, or that they were quickly covered. In the Greenlandic middens there was abundant evidence of colonisation by phytophagous and algaecolous flies, but there is no such evidence in these Bessastaðir horizons.

29 EINHYRNINGUR (Rangarvallasýsla)

Introduction Located in the upper reaches of the Markarfljót above Fljótshlid, this raised-bog site was surveyed for possible relevance to discussions on Iceland's pre-Landnám fauna (Buckland *et al.* 1986, Buckland in Dugmore 1991).

Interpretation Only two Dipterous fragments were recovered from this site, namely fragments of two Tipulid pupae from a sample having the code "..section 1 Bulk 1779 First-110-120m". Only three species of Tipulid are known today in Iceland, namely *Prionocera turcica* and *Tipula confusa* and *T. rufina*. The last two are very closely related and have humicolous or muscicolous larvae, whilst those of *Prionocera* breed in wet places, especially in peaty areas. The Einhyrningur pupae could belong to any of these three species, none of which is in any way synanthropic. The sample therefore shows no evidence of human presence. The condition of preservation of this material was also extremely poor.

30 FINNBOGASTAÐIR (Strandasýsla) (Analysis on page 378)

Introduction This medieval farmstead site is situated on the coast near Árnes, in northern Strandasýsla. The site was excavated as a rescue operation on behalf of the Icelandic Government, precipitated by the rebuilding of the farmhouse. The stratigraphy for this site has not been seen, so spatial and temporal relationships between the samples are unknown at present.

Interpretation In terms of the total number of Dipterous specimens recovered, this was by far the most productive of Icelandic sites examined in the current research programme, yet the species diversity was spectacularly less than the other sites. Indeed, apart from those species clearly owing their presence to human activity, a Dipterous fauna was virtually absent. Thus, three of the nine taxa present make up over 99.9 per cent of the entire material (ie. *Heleomyza* 91.6, *?Allopiophila* 6 and *Scathophaga* 2 per cent respectively) (Table 22). The inference here may be that the fly fauna of Finnbógastaðir was in fact extremely impoverished. Puparia of only two phytophages (ie. *Botanophila fugax* and *?Pegoplata infirma*) and one algaecole (*Scatella* sp.) were found. This contrasts strongly with the Norse sites in West Greenland. Out of the total Finnbógastaðir Dipterous material of 2136 specimens, almost 98 per cent belonged to the genera *Heleomyza* and *?Allopiophila*. The virtual absence of exophilic Calliphorines probably indicates a lack of suitable breeding sites in the form of exposed carrion. Whilst *Heleomyza* and *?Allopiophila* are primarily necrophagous, the former is strongly addicted to dung with an animal protein content (eg. human faeces) in places shaded from direct sunlight. Piophilids on the other hand are heliophilous but predominate on dry carrion in a very advanced state of decay. A highly characteristic habitat for them is in masses of skeletal material where they develop in the marrow in cracked and shattered bones. *Heleomyza* makes up 91.8 per cent of the Dipterous fragments of most of the samples from Finnbógastaðir; the Piophilids are present in modest numbers in most of these. As in other sites, a small number of *Heleomyza* puparia were very large and may have belonged to *H. serrata* but specimens containing the male surstyli all belonged to *H. borealis*, the dominant one in more northerly areas and the only one positively recorded from the Norse sites in West Greenland.

The over-riding impression indicated by the Dipterous inhabitants of the midden is of a highly artificial community in a hostile environment. The main materials tipped onto the midden were probably fouled domestic floor-coverings from the farmstead and some skeletal material from butchered animals cleaned of all flesh. The most abundant Blowflies in Iceland are *Calliphora uralensis* and *Phormia terrae-novae*. The latter abounds on exposed carrion throughout the more northerly parts of the temperate areas of the Holarctic, northwards to Ellesmere Island and Cape Morris Jesup. It is a highy heliophilous exophile. *Calliphora* species have a slight though marked preference for ovipositing in carrion lying in somewhat shaded situations (Smith 1986). *C. uralensis* however, according to Smith (*op. cit.*) is unusual in preferring to breed in liquid human faeces rather than carrion. But the abundant occurrence of this fly throughout even the uninhabited parts of Iceland and Greenland strongly suggest that this is not the case in these areas and it is far more likely that it shares the necrophagous habits of its congeners. Furthermore, were it to develop in liquid human faeces in dark situations it should figure far more abundantly in discarded floor covering deposits on medieval middens with *Heleomyza*.

Table 22 Diptera of Finnbógastaðir

Taxon	a	b	c	d	e	f	g	h	em.	unh.	MNI	%
Megaselia sp.	1								1		1	0.05
Heleomyza borealis	348	21	7	7	48	163	307	1055	1737	219	1956	92
H. ?serrata		1			3			1	5		5	0.2
?Copromyza sp.			1				1		2		2	0.1
?Allopiophila vulgaris		1	1	1	4	10	45	66	128		128	6
Scatella sp.	1								1		1	0.05
Calliphora sp.		1							1		1	0.05
Scathophaga sp.	2				1	9	6	21	38	1	39	2
Botanophila ?fugax			1						1		1	0.05
?Pegoplata infirma	1							1	2		2	0.1
Total taxa 10 MNI	353	24	10	8	56	182	359	1144	1916	220	2136	

Key to Samples a 4901Sv 1; b 4901-39 21/7/90 Road cut profile Col.SU 9; c 4901-30 Road cut Profile C 12 sample; d 4901-39 21/7/901 Road cut Profile Col sample SU 11; e 4901-39 SU 11; f 4901-39 Road cut (12 Sam) 7.12.90; g R.C.Prof.col.Sam SU 14 21/7/90; h 4901-39 21/7/90 Road cut prof.column Sample SU 14 (tubes 1,b, and c). Column *em* gives the total number of emerged, and *unh* of unhatched, puparia, whilst the final column gives the percentage of the total MNI for each taxon.

Indoor temperatures at Finnbógastaðir were probably decidely lower than in the other farmsteads studied here in Iceland and Norse Greenland. This may be inferred by the complete absence of the endophilous necrophagous Sphaerocerids *Telomerina flavipes* and *Herniosina bequaerti.* The occurrence of the former at least in several other contemporary sites in Iceland and Norse Greenland, but not in Finnbogastaðir appears noteworthy. *Herniosina* has not yet been recorded from Norse Greenland and was much scarcer in Icelandic sites, but, since *Telomerina* was clearly transported by Norse commerce to the Western Settlement in Ameragdla, it appears inconceivable that it would not have been spread throughout Iceland where suitable conditions prevailed in the homesteads. Its marked thermophily in these cold regions would appear to be the major factor in preventing its colonisation, and it would not therefore breed in colder buildings.

Conclusions This site showed the lowest Dipterous diversity of any of the major sites examined in this programme, and provided a remarkable contrast in this respect to the major sites in southern Iceland and West Greenland. The deposits appeared again to consist mainly of ejected floor-coverings from the farmstead, *Heleomyza* comprising 92 per cent of the total MNI from the site. A total absence of *Telomerina* probably inferred an indoor thermal regime below the threshold for this fly. A 6 per cent Piophilid presence suggested a small quantity of bone marrow or dessicated carrion on the midden, and there may also have have been some sheep dung.

31 GJÖGUR (Strandasýsla) (Analysis on page 379)

Introduction This farmstead site is located a little to the north of Finnbógastaðir and was also excavated as a rescue operation.

Interpretation. The number of Dipterous specimens from this site was very limited, comprising only 116 specimens and six species. The fauna was very similar to that of Finnbógastaðir, the same three species accounting for 95 per cent of the total (Table 23). Here however the proportions of *Heleomyza* and *?Allopiophila* were reversed, the latter being most numerous (ie. *Heleomyza* 31, *?Allopiophila* 59 per cent).

Table 23 Diptera of GjÖgur

Taxon	a	b	c	d	e	MNI	%
Heleomyza borealis	1;	14;	12;	6;		33	28
H. ?serrata		3;				3	3
?Allopiophila vulgaris			66;	1;	1;	68	59
Scatella sp.			1;			1	1
?Calliphora sp.		1;			1;	2	2
Scathophaga sp.			8;	1;		9	8
Total taxa 6 Total MNI=	1;	18;	87;	8;	2;	116	

Key to samples *a* 4901-7 Gjogur SU 38 J.S; *b* 4901-7 Gjogur SU 40 J.S; *c* 4901-7 Gjogur SU 47/48 J.S; *d* 4901-7 Gjogur SU 60-61 J.S; *e* 4901-7 Gjogur SU 67 J.S. The final column gives the percentage of the total MNI for each taxon.

Since Piophilids are primarily exophilous, these deposits would appear to have accumulated mainly outdoors. The inferred habitat would be a disposal area for bone material containing quantities of marrow, or for dessicated carrion. The extreme scarcity of Calliphorids suggests there was very little decaying flesh. The *Heleomyza* may have been breeding outdoors with the Piophilids, but an indoor floor-covering origin, as in other sites studied here, cannot be ruled out. It is however relevant to note that other taxa from this site are exophilous. As at Finnbógastaðir, the absence of *Telomerina* suggests that if floor-débris did account for part of the samples studied, the indoor temperatures were lower than normal.

Again the specific identity of the *Scathophaga* which constituted 8 per cent of the total MNI at Gjögur was not established. If it was one of the coprophagous species (ie. *furcata* or *stercoraria*), a presence of sheep in the vicinity of the site could possibly be inferred.

Conclusions The most interesting feature here was the major role of Piophilids, possibly inferring that this may have been primarily an outdoor disposal area for waste skeletal or dried meat products.

32 HOLT (Rangarvallasýsla)

Introduction This study involved the cleaning and sampling of horizons exposed by drainage operations at Holt in Eyjaflallasveit, which offered opportunities of examining pre-Landnám surfaces. The single sample received from this study however, labelled " Holt/2/1980 " cannot be related to the stratigraphies figured in Buckland *et al.* (1991), who provide a detailed account of the site. The ditching work also cut through an old farmstead site, and from the midden section of column HO3 they recovered a *Melophagus ovinus* and an unstated number of Chironomid larval head-capsules and undetermined puparia.

Interpretation The single sample seen by me from Holt contained two empty puparia of a *Hydrellia* species, probably *H. griseola*, the only member of the genus known from Iceland. The larvae are leaf and stem miners, often of grasses, and pupariation occurs in the soil. Another incomplete puparium apparently belonged to the family Anthomyiidae, most species of which are phytophagous.

33 ÓSABAKKI (Rangarvallasýsla)

Introduction A column comprising 13 samples was collected from this site in order to investigate the pre-Landnám birch forest fauna. Buckland, Greig & Sveinbjarnardóttir (1980) figure the stratigraphy, and the sample came from deposits immediately pre-dating settlement. Labelled "Ósabakki 1979 Vol./7", this contained only two Dipterous fragments.

Interpretation The Dipterous fragments just mentioned were two muscid puparial end-segments, probably of a *Spilogona* species. In the larval stage these are obligative carnivores, feeding on other small, soft-bodied invertebrates, usually in mud or silty sand, wet moss or algae; sometimes in shallow water.

34 PAPEY (Suðurmúlasýsla)

Introduction Two samples only from this site, which was occupied from Landnám to the thirteenth century, contained any Dipterous material. The site is discussed in Buckland *et al.* (1980).

Interpretation The two Dipterous specimens recovered were a *Scatella ?stagnalis* wing and a "false puparium" of *?Mayetiola*, indicating the proximity of organic mud and of a species of grass.

35 REYKHOLT (Borgarfjarðarsýsla) (Plan; pl. 30) (Analysis; p. 380)

Introduction. Reykholt farm, standing in Reykholtsdalur in Borgarfjörður was owned by Snorri Sturluson and was the site of his murder in 1241 AD. The samples, however, came from a post-medieval passage house (plate 30). The palaeoecology of the site was discussed, and the subfossil insects listed, by Buckland, Sadler and Sveinbjarnardóttir (1992), who used a Twinscan analysis of their extensive data. The Dipterous material from the site is far less numerous and consequently the end-groups proposed by them are unconvincing from a Dipterous standpoint. *Melophagus ovinus*, the Sheep Ked, was more abundant at Reykholt than at any other North Atlantic site studied, with the exception of Stóraborg.

Interpretation Most of the Dipterous material from Reykholt emanated from the passage between Rooms 1 and 2, and from Room 2 itself (plate 30). In Table 24 the results are given under these main headings. The tabulation reveals a number of spectacular differences between the Dipterous assemblages from the passage and room 2 as follows.

a A much greater species diversity in the passage than in room 2 [Passage, 5 samples; 107 specimens; 15 taxa. Sample 14 showed the greatest diversity of any from Reykholt- 42 specimens; 12 taxa.] [Room 2, 5 samples; 225 specimens; 14 taxa. Sample 22 showed the greatest diversity of any from this room- 102 specimens; 9 taxa.]

b A far larger proportion of hygrophiles, humicoles and phytophages in the passage [Passage, 22 specimens; 8 taxa] [Room 2, 4 specimens; 3 taxa]

c The exophilic necrophage *Allopiophila* was far more numerous in the passage [Passage, 26 specimens] [Room 2, 2 specimens]

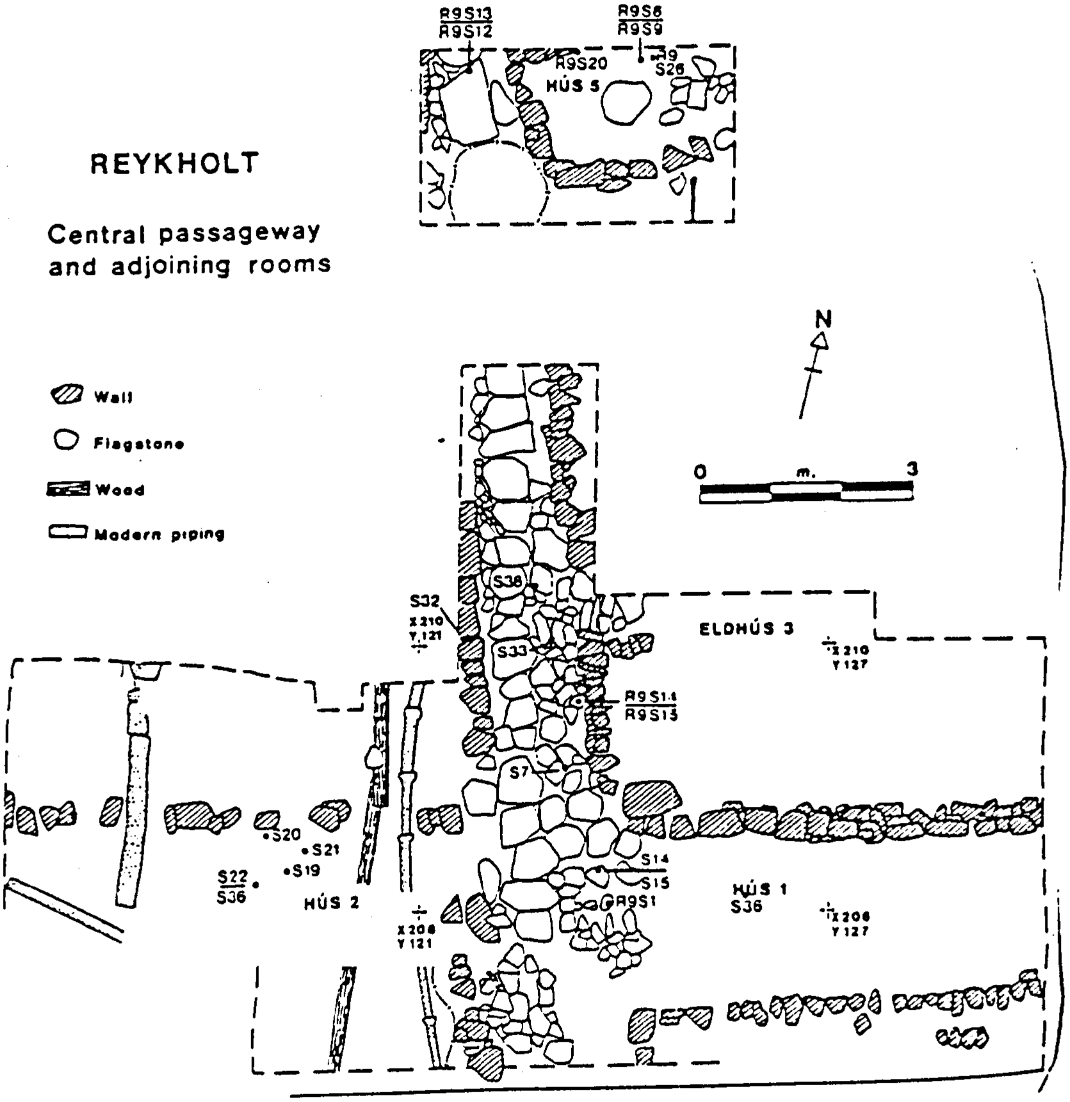


Plate 30. Plan of Reykholt Farm (after Buckland, Sadler and Sveinbjarnardóttir, 1992)

d A much larger number of necrophages tolerant of darkness in Room 2; *Megaselia* [passage 6; Room 2; 61] *Heleomyza borealis* [passage 16; Room 2; 26).] The 15 larval head-capsules of *Trichocera* from Room 2 (sample 22) probably belonged to the strongly troglodytic *T. maculipennis*, a prominent member of the ombrophilous fauna of Stóraborg.

e A great disparity in the numbers of *Melophagus ovinus* in the two areas [Passage; 32 specimens] [Room 2; 105 specimens] [NB. A total of 210 additional *Melophagus* from the three R9S samples, from Room 5 etc., were noted by Buckland et. al. (1992).] The impression conveyed by the above is of a darkened room and an adjacent, lighter passage, which would appear to have been open to the elements, and in which some decaying organic matter, bones and dung were exposed. Whether the hygrophilous species were actually breeding *in situ*, or had been brought in in a subfossil state in peat and turf is not evident.

Fly fauna associated with sheep The presence of the Sheep Ked *Melophagus ovinus* in such profusion indoors at Reykholt is suggested by Buckland et al. as probably resulting from wool-processing in the room, rather than evidence of a stalling area. The results noted under item 'e' above would support this view. This was the most abundant Dipteron in the samples studied from Reykholt, accounting for 42 per cent of the Dipterous material recovered from samples examined by me. A further 210 specimens were recovered from samples not seen by me and which otherwise apparently contained no Diptera. Therefore the Sheep Ked actually accounted for about 64 per cent of the total Diptera present in all of the samples studied.

The fly fauna associated with sheep dung was very little in evidence at Reykholt. None of the 12 Sphaerocerid and *Scathophaga* puparia could be identified to species, and hence positively associated with sheep dung, but this figure (4 per cent of the total Reykholt MNI) represents the maximum that could possibly be referred to this faunal community. For a farm in which sheep rearing was of such overriding importance this appears remarkable, but is also reflected in the very small numbers of *Aphodius lapponum* noted in Buckland *et al.* This also lends support to the hypothesis that room 2 was not a stalling area.

Endophilous fauna As stated above, *Melophagus* outnumbered all of the other Diptera combined at Reykholt. But excluding this species, Reykholt was unique amongst the Icelandic farms studied here in that *Heleomyza* was not the most abundant taxon, being replaced by *Megaselia* cf. *rufipes*; respective percentages of the total Reykholt MNI being 8 and 12 per cent. The *Megaselia* populations were centred almost wholly in room 2 (ie. 77 per cent of the total for this taxon), whilst *Heleomyza* showed less bias, about a third of the specimens emanating from the passage, although there were striking differences between samples from Room 2. Thus, sample 30 had the largest number of *Heleomyza* of any sample from Reykholt (76 per cent of the total from the sample), whilst *Megaselia* was absent. In sample 20 on the other hand, *Megaselia* populations reached a peak, whilst *Heleomyza* numbers were small (80 and 17 per cent respectively). *Megaselia* species will breed in a very wide range of putrifying substances, including rancid dairy products, dead insects, fermenting organic matter, buried corpses etc. In many such situations they may be the only breeding Diptera present.

Scatopse notata and *Heleomyza borealis* breed commonly in guano accumulations below bird cliffs and in similar masses of decaying material, and both were evidently common, along with *Trichocera maculipennis*, in medieval Icelandic homesteads. At Reykholt, all three were breeding in Room 2 with *Megaselia*, although each exhibited a different, presumably ecological bias.

Compared with the West Greenland sites and those at Bessastaðir and Stóraborg, a surprising absentee from Reykholt was the endophilous thermophile *Telomerina flavipes*, a common inhabitant in Norse houses, where it was dependant upon the warmer conditions these provided. *Herniosina* was also not noted from Reykholt, but this appears not to have been carried to Greenland by the Icelanders, or at least not to have formed viable populations there. The absence of *Telomerina* at Reykholt suggests that temperatures, at least in Room 2, were inadequate, but it may have existed elsewhere in the farm.

Exophilous necrophages The absence of first-wave colonisers amongst the exophilic necrophages, such as *Phormia*, *Cynomya* and *Calliphora*, is taken as an indication again that very little carrion was left exposed, at least in the passage-way. *Allopiophila*, indeed most Piophilids, belong to the last wave of carrion-colonisers, being characteristic utilisers of decaying bone marrow, etc. Hence they can breed for many generations in piles of bones from which all sign of flesh has been lost. Piophilids were far more numerous in the passage than in room 2, percentages of the Reykholt total for this taxon being 93 and 7 respectively. The heliophilous propensity displayed by Piophilids suggests that the passage was at least partially sunlit. There was a strong presence of *Heleomyza* with the Piophilids in the passage, underlining the fact that members of the genus can breed with

Table 24 Diptera of Reykholt

Taxon	Passage					Room 2					R1	?		
	4	14	15	32	33;	19	20	21	22	30;	36	S?	R9S*	MNI
Trichocera sp.									15					15
?Tipula rufina/confusa			1	1										2
Prionocera turcica		8												8
Bibio pomonae									2					2
Scatopse notata							1		3					4
Rhamphomya simplex		2												2
Dolichopus plumipes				1					1					2
Megaselia cf. *nigra*		3								1				4
M. cf. *rufipes*	1	1		1		1	33		26		2			65
Heleomyza borealis		11	1	4			7			19				42
Copromyza sp.									3					3
Sphaerocerid sp.						1				1				2
Limosinine sp.									1					1
?Allopiophila vulgaris		4		22		1			1					28
?Philhygra vittipennis		1												1
?Drosophila sp		1												1
Scathophaga sp.		4								2				6
Botanophila ?fugax		4												4
Anthomyiid sp.		1												1
?Spilogona sp.		2	1			1								4
Melophagus ovinus	19		3	2	8	10		43	50	2	1	9	210	357
Total MNI=	20	12	6	31	8	14	41	43	102	25	3	9	210	554
Total taxa c.21	2	12	4	6	1	5	3	1	8	5	2	1	1	

Piophilids in lighter situations

Non-synanthropic fauna Apart from *Melophagus*, the presence of which is discussed by Buckland *et al.*(1992), this assemblage comprises a mixture of non-synanthropic elements and those which in Iceland may be classed as semi-synanthropic. In the former group belong *Tipula*, *Prionocera*, *Bibio*, *Rhamphomyia*, *Dolichopus*, *Philygra* and *Spilogona*. All but *Bibio* and some *Tipula* and *Spilogona* species breed in wet places, *Prionocera* especially favouring peaty pools. This assemblage was eight times more numerous in the passage than in room 2.

Conclusions Of the Icelandic sites studied here, Reykholt provided the second-largest number of specimens of the Sheep ked *Melophagus ovinus*, and the greatest Dipterous diversity. The samples came from two parts of the farm, namely room 2 and the adjoining passage, and the dipterous fauna indicated spectacular differences between them. Room 2 appeared to be primarily used for fleece-cleaning, whilst the adjoining passage afforded access from the outside. Compared with all other farm sites studied here, the Reykholt subfossil fly fauna comprised an unusually large non-synanthropic element (ie.5 per cent), 87 per cent of which was from the passage, the remainder from room 2. Within room 2, *Melophagus* massively predominated, but the populations of the three main "decomposers" in that room, namely *Trichocera*, *Megaselia* and *Heleomyza* showed conspicuous fluctuations.

36 STÓRABORG (Rangarvallasýsla) (Analysis on pages 382- 386)

Introduction. Located on the relatively benign south coast of Iceland, sheltered from the north by the Eyjafjallajökull and from the north east by the Myrdalsjökull, Stóraborg is in one of the climatically mildest, and entomologically richest, parts of the island. This account discusses the subfossil Dipterous material from the Stóraborg excavation. In the 38 samples studied by me there were over 30 taxa and 1873 specimens. Twelve of the samples, labelled "F Trench" and "G Trench" and containing 332 specimens, were from the midden. This material clearly originated from indoors, as will be seen from the species assemblages, but the endophilous fauna was diluted by exophiles. In Table 25 midden samples and specimens are underlined and totalled seperately.

The history of Stóraborg, and the results of the archaeological work carried out there are discussed in detail by Sveinbjarnardóttir *et al* (1981), and in summarised form by Snæsdóttir(1991). First noted around 1200 AD, Stóraborg comprised a farm and a chapel, but the latter was abolished about 1700 and the foundations were covered by the sea some years ago. Prompted by further marine encroachment, excavation of the cemetery was commenced by Snæsdóttir in 1978, and of the main farm midden in 1979. Two preliminary samples were analysed and these form the subject of the report by Sveinbjarnardóttir *et al.*(1981), in which the Coleoptera were discussed. Subsequently many further samples have become available from actual building interiors and this report covers all of the Dipterous material seen by me from these sources. Dr. P. C. Buckland provided me with species lists of subfossil insects from a further 42 samples which included a total of 389 *Melophagus ovinus*. A discussion of the occurrence of this species in Stóraborg appears in Buckland and Perry (1989).

Interpretation All of the samples seen by me, except those from 'F' and 'G' trenches, which came from the midden, were from floors of farm-buildings, pits and drains beneath them. This doubtless explains the specialised Dipterous fauna present in these deposits. Four faunal associations were almost, or quite, absent. These are discussed first.

a **Fucicolous and littoral fauna** For this coastal location a complete absence of any littoral Diptera, even of adults, was surprising. There was therefore no Dipterous evidence of seaweed utilisation on the farm.

b **Exophilous necrophages** *Calliphora* and *Allopiophila* were predictably almost absent from these deposits.

c **Humicoles** These accounted for only about one per cent of the total, but this is perhaps less remarkable as many humicoles normally occur at very low population densities. *Dilophus*, a typical humicole, occurred only as adults. These have a very short flight period but occur in great swarms and they may have been amongst vegetation brought into the house during a change of floor-covering. *Fannia postica*, a humicole could have been introduced into the house in peat.

d **Phytophages** Apart from *?Mayetiola*, which is discussed below, the only phytophagous Diptera present were seven *Hydrellia* and one *Scaptomyza*. In total these three taxa constituted eight per cent of the Dipterous fauna. *?Mayetiola* was found in six samples, and in 1, 7 and 29 it was the most abundant Dipteron present. Interestingly, samples 1 and 7 showed extremely low numbers for the endophiles discussed below, inferring little contamination by domestic faecal material, although all three samples were from indoors. Also, sample 7 showed the highest count for puparia of *Scathophaga*, presumably either *furcata* or *stercoraria*. The biology of the genus *Mayetiola* is discussed on page 67. Their presence at Stóraborg, almost unique amongst the Norse sites studied, suggests these were deposits of grass, probably hay. Today species which produce these "False puparia" are unknown in Iceland.

Endophilous fauna Endophiles constituted 80 per cent of the total dipterous material from Stóraborg. Five taxa were present in some quantity, namely *Trichocera maculipennis, Scatopse notata, Heleomyza serrata* and *H. borealis, Herniosina bequaerti* and *Telomerina flavipes*. Of the two *Heleomyza* species, *serrata* predominated. The apparent absence of *Heleomyza captiosa* from any Icelandic material seen by me is probably climate-related, but could be the result of the original introduction of *serrata*, but not of *captiosa*, by the Norsemen from Scandinavia.

Telomerina flavipes accounted for only 8 per cent of the Dipterous material from Stóraborg. This appears curious in view of the huge populations of this fly in several other sites, especially in Norse West Greenland where it was inadvertently transported by the Icelanders. It is unlikely that indoor temperatures were inadequate for it at Stóraborg and other limiting factors must have been operative. Competition from *Trichocera maculipennis* and *Herniosina* seems an improbable cause as they were in smaller numbers than *Telomerina*. It will be seen from the Stóraborg analyses in Appendix 2 that many of the samples were from drains below the floors of the buildings, and it was in these samples that peak numbers of *Trichocera, Heleomyza* and *Telomerina* were found (see samples 16 and 32).

Exophilous fauna Table 24 shows that an exophilous fauna of about 15 per cent was present in the Stóraborg material, the bulk of which belonged to the coprophagous community. For *Copromyza* and *Leptocera*, the majority of specimens were from F Trench, which were midden horizons. *?Mayetiola* would normally be regarded as an outdoor species but it may have been brought indoors amongst hay.

Coprophilous Fauna Sheep-rearing was evidently a function of the Stóraborg farm, as shown by the presence of the Sheep Ked, *Melophagus ovinus*. The dung of these animals probably supported the genera *Scathophaga* and *Copromyza*, which together accounted for ten per cent of the exophilous Stóraborg material.

Non-synanthropic Fauna Although around 82 per cent of the total dipterous material from the Stóraborg consisted of obligative and facultative synanthropes, a quite substantial 18 per cent presence of non-synanthropes testifies to a fairly rich "background fauna" in contrast to the extremely impoverished sites at Finnbógastaðir and Gjógur in the far north of Iceland.

Conclusions As with other studies of material emanating from interiors of dwellings, the Stóraborg samples infer living conditions of extreme squalour when viewed through modern eyes. Sheep-rearing was an important element in the farm economy, as shown by the frequency of the Sheep Ked, *Melophagus ovinus*, and sheep dung may have been used indoors, perhaps as fuel. Uniquely amongst the sites studied here, the "false-puparia" of *?Mayetiola* were a prominent feature of several samples, possibly indicating a presence of hay, or other graminaceous source. The results from Stóraborg indicate a much richer background fauna than in sites on Iceland's north coast, but no greater than in the Norse Western Settlement around Sandnes in West Greenland.

Table 25 Diptera of Stóraborg (samples 1- 10)

Taxon	Sample numbers 1;	2;	3;	4;	5;	6;	7;	8;	9;	10;
Dilophus sp.	2;						5;			
Sciarid sp.			1;							
Scatopse notata								1;		6;
Mayetiola sp.	8;						120;	4;		
Heleomyza serrata	1;	9;		1;		2;	3;	31;	96;	250;
?Copromyza sp.	2;							1;	2;	
Herniosina bequaerti								8;		1;
Telomerina flavipes										9;
Sphaerocerids(3 species)							7;			
Hydrellia ?griseola			1;	1;			3;			
Drosophila sp.			1;							
Calliphora sp.									4;	
Scathophaga sp.	4;		1;				10;			
Anthomyiid sp.					1;					
Fannia ?postica	1;						2;			
?Hydrotaea dentipes								-	1;	
?Thricops sp.							1;			
Spilogona sp.	1		1;				1;			
Melophagus ovinus						1				
Totals/sample	19	9	5	2	1	3	152	45	103	266

Key to Samples *1* Pit under Hús 14 Det.(1981); *2* Passage floor Hús 30 (1984); *3* Hús 32 floor(1984); *4* Hús (12) 13-17 floor (1985); *5* Hús 33 floor; *6* Str 85 floor (1985); *7* Hús 14 under floor (1981); *8* Hús 18; *9* Stb 81 F Trench S.Profile 40-45cm; *10* Pit under Hús 14.

(Table 25 contd.)	11;	12;	13;	14;	15;	16;	17;	18;	19;	20;
Trichocera maculipennis						6;				
Chironomid sp.				1;						
Dilophus sp.						1;				
Scatopse notata					2;	34;		3;		
Heleomyza serrata	3;	2;	1;	26;	9;	201;		44*	1;	6;
H. ?borealis							1;	40*		
?Themira dampfi	1;	2;								
Copromyza sp.						3;	9;			3;
Leptocera ?fontinalis										12;
Herniosina bequaerti						14;				
Telomerina flavipes					6;	48;		3;		
Spelobia sp.						1;				
Limosinine sp.	1;							1;		
?Scaptomyza sp.						1;				
?Agromyzid sp.					1;					
?Acalypterate indet.		3;								
Scathophaga sp.		2;	1;	2;	5;					
Anthomyiid sp.				2;						
Fannia ?postica	1;									
Melophagus ovinus						4;				
indet pup.(sp.5,6)		3;			2;					
Totals/sample	6	12	2	31	25	313	10	91	1	21

Key to Samples *11* Stb 81 F Trench W.Profile Column 35-40cm; *12* Stb F Trench S.RPro.10-15cm; *13* Stb 81 F Trench/W.Profile Column; *14* Stb 81 F Trench; *15* Stb 6 Trench N.Prof.65-70cm; *16* Drain under H14 Upper Layer; *17* Stb F Trench S Profile Column 25-30cm, 12.8.81; *18* Hús 18 Floor; *19* Hús 14 Pit; *20* Stb F Trench Prof.Col.35-40cm.W7 4RS.

(Table 25 contd.)	21;	22;	23;	24;	25;	26;	27;	28;	29;	30;
Trichocera maculipennis		1;							1;	
Scatopse notata	1;		1;	3;				5;		
Mayetiola sp.								8;	8;	
Heleomyza	1;	8;	9;	89;	13;	64;	2;	23;	3;	11;
?Copromyza sp.	33;				1;			2;		
?Leptocera fontinalis							1;	3;		
Herniosina bequaerti				22;					5;	
?Minilimosina sp.	1;	1;	10;							
Telomerina flavipes										1;
?Trachyopella sp.	1;	1;								
Limosinine sp. indet.					2;					
Allopiophila sp.	1;		1;					4;		
?Meonura sp.								1;		
Hydrellia ?griseola										1;
Calliphora sp.									1;	
Scathophaga sp.	1;			3;		1;				
Anthomyiid sp. indet.								1;	2;	
?Spilogona sp.			1;			1;	1;			
Melophagus ovinus			1;						- 1;	
Totals/sample	39	11	23	117	16	66	4	47	21	13

Key to samples *21* Stb 81 F Trench S Profile 25-30 12.8.81; *22* Stb C; *23* Stb E; *24* Stb F; *25* Stb K; *26* F Trench(W) 0-5 Sto; *27* Stb Charcoal I Pit under Hús 14 Sto; *28* Sto 1; *29* Sto 2; *30* F Trench(W) Sto 95-100.

(Table 25 contd.)	31;	32;	33;	34;	35;	36;	37;	38;	MNI	Midden
Trichocera maculipennis	1;	20;					1;		30	1
Chironomid sp.									1	1
Dilophus sp.		1;							9	
Sciarid sp.									1	
Scatopse notata	1;	4;			1;		1;		63	3
?*Mayetiola* sp.				1;					149	1
Heleomyza serrata	41;	50;							777	219
H. borealis					8;				49	1
Heleomyza sp.						78;	16;		317	
?Themira dampfi									3	3
Copromyza sp.	4;	2;		1;			1;	1;	65	48
Crumomyia nitida		1;							1	
Leptocera ?fontinalis									16	12
Herniosina bequaerti	25;	5;				2;		1;	83	
?Minilimosina sp.									12	1
Telomerina flavipes	55;					7;	16;		145	7
Spelobia sp									1	
Limosinine sp. indet.		31;					1;		36	1
Trachyopella sp.							1	-	2	1
Sphaerocerid sp.									7	
Allopiophila sp.									6	1
?Neonura sp.									1	
Hydrellia ?griseola				1;					7	2
Scaptomyza/Drosophila sp.									1	
?Agromyzid sp.									1	1

Taxon	Samples-	31;	32;	33;	34;	35;	36;	37;	38;	MNI	Midden
Acalypterate sp.										3	3
Calliphora sp.										5	4
Scathophaga sp.		2;	2;					2;		36	12
Anthomyiid sp.										6	2
Fannia ?postica										4	1
?Hydrotaea dentipes										1	1
Thricops sp.										1	
Spilogona sp.										6	
Cyclorrhaphous sp. (sp. 5, 6)										5	5
Melophagus ovinus		1;	10;	1;	1;	2;				22*	1
Totals/sample		130	126	1	4	11	87	38	2	1873	332

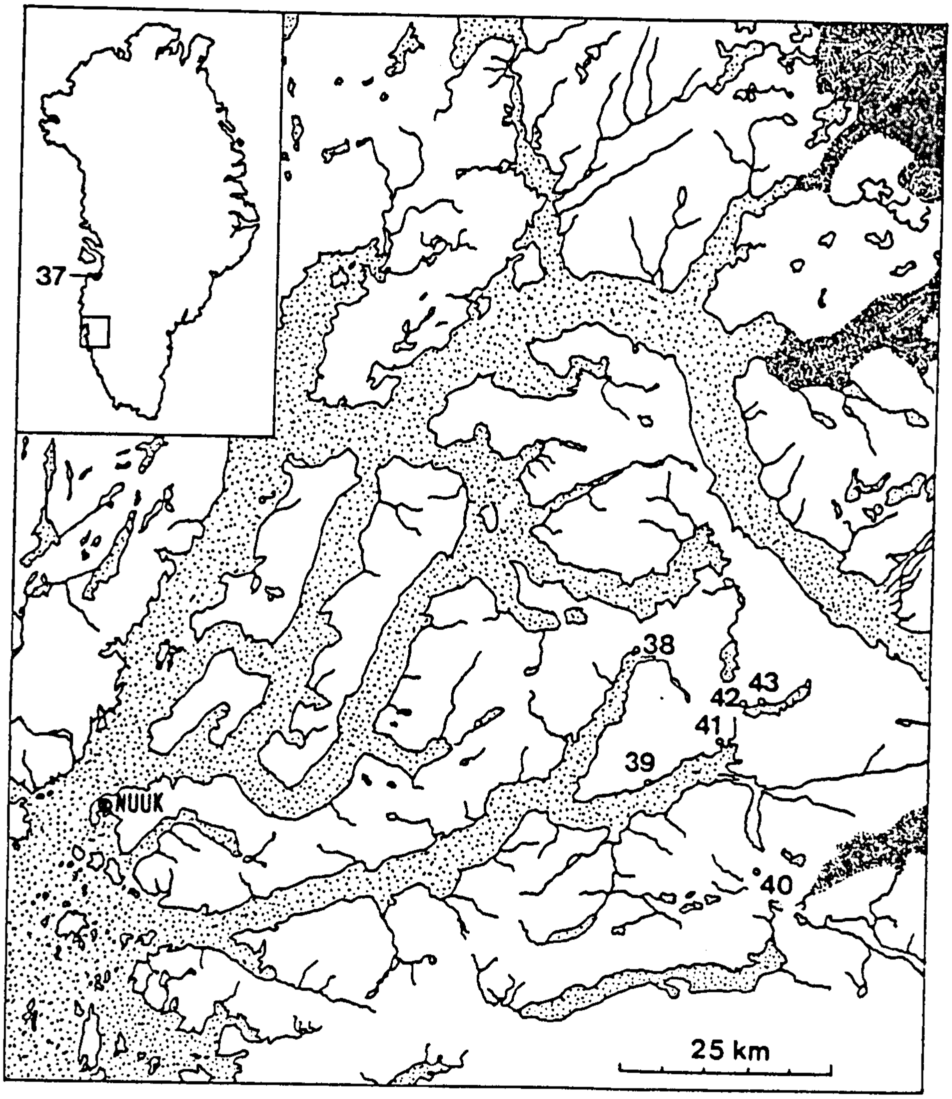
Key to samples *31* Stb 82 Hús 19; *32* Stb. House 17 Drain under hús 9U St B81. R. Nichols; *33* Stb Drain under Hús 17; *34* Stb E Trench 20-25cm St13-81; *35* Stb Hús 18 Pit 3 S of section; *36* Stb Hús 18 floor; *37* Stb 1982 Hús drain (1982); *38* Stb (1982) 3 Rak

NB. In Table 24 samples from the midden (ie. Trenches F and G) are underlined. * As noted above, a further 389 specimens of *Melophagus ovinus* were recovered from samples not seen by me. Apart from *Melophagus ovinus*, the six most abundant taxa were- Heleomyza spp. (1143); *Mayetiola* sp. (149); *Telomerina flavipes* (145); *Herniosina bequaerti* (82); *Copromyza* sp. (65) and *Scatopse notata* (63). Total= 6 taxa; 1647 MNI; % of total taxa= 18,75; % of total MNI = 93 %

WEST GREENLAND Map 3, page 238

37 QEQERTASUSSUK (Disko Bay) (Analysis on pages 387- 389)

Introduction A comprehensive report on the Palaeo-eskimo midden site at Qeqertasussuk, a small island on the southern shores of Disko Bay, West Greenland, has been published by Böcher and Fredskild (1993). This



Map 3 Sites in Greenland

showed that the Dipterous fauna of the midden was very different from those in the Norse Western Settlement, although few of the taxa present had been positively identified to genus. Through the kindness of Dr. J. Böcher, I was able to examine some 2200 puparia from nine samples from the site. The interpretation of this material confirms the findings of Böcher and Fredskild regarding the dominance of Piophilids and Calliphorids.

Interpretation Table 26 shows the subfossil dipterous fauna of nine samples from the midden at Qeqertasussuk and includes the trophic groups to which each taxon broadly belongs. Sites 1 to 5 inclusive are from the midden in Area B, whilst 6 to 9 area from the habitation site at Area C.

It will be seen that the exophilic necrophages (ie. *Neoleria*, *Allopiophila*, *Lasiopiophila*, *Hydrotaea* and *Phormia*) combined account for 1411 (or 64 per cent) of the 2194 puparia recovered from the samples examined. Also present were 486 puparia of another necrophage, *Heleomyza*, which breeds in light or dark situations, but here it was evidently breeding in the former. So the total necrophagous component of the Dipterous fauna of these two dumps was over 86 per cent, showing that carrion formed the bulk of these deposits. *Phormia* was found by Böcher and Fredskild (*op. cit.*) to dominate some of the horizons, and in sample 3 studied here, it reaches 33 per cent of the total. A pioneer coloniser of fresh carrion, its abundance here shows that the human inhabitants were throwing large quantities of soft animal tissue onto the middens. Whilst it is most likely that the species concerned here is *Phormia terrae-novae*, it could be the closely related, exclusively arctic, *P. atriceps*. Their biology is very similar, but the restricted range of the latter suggests it has different thermal tolerances. Böcher and Fredskild note that the incidence of *Phormia* decreases in the upper layers of the dumps as human influence on the site declines.

Table 26 Diptera of Qeqertasussuk

Taxon	T	1	2	3	4	5	6	7	8	9	Total
Sciarid sp.						1					1
Neoleria prominens	c	7		14	63	3	3	170		4	264
Heleomyza borealis	*	25	51	40	323	6	1	22	1	17	486
Allopiophila vulgaris	c	11	49	49	229	6	29	126	62	56	617
Lasiopiophila pilosa	c	5	38	70	108	1			2	5	229
Scatophila cribrata	e									1	1
Scatella ?stagnalis	e							1			1
Scathophaga sp.	a			1		1					2
Fucellia sp.	f			70	90		2	7	25	9	203
Delia fabricii	d								1		1
Zaphne sp.	e								1	1	2
?Paregle sp.	d				36	8		21	2	1	68
Hydrotaea anxia	c	2	6		1		1	1			11
Spilogona sp.	e				1			2	4	7	14
Phaonia sp.	h	2									2
Phormia terrae-novae	c	7	40	123	21	24	26	34	11	4	290
Tachinid sp.	(i)									1	1
Gen. sp. indet.					1						1
Total MNI		59	184	368	873	49	62	384	109	106	2194
Total taxa 11		7	7	8	9	7	6	9	10		

Piophilids occur throughout the Qeqertasussuk sequence according to Böcher and Fredskild. These flies are amongst the last wave of carrion-colonisers, favouring bone marrow. Of the total necrophagous fauna in the samples examined, Piophilids accounted for 44.5 per cent, suggesting that skeletal material was probably left exposed on the sites over several summers.

The evident abundance of carrion and bone-marrow on this Palaeoeskimo site is in complete contrast to the Norse middens, both in West Greenland and Iceland.

Apart from the necrophages, there was a strong and constant presence of seaweed, indicated by large numbers of *Fucellia* puparia. These again were rare in the Sandnes middens, although some of them were close to the shore. As at Niáqussat, there were probably some areas of organic slurry supporting colonies of freshwater algae on the midden edges at Qeqertasussuk , as the same group of taxa occurred in both locations. The only positive phytophage found in the Qeqertasussuk material was a single puparium of *Delia fabricii* which feeds on the grass *Poa pratensis.* This species was very common in the Sandnes middens. The taxon queried as *?Paregle* may belong to another Anthomyiid genus, but the trophic group is unknown. Most Anthomyiids are phytophagous.

According to the analysis of Dipterous subfossils, the greatest diversity occurred at the bottom of the midden in Area C

NORSE WESTERN SETTLEMENT SITES IN WEST GREENLAND

38 EGALUGIALIK (V 45) (Analysis on page 389)

Introduction One of the lesser Norse farms listed by Bruun (1928), this stood at the head of Itivdleq, 15 km north-west of Sandnes. Only six samples were seen from this site, comprising five taxa and 64 specimens as listed in Table 27a. Table 27b gives the percentage representation of the trophic groups to which taxa present belonged.

Interpretation A very restricted Dipterous fauna with *Heleomyza* accounting for 86 per cent of the total Dipterous MNI. The absence of exophilic necrophages suggests a dark environment like the other Norse farms, but here only one *Telomerina* was found, perhaps inferring

Table 27a Diptera of Egalugialik (V 45)

		Samples						
Taxon	TG	MF1;	MF2;	MF3;	MF4;	MF5;	MF6;	MNI
Simulium	g	-	-	-	-	-	1	1
*Heleomyza**	b	2	3	2	11	11	26	55
Telomerina	b	-	-	-	1	-	-	1
Delia(fabricii)	d	-	-	1	3	-	2	6
Hydrotaea	c	-	-	-	1	-	-	1
Total taxa 5	Total MNI	2	3	3	16	11	29	64

* A very large *Heleomyza* from MF5 may be *serrata*; rest probably *H. borealis*.

Table 27b Percentage Representation of Trophic groups at Egalugialik

Sample,	Trophic group									MNI,	Sample,										MNI
	a	b	c	d	e	f	g	h	i			a	b	c	d	e	f	g	h	i	
MF1		100								2	MF5		100								11
MF2		100								3	MF6		90		7			3			29
MF3		67		33						3											
MF4		75	6	19						16	Total Taxa 5 Total MNI= 64										

lower temperatures than in most of the other farms. *Delia fabricii* may have been in *Poa pratensis* turf used indoors, perhaps as fuel. The *Simulium* had presumably entered the house for a blood meal from the occupants, whilst the single *Hydrotaea anxia* puparium may have been accidentally introduced from the midden outside, where it could have been feeding in any decomposing animal matter. An exophilic fly, its larvae are facultative carnivores, preying on other insect larvae in putrifying organic matter. It is unlikely to have entered the house to oviposit amongst the *Heleomyza* as it should have been much commoner in the samples. It is a very common fly in West Greenland today.

Whilst the Dipterous material from V 45 is in limited quantity, several peculiar features are apparent when compared to the other sites. Most strikingly, there is no evidence of herbivore dung (ie. no *Scathophaga furcata*), despite the proximity of *Poa pratensis* swards as indicated by the puparia of *Delia fabricii*, which accounted for almost 10 per cent of the entire Dipterous material present. Again, for a coastal site, the total lack of Dipterous evidence for any utilisation of seaweed is noticable, though in broad agreement with other Western Settlement farmsteads. The total absence of exophilic necrophages is again conspicuous, although the occurrence of a single *H. anxia* puparium is problematical as this fly would be likely to occur in greatest abundance with Calliphorids in rotting carrion. The closely related *H. dentipes*, which replaces *anxia* in more temperate regions, breeds in a very wide range of media (Skidmore 1985) and will breed in chicken manure and similar putrifying residues which are infested with *Heleomyza captiosa* larvae.

39 Niáqussat (V. 48) (Analysis on pages 390- 393)

Introduction Niáqussat farm midden produced the largest quantity of Dipterous material seen by me from any Western Settlement site, totalling 2662 specimens in 28 taxa from 18 samples. McGovern (in prep.) notes that animal dung made up a large proportion of the midden from this site which is situated on a steep south-facing slope. Sadler (1992) describes the midden deposits in detail and discusses the 28 Coleopterous taxa which he recovered from the site. Deposition in the midden is believed to have commenced around 1000 AD and continued until about 1350 AD. A major component consisted of sheep dung and bone fragments with lenses of brushwood. Table 28a-c lists the Dipterous taxa present and Table 29 the percentage representation of the relevant trophic groups. The this was a site of human habitation was indicated by the large numbers of the Human Flea *Pulex irritans* (Buckland & Sadler 1989) and lice *Pediculus humanus* (Sadler 1992).

Interpretation In that the dominant species in most of the midden horizons at Niáqussat were the endophilous necrophages *Heleomyza borealis* (47.3%) and *Telomerina flavipes* (20.6%), this site much resembles the other Western Settlement farms discussed here. Along with the Human fleas and lice mentioned earlier, this Dipterous species combination indicates that these horizons were ejected floor-coverings, showing that the human living quarters were again squalid and cave-like, but the large populations of *Telomerina flavipes* perhaps infer relatively warmer conditions. Niáqussat differs from other Norse farmsteads discussed here in that the fourth most abundant species was the Piophilid *Allopiophila vulgaris* (149 spp., 4.9%). This, together with single specimens of the blowfly *Calliphora uralensis and* the arctic Piophilid *Lasiopiophila pilosa*, eighteen *Neoleria inscripta* and nine *Hydrotaea anxia*, suggest that the midden here may have had more carrion than the other farms. The Piophilids (*A. vulgaris* and *L. pilosa*) and *Hydrotaea anxia* are usually regarded as exophiles.

Table 28a Diptera of Niáqussat (C9, samples 1 to 10)

Taxon	TG	1	2	3	4	5	6	7	8	9	10	MNI
Tipula arctica	h	-	-	-	-	-	-	1	-	-	-	1
Trichocera sp.	h	-	-	-	-	-	1	-	-	-	-	1
Simulium sp.	g	-	-	-	-	1	-	-	-	-	2	3
Heleomyza borealis	b	11	1	157	97	341	251	15	49	10	12	944
Neoleria prominens	b	-	-	1	3	2	3	-	1	2	1	13
Telomerina flavipes	b	2	1	76	9	174	130	22	1	8	16	439
Allopiophila vulgaris	c	44	5	-	-	-	-	-	20	1	47	117
Lasiopiophila pilosa	c	-	1	-	-	-	-	-	-	-	-	1
Philygra vittipennis	e	-	-	-	-	-	-	1	-	-	-	1
Scatella sp.	e	-	-	-	-	-	-	1	2	1	-	4
Scatophila cribrata	e	-	-	-	-	-	-	-	1	1	-	2
Agromyzid sp.	d	-	-	-	-	-	1	-	-	-	-	1
Scath. furcata	a	2	6	2	-	6	5	2	2	3	28	56
S. litorea	f	-	1	-	-	-	-	-	-	-	-	1
Pegomya sp.	d	-	-	1	-	-	1	-	2	-	4	8
Zaphne sp.	e	-	-	-	-	-	-	-	1	-	-	1
*Botanophila**	d	47	-	1	11	8	-	1	4	-	-	72
Delia fabricii	d	12	1	4	2	5	2	9	16	13	12	76
D. ?platura	d	-	-	-	-	2	-	2	-	-	2	6
Hydrotaea anxia	c	-	-	2	-	4	1	-	-	-	-	7

Taxon	TG	Samples (C 9 contd.)										MNI
		1	2	3	4	5	6	7	8	9	10	
Spilogona sp.	a	-	-	-	1	-	-	1	-	1	-	3
Phaonia pallidisquama	h	-	-	-	-	1	-	-	1	-	-	2
Melophagus ovinus	i	1	-	-	-	-	1	-	-	-	-	2
Calliphora uralensis	b	1	1	-	-	-	-	-	-	-	-	2
"segmented pupa"	?h								8			8
Total taxa 25 MNI=		120	17	244	123	544	396	56	119	44	125	1788

Key to C9 samples 1, #; 2, 14c; 3, 20-30cm; 4, 30-40cm; 5, 60-70cm; 6, 90-100cm; 7, 120-130cm; 9, 130-140cm; 10, 140-base. ‡ At least two species, probably *betarum* and *profuga*. For discussion on Trophic groups (TG), see under Sandnes, p.257

Table 28b Diptera of Niáqussat (C10, C11 and D9 samples)

Taxon	TG	C10		C11	D9					
		1	2		1	2	3	4	5	MNI
Heleomyza borealis	b	92	19	166	2	22	1	26	5	333
Neoleria prominens	b				1			3	1	5
Telomerina flavipes	b	34	1	54	2	1	-	-	-	92
Allopiophila vulgaris	c				-	7	-	5	-	12
Scatella ?stagnalis	e				-	-	27	6	24	57
Scatophila *cribrata*	e				-	-	48	5	35	88
Calliphora uralensis	b				-	-		1	-	1
Scathophaga furcata	a			1	-	-	-	1	5	7
Botanophila betarum	d				8	1	5	42	-	56
B.profuga	d		2		-	-	-	-	4	6
?*Lasiomma* sp.	d			-	1	-	13	40	12	67
Fucellia sp.	f				-	-	-	3	-	3

Taxon	T6	C10		C11	D9					
		1	2		1	2	3	4	5	MNI
Delia fabricii	d				31	1	18	73	10	133
Delia ?platura	d				1	-	2	2	-	5
Zaphne sp.	e				-	-	1	-	-	1
?Pegomya sp.	d			1	2	-	1	1	-	4
Hydrotaea anxia	c	1	1							2
Spilogona sp.	e				-	-	1	-	-	1
Melophagus ovinus	i			1	-	-	-	-	-	1
Total taxa 19 Total MNI=		127	23	223	48	32	117	208	96	874

Key to C10, C11 and D9 samples. C10 1 67.5cm; 2 117.5cm; C11 120cm; D9 1 112.5-115cm "Floor depression"; 2 127.5-130cm; 3 125cm; 4 130cm "wet above underground"; 5 130-140cm "old ground surface". For discussion on Trophic groups (T6), see under Sandnes, p.257

Phytophages constitute 11 per cent of the total and include *Delia fabricii*, which in D 9 sample 2 reaches 74 per cent of the Dipterous fauna. A herbivore dung fauna, indicated by the dung fly *Scathophaga furcata* is present in most samples and reaches 35 per cent of sample 2, which is also unusual in almost wholly lacking both *Heleomyza* and *Telomerina*. Only 17 Dipterous specimens were present, mostly as single specimens but including 5 *Allopiophila* and 6 *Scathophaga furcata*, signifying a mixture of herbivore dung and carrion lying in an open place.

In D9 there is a very low count for the endophilous necrophages, except in sample 3 (72%) where there is also a 22 per cent presence of *Allopiophila*.

In samples 1 and 2 the phytophages *Delia fabricii* and *Botanophila* form the dominant group (56.6 and 91% respectively), whilst in 4 and 5 it is the algaecoles *Scatella* and *Scatophila* which dominate (63.3 and 61.5), the phytophages forming the bulk of the remaining fly fauna (34.2 and 26.9).

Table 28c Complete List of Dipterous taxa from Niáqussat

Taxon	TG	C9	C10	C11	D9	MNI	Taxon	TG	C9	C10	C11	D9	MNI
Trichocera sp.	h	1				1	*Scathophaga litorea*	f	1				1
Tipula arctica	h	1				1	*Calliphora uralensis*	b	2			1	3
Simulium sp.	g	3				3	*Botanophila* spp*	d	72	2		59	133
"segmented pupa"	?h	8				8	*Zaphne* sp.	e	1			1	2
Heleomyza borealis	b	944	111	166	56	1277	*Fucellia* sp.	f	1			3	4
Neoleria prominens	c	13			5	18	*?Lasiomma* sp.	d	15			66	81
Telomerina flavipes	b	439	35	54	3	531	*Pegomya* sp.	d	8		1	4	13
Allopiophila vulgaris	c	117			12	129	*Delia fabricii*	d	76			133	209
Lasiopiophila pilosa	c	1				1	*D. ?platura*	d	6			5	11
Philygra vittipennis	e	1				1	*Hydrotaea anxia*	c	7	2			9
Scatella ?stagnalis	e	4			57	61	*Spilogona* sp.	e	4			1	5
Scatophila cribrata	e	2			88	90	*Phaonia pallidisquama*	h	2				2
Agromyzid sp.	d	1				1	*Melophagus ovinus*	i	2		1		3
Scathophaga furcata	a	56		1	6	63	Total taxa 28 Total MNI=		1788	150	223	500	2661

Table 29 Percentage Representation of Dipterous trophic groups at Niáqussat

Sample	a	b	c	d	e	f	g	h	i	MNI
				Trophic groups						
C9										
1	2	11,8	37	49	-	-	-	-	0,8	120
2	35	18	36	6	-	-	-	-	-	17
3	0,8	95,4	0,8	2,4	-	-	-	-	-	244
4	-	88,7	-	10,5	0,8	-	-	-	-	123
5	1	95,4	0,8	2,8	-	-	0,2	0,2	-	544
6	1,3	97,6	-	0,8	-	-	-	0,2	0,3	396
7	3,6	66	-	27,2	5,4	-	-	1,8	-	56
8	1,7	43,8	17	27,8	5,3	-	-	?8,8	-	119
9	6	37,1	2	32,5	12	2	-	?10,2	-	44
10	6	23,8	38	31,6	0,8	-	2	-	-	125
C10	a	b	c	d	e	f	g	h	i	MNI
1	-	99,2	0,8	-	-	-	-	-	-	127
2	-	87,3	4,3	8,7	-	-	-	-	-	23
C11	0,4	99	-	0,4	-	-	-	-	-	223
D9										
1	0,4	14	2,5	77,6	5,5	1,5	-	-	-	208
2	-	8,4	-	91	-	-	-	-	-	48
3	-	72	22	6	-	-	-	-	-	32
4	-	4,1	-	32,6	64,9	-	-	-	-	117
5	6,2	6	-	26,9	61,5	-	-	-	-	96

Total samples 18 Total MNI= 2661

NB, For discussion of trophic groups see under Sandnes, p.258

40 NIPÁATSOQ (V. 54) (Plan, plate 31) (Analysis on page 394)

Introduction. The published account of this site by Buckland, et al. (1983) details the excavation strategy, lists the subfossil fauna and flora, and interprets the rooms making up the farmstead. A short list of Diptera with interpretive comments was also included. The study by McGovern (1994a) of bone material from the rooms strongly emphasises their function. The major revision of the Dipterous material is discussed below. Table 30 shows that the Dipterous material consisted of 1087 specimens in ten taxa from 5 samples

Interpretation As stated above, the presence of *Heleomyza serrata* in the Western Settlement material remains unproven, but the comments relating to it in Buckland *et al.* (1983) are broadly applicable also to the species referred to in that paper as *Leptocera* sp., but now positively identified as *Telomerina flavipes.* This fly was unquestionably taken to Greenland by the Icelanders and could only have survived in the warmest parts of the settlers' homes where it bred in darkness on their fouled floors etc.

Nipáatsoq differs from the other Ameragdla farms in several respects. The samples collected were all from the actual floors inside the house, not from the middens, so they provide a remarkable insight in Dipterous terms, into the interior of a Norse dwelling in the Western Settlement. The most obvious feature is the massive predominance of *Telomerina flavipes* in two of the five samples, from Rooms III (the Hall) and VI (the Bedroom), where there were clearly colossal populations. In these Norse farms *Telomerina flavipes* was a thermophile, capable of survival only in the warmest parts of the dwellings. The precise lower threshold for its survival is not known at

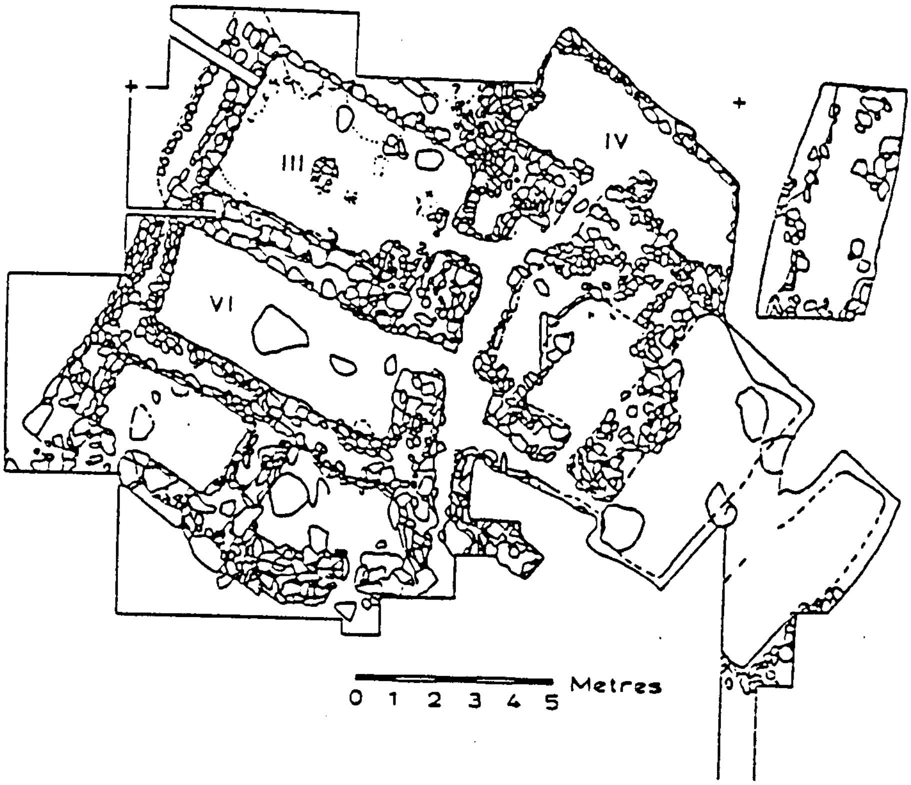
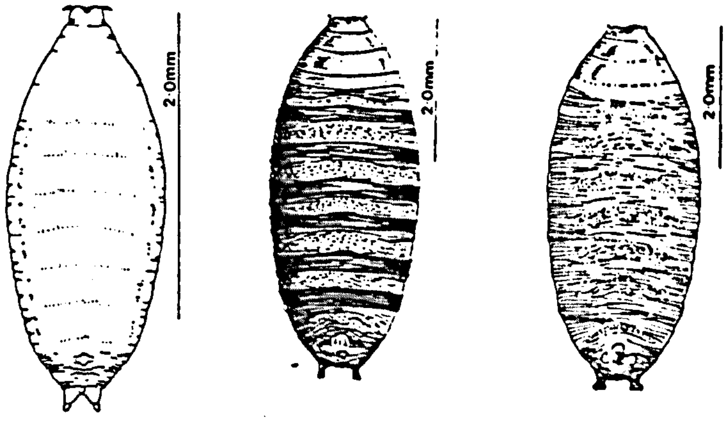
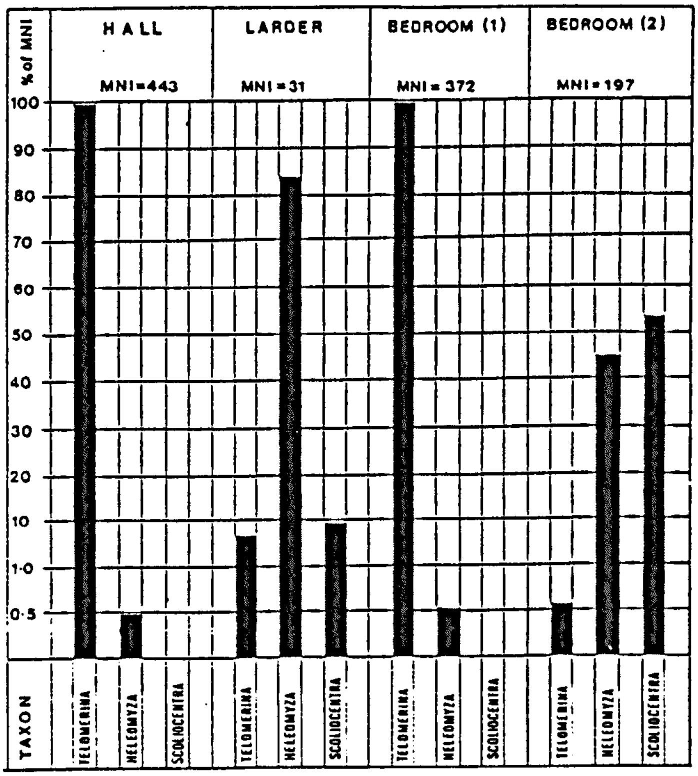


Plate 31 Plan of Nipáatsoq farm showing rooms III (Hall), IV (Larder) and VI (Bedroom). (After Andreasen, in Buckland *et al.*, 1983).

present. Where thermal regimes permitted, the dark interiors of the Norse houses provided conditions ideal for this troglodytic fly.



Text-Figure 15



Text-Figure 16

Text-figure 15 Puparia of *Telomerina, Heleomyza and Scoliocentra.*

Text-figure 16 Relative abundance of the above three taxa on the floors of the three rooms at Nipáatsoq.

Text-figs. 15 and 16 show that *Telomerina* massively predominated in sample 2 from the Hall (Room III) and in sample 5 from the Bedroom (Room VIb). The relative abundance of *Telomerina* and *Heleomyza* in these two samples was identical, strongly inferring that the two rooms had similar thermal regimes, organic contamination and poor light-intensity. Defaecation and other activities of human and canine inhabitants probably took place mainly in these two rooms. Indeed conditions prevailing in these rooms were probably the norm in Norse homesteads in Greenland. The analyses on page 418 show that *Telomerina* was enjoying almost optimum conditions in these rooms, with a very low mortality. Interestingly, the analyses also show that single specimens of the mosquito *Aedes* were found in these rooms, clearly having entered for blood-meals from the occupants.

The Larder (Room IV) was very different, being obviously colder, although it is not clear whether this alone accounted for the dominance of Heleomyzids over *Telomerina*. It is probable that there was also some difference in the nature of contaminants- perhaps more decaying meat-products in the Larder than in the Hall or the Bedroom. Two Heleomyzids (*Heleomyza* and *?Scoliocentra*) were breeding in the Larder, the former greatly predominating. The latter was queried as *Neoleria septentrionalis* in Buckland *et al.* (*op. cit.*).

Comparison of the Bedroom samples 4 and 5 (Room VIa and b) show hugely different fly faunas (Text-figs. 15 and 16), clearly indicative of a catastrophic event which brought about the following changes:- *a* a huge crash in *Telomerina* numbers (down to 2.5 per cent of the fauna, with a concurrent massive increase in mortality.

b an explosion in Heleomyzid populations (to 94 per cent of fauna).

Of the two Heleomyzids present it was *?Scoliocentra* which became dominant. It will be seen that a small population of these flies lived in the Larder and it seems that they moved into the Bedroom in response to a sudden increase in attractants there- most probably carrion.

c a massive increase in species diversity, including trace presence of exophilic necrophages (one adult *Cynomya* and one *Phormia* puparium).

d an absence of *Aedes*.

These changes in the Dipterous fauna suggest a sudden great drop in temperature in the Bedroom, resulting in a total collapse of the

Table 30 Diptera from the Nipáatsoq Farm floors

Taxon	TG	1;	2;	3;	4;	5;	Total
Aedes impiger/nigripes	g	-	1	-	-	1	2
Heleomyza borealis‡	b	9	2	26	87	2	126
?Scoliocentra fraterna	b	-	-	3	103	-	106
Telomerina flavipes	b	27	441	2	5	370	845
Calliphora uralensis	b	1	-	-	-	-	1
Cynomya mortuorum	c	-	-	-	1	-	1
Phormia terrae-novae	c	-	-	-	2	-	2
Scathophaga furcata	a	-	-	-	1	-	1
Delia fabricii	d	-	-	-	2	-	2
Spilogona	e	-	-	-	1	-	1
Total taxa 10 Total MNI=		37	444	31	202	373	1087

Key to samples; 1 "jord fra område; omvr.mosens; 2 Rum III; 3 Rum IV; 4 Rum VI; 5 Jordprøve fra Rum VI. ‡ 20 *Heleomyza* puparia from sample 4 much larger than rest and may be *serrata*; remaining 106 probably *H.borealis*. For discussion on Trophic groups see Sandnes account below.

Table 31 Percentage representation of Trophic groups at Nipáatsoq

Samples	Trophic groups									
	a	b	c	d	e	f	g	h	i	MNI.
1	-	100	-	-	-	-	-	-	-	37
2	-	99,5	-	-	-	-	0,2	-	-	444
3	-	100	-	-	-	-	-	-	-	31
4	0,5	96,5	1	1	-	-	-	-	-	202
5	-	99,5	-	-	-	-	0,3	-	-	373
								Total		1087

Telomerina population. The cold-resistant Heleomyzids move in from the Larder in response, almost certainly, to an increase in carrion in the Bedroom. *Scoliocentra* species, much more so than *Heleomyza*, appear to be obligative troglodytic necrophages which frequent carrion in caves and animal burrows. It is clear that the Bedroom ceased to function as such and it seems likely that after the troglodytic necrophages from the Larder had colonised the contents of this room, the "outside world" came in, manifested by a large increase in Dipterous diversity. Perhaps as a result of a roof-collapse, the sun was able to penetrate and the exophilic necrophages *Cynomya* and *Phormia* gained entry. The testimony of these flies appear to support the hypothesis that the last occupants of Nipáatsoq may have met a tragic end (Jones 1986), but it would have been desirable to see further samples from all of the rooms.

Nipáatsoq is very unusual amongst this group of Norse farms in three other respects. *Simulium* adults were absent from the material, being replaced by just two *Aedes*. In view of the large numbers of blackflies in some other samples this is curious and may reflect an absence of running water nearby, but proximity of stagnant water. Also very curious is the virtual absence of any indication of herbivore dung, there being just one puparium of *Scathophaga furcata*. Unlike farm V 45, which shares this peculiarity however, the extremely low incidence of *Delia fabricii* at Nipáatsoq may infer a local scarcity of *Poa pratensis*. This fly was referred to as *Delia* sp./*Calythea micropteryx* Thoms. in Buckland *et al.*(1983).

Buckland *et al.* (*op. cit.*) query the presence amongst the material from Nipáatsoq of a single *Melophagus ovinus*. It is not possible to verify this record, but as stated above there is no further Dipterous evidence for sheep or cattle at Nipáatsoq.

41 SANDNES (V. 51) (Analysis on pages 395- 402)

Introduction The main farm in the Western Settlement, Sandnes has been the subject of much research and many publications, and is fully discussed in Roussell (1936) and McGovern (1994b). The material forming the basis for this interpretation consists of 1986 Dipterous specimens from 40 samples. In Tables 34a- 34d the total numbers of Dipterous specimens are listed under their respective samples arranged under the appropriate Felt (*Danish;* Trench) numbers I to VII. Table 35 summarises these data and gives the total minimum number of individuals of each taxon in each Felt number.

Interpretation For interpretation purposes taxa are grouped according to broad larval pabula. These " trophic groups" are indicated for each taxon in Table 33 by letters a to i, and are as defined below, where the square-bracketed figures give the number of individuals from the

Table 32 The Dipterous Trophic types in the Sandnes Middens(Felt I-VII)

Felt/Au.	a	b	c	d	e	f	g	h	i	Spp.
Felt I										
Au I	2	364	1	16	-	1	3	-	5	392
Au III	52	7	-	10	-	1	26	-	1	97
Au IV	7	69	-	18	11	1	6	-	1	113
Au V	26	161	?2	57	155	2	2	-	-	405
Au VI	-	17	-	2	-	2	-	-	-	21
Au ?(1287)	10	34	2	26	2	-	-	-	-	74
Felt II	6	721	4	2	3	-	-	-	1	737
Felt III	3	40	-	15	8	-	-	1	-	67
Felt V	-	-	-	-	-	1	-	-	-	1
Felt VI	8	11	-	30	1	1	12	1	-	64
Felt VII	-	-	-	-	-	-	3	-	-	3
Totals/TG	114	1424	8	176	180	9	52	2	8	1974

Key

a) stercoricolous in herbivore dung (eg. *Scathophaga furcata)*

b) endophilic coprophages/necrophages (eg. *Heleomyza/Telomerina)*

c) exophilic necrophages (eg. Piophilids, Calliphorids)

d) phytophages (eg. Agromyzids, *Delia, Botanophila, Pegomya)*.

e) algaecoles (eg. Ephydrids, *Zaphne, Spilogona*).)

f) fucicoles (eg. *Orygma, Fucellia*)

g) ripicoles (eg. *Simulium*)

h) humicoles (eg. *Tipula* and *Phaonia*)

i) ectoparasites (*Melophagus*)

Sandnes material belonging to each trophic group, followed by the percentage of the total Sandnes MNI that figure represents.

a. **stercoricoles**; breeding in dung of herbivores (eg. sheep and cattle) (*Scathophaga furcata*). [114; 6 %]

b. **endophilous necrophages**; breeding indoors in carrion and excrement of carnivores/omnivores, including human, in which animal protein is present (*Heleomyza*, *Neoleria*, *Telomerina* and *Calliphora*) [1422; 72 %]

c. **exophilic necrophages**; breeding outdoors in carrion (Piophilids and *Phormia*) [9; 0.4 %]

d. **phytophages**; feeding on vascular plants and/or fungi (Agromyzids, *Pegomya*, *Botanophila* and *Delia*) [176; 9 %]

e. **algaecoles**; feeding on green and blue-green algae in shallow water (Ephydrids and *Zaphne*), or predatory on these (*Spilogona*) [179; 9 %]

f. **fucicoles**; feeding on rotting seaweed or beach litter (*Orygma*, *Scathophaga litorea* and *Fucellia*). [13; 0.6 %]

g. **hydrophiles**; breeding in water (*Simulium*) [52; 3 %]

h. **humicoles/muscicoles**; breeding in humus soil and/or moss-cushions (*Tipula* and *Phaonia*). [2; 0.1 %]

i. **ectoparasite on sheep** (*Melophagus*). [8; 0.4 %]

Table 33 shows the percentage representation of the nine trophic groups in each Felt. In Felt 1, 2 and 3 the endophilic necrophages predominated although it is clear from Tables 34 to 36 that there were considerable differences in this respect between closely adjacent sample numbers. In Felt 1, Au I for example, group b predominated in all samples, whilst in Felt 1, Au III, group b was of minor importance. In Felt 6, group d formed the dominant group. Felts 5 and 7 contained one species each, in single numbers (groups f and g respectively). It is clear therefore that each sample must be considered separately for detailed interpretation.

Table 33 Percentage representation of the nine Trophic Groups in the Sandnes Dipterous Material.

TG;	Felt 1;	Felt 2;	Felt 3;	Felt 5;	Felt 6;	Felt 7;	
a	7	0,8	4	-	8	-	
b	57	98	61	-	17	-	
c	0,4	0,1	-	-	-	-	
d	11	0,2	21	-	48	-	
e	14	0,4	12	-	1,5	-	
f	7	0,4	-	100	1,5	-	
g	3	-	-	-	18,5	100	
h	-	-	1,5	-	1,5	-	
i	0,6	0,1					
MNI=	1112	740	66	1	64	3	Total= 1986

NB. Bold figures indicate the dominant trophic type in each Felt, and numbers at foot of each column give total specimens per Felt.

It will be seen from Table 33 shows that groups c, f, g, h and i are very poorly represented in the Sandnes material, together accounting for only about 6 per cent of the entire specimens present. In fact the middens contained virtually no carrion or seaweed, and humicoles were practically non-existent. The vast bulk of the material inferred by the Dipterous taxa recovered consisted of faeces with a strong animal protein content which had accumulated in a dark environment.

Although Felt I contained by far the greatest number of specimens (1112 Diptera) it also included the largest number of samples (23), so the actual mean number per sample was only 48. Corresponding numbers for the other Felt numbers were- Felt II (740 Diptera, 4 samples, 185 per sample); Felt III (66 Diptera, 3 samples, 22 per sample); Felt IV (none); Felt V (1 Dipteron, 1 sample, 1 per sample); Felt VI (64 Diptera, 7 samples, 9 per sample); Felt VII (3 Diptera, 2 samples, 1.5 per sample). Since over 97 per cent of puparia in Felt II belonged to a trophic group b species (*Heleomyza*) this appears to have been the most squalid of the Sandnes sites examined.

In interpreting the Dipterous content of the Sandnes excavations three major uncertainties arise.

a the juxtaposition of the samples within each Felt is unclear from the basic excavation data. It is possible that some contamination across sampling sites could have occurred shortly after deposition, as mature larvae vacated their pabula to pupariate. Thus a coprophagous larva may have left its pabulum for adjoining matrices. Lateral and vertical migration could have occurred, modifying the implications.

b Presumably putrid floor covering from the habitations would have been cast onto the midden during the warmer months of the year, most likely between May and mid September. A time-consuming operation, this was probably not repeated annually (McGovern 1994b).

c The frequency of deposition is not known on any particular part of the midden, and hence the length of time any surface was exposed to the atmosphere is unknown.

With the possible exception of *Phormia*, it is most improbable that any exophilic Greenlandic fly would have more than one emergence of adults annually, or that any would hibernate in the adult state. It is well known (Downes 1964) that many insects, which are polyvoltine further south, may pass more than one winter in their larval stage in the Arctic. There, overwintered larvae produce a summer emergence of imagines, the progeny of which do not reach maturity until the following summer, at the earliest. This is clearly the case with the phytophage *Delia fabricii* in northern Norway as shown by Johansson (1989). It should be noted here that Johansson's study area, unlike the Western Settlement area, is not technically inside the Arctic, as defined by the 10 degree July Isotherm, although it lies north of the Arctic Circle. Greenland under the same definition lies entirely within the Arctic today (Sage, 1986), and probably did so during the Norse occupation.

The "twig layers" at Sandnes and elsewhere have been interpreted as floor covering in the Norse homesteads, composed of brushwood from birch, willow and/or alder scrub (Buckland et. al., 1984). Two of the 10 taxa retrieved in quantity from Sandnes can be regarded as indicative of human faeces and animal protein accumulated in dark places, namely *Heleomyza* and *Telomerina flavipes*. It could be expected that the populations of these would be highest in the "twig layers". In fact, the samples having the largest populations are, for *Heleomyza*, 1046, matrix not stated (134 puparia), 1204, "fire-place material"(325) and 1238, matrix not stated (569), and for *Telomerina flavipes*, 540,"turf"(33). The total Dipterous MNI from Sandnes (FeltI-VII) was 1986, of which 1363 were *Heleomyza* and 60 were *Telomerina*, and the total number of samples containing Dipterous material was 40. If one omits the above four samples (540, 1046, 1204 and 1238) from the sum, the corresponding figures are total Diptera 918, *Heleomyza* 335, *Telomerina* 27 and samples 36. Of these samples, 9 are designated "twig layers", which collectively contain 143 *Heleomyza* and 11 *Telomerina*. If all of the samples were equally attractive to all species, it could be predicted that the nine twig-layers would contain 9/36 x 335 = 83.75 *Heleomyza*, and 9/36 x 27 = 6.75 *Telomerina*. These results show that the twig layers obviously had above-average populations of these two flies, a result supportive of the proposition that the twig layers were fouled floor-coverings from the rooms occupied by the human inhabitants of the farms. Again, human lice and fleas are widely scattered through these deposits (Sadler 1987). In this connection, the huge *Heleomyza* population in sample 1204, described as a fire-place, is highly significant since the fire place, being the warmest part of the house, was presumably the centre of human, and endophilic Dipterous, activity.

Several of the "twig-layers" from Sandnes contain puparia of *Heleomyza* and *Delia fabricii*. The former will certainly breed outdoors, notably in guano and scraps of carrion below bird cliffs up to the northernmost parts of the High Arctic. But there can be little doubt that in the Western Settlement it constituted the "House-fly", breeding in human excrement and decaying animal matter on the floors of the houses. These would have provided optimum breeding conditions for the fly, and the success of the populations was adequately demonstrated by the very small proportion of unhatched puparia in the Sandnes excavations. *D. fabricii* on the other hand feeds on the grass *Poa pratensis*, the females laying in swards of this grass in summer and the eggs overwintering in the soil. In early spring the larvae hatch and feed up rapidly on the young growth, pupating in the soil in late spring, the adults hatching a few weeks later. In the samples containing puparia of these two species, they were evidently not breeding in the medium concurrently. Three possible models could account for these two taxa occurring together.

1) the contaminated twig layer was thrown onto a sward of *Poa pratensis* containing hatched *Delia* puparia.

2) *Poa* turf containing emerged *Delia* puparia was amongst the twig-layer material when it was laid on the house floor.

3) *Delia* bred in the twig-layer material on the midden after it was deposited there.

The last model is perhaps the most likely explanation and a possible sequence of events would be as follows.

Year one (spring). Putrid floor covering of twigs contaminated with human faeces and carrion and infested with *Heleomyza* removed from the house and cast onto the midden.

Year one (summer). Seeds of *Poa pratensis* from adjacent swards fall onto the midden surface.

Year two (spring). Seeds of *Poa* germinate to form a covering on the old midden surface.

Year two (summer). The grasses attract female *D. fabricii* from colonies nearby and these scatter their eggs across the sward.

Year three (spring). The *D. fabricii* larvae hatch and feed on the fresh growth of *Poa*, the adult flies emerging a month or so later.

Assuming that the fouled twig layer was cast onto the midden in spring and that *Poa* seeds fell onto its surface during the first summer, this model shows that a minimum of two years must have passed before the emergence of *Delia fabricii.*

Johanssen (1989) states that other grass species may be affected by *D. fabricii* in northern Norway and indeed this, in an Arctic environment, would be highly advantageous. However, the foregoing model stands, insofar as a dominance of an acceptable host plant must develop before the gravid female flies will be attracted for oviposition purposes, and hence at least one full season between creation of a new midden surface and emergence of phytophagous flies must have occurred.

As stated above, *Heleomyza borealis* could have bred either in the floor covering in the houses, or after the material was cast onto the midden. A non-thermophilous species even in the Arctic, this could have bred outdoors, needing only the presence of animal protein. But the extreme scarcity of such heliophilous necrophages as *Phormia terrae-novae* and *Allopiophila vulgaris* suggests that the *H. borealis* populations built up indoors. Outdoor temperatures were certainly adequate for these three to survive at Sandnes, since they breed commonly into the High Arctic anyway. McAlpine (1965) for instance found *Phormia terrae-novae* "in extreme abundance" at Lake Hazen, Ellesmere Island at 81° 49' N, and it has been recorded from Kap Morris Jesup, the northernmost cape of Greenland and the nearest land to the the North Pole. Many Piophilids are noted for their great resistance to intense cold. Both taxa predominated at Qeqertasussuk (see above).

Heleomyza borealis was by far the most abundant species in the Western Settlement Dipterous material, but it is probable that the closely related *H. serrata* was also present. Although not confirmed by male genitalic characters, some of the puparia were well above the normal size range for *borealis*. In excavations of a similar date in southern Iceland, *serrata* was more abundant than *borealis* (see above), and it seems inevitable that the species would have been transported to Greenland by the emigrating Icelanders.

A fly having similar biological requirements to *Heleomyza* which was certainly carried to the Western Settlements from Iceland was *Telomerina flavipes*. Favouring dark situations this normally necrophagous fly would have found suitable living conditions in the dark interiors of the colonists' houses with their faecally contaminated floors upon which scraps of decaying carrion gathered. On the extreme northern edge of its range, the fly would have been a thermophile, whose very survival depended upon the elevated temperatures of the farm interiors. Of all of the species found in the midden deposits, this is the one fly which would have been least likely to have survived outdoors in Greenland, where it must have been an obligative endophilous eusynanthrope. A success rate of 95 per cent infers that it was enjoying near-optimum conditions. The fly was common in Icelandic houses during the same period, but is now regarded as a rare southern species (Lindroth et al., 1973). Unknown in Greenland today, it evidently shared the demise of the Norse colonists, the Sheep Ked *Melophagus ovinus* and several of the Coleoptera (Buckland 1988), when climatic deterioration set in in the fourteenth century. If indeed the very large *Heleomyza* puparia do belong to *H. serrata* as suggested above, this would constitute a third lost Greenlandic eusynanthrope.

An interesting feature of the Norse middens, mentioned above, is the almost total absence of puparia of exophilic necrophages. This must mean that the Norse middens contained virtually no carrion, and that any bone material had been completely cleared of flesh before it was committed to the "scrap-heap". Since Piophilids breed profusely in the marrow of larger bones their virtual absence from the middens infers that even the bone marrow had been largely removed. The level of bone-fragmentation noted by McGovern (1994b) supports this view. In total contrast, the exophilic necrophages so scarce in the Sandnes middens, namely Piophilids and *Phormia*, were the dominant taxa in the Palaeoeskimo midden at Qeqertasussuk (Böcher & Fredskild 1993) (see above).

There is ample evidence in the Western Settlement that the combination of *Heleomyza* and *Telomerina*, in the absence of the exophilic necrophages just mentioned, identifies deposits with the interiors of human habitations, and as such provides a useful tool for archaeological investigations. Where this fauna dominates an assemblage, as in Felts 1, 2 and 3 at Sandnes it indicates a mainly domestic origin of the material.

One of the commonest species in the middens was *Scathophaga furcata*, an ubiquitous stercoricolous fly throughout much of the Holarctic, extending well into the Low Arctic. It breeds in the dung of many mammals, including man and dog (Ferrar, 1987), and can often occur where no mammals are in evidence. But in northern and montane areas, where it is most abundant, sheep dung is probably the favoured pabulum (Skidmore 1991). Its presence in the Western Settlement middens probably indicates dung from sheep and/or cattle which had accumulated in stables. In one sample(Felt I, Au III 1052) a huge predominance of this fly (82 per cent) suggests a major input from such a herbivore source, probably a clear-out of stable litter. In this sample the success rate was 86 per cent, and of the unhatched puparia three (6 per cent) contained parasitic ichneumons; this constituted the highest incidence of parasitism of any fly in the Sandnes deposits. It is not clear whether the *Scathophaga furcata* bred indoors, or in byre debris already thrown onto the midden, but the incidence of parasitism, and heliophilous habits of adult *Scathophaga* species would suggest colonisation occurred on the midden.

Where wet situations existed on the middens, or their periphery, colonisation by green and blue-green algae occurred, as indicated by large breeding populations of Ephydrid flies. Although their specific identity cannot be ascertained, there are clearly four different genera and probably, as here proposed, they belong to taxa currently known from Greenland. In any case, known habitat requirements of these four genera are alike (Ferrar, 1987), so identification to species would probably add very little information. The Anthomyiid *Zaphne* shared this habitat with at least two species of the Muscid genus *Spilogona*, which acted as the main Dipterous larval predators (Skidmore 1985); significantly *Spilogona* occurred with peak Ephydrid populations.

In addition to the above, there was a distinctive community of Agromyzid and Anthomyiid phytophages, by far the most numerous of which was *Delia fabricii*, which has been discussed above. There were also at least two *Pegomya* species, doubtless belonging to the mycetophagous section of that genus (Ferrar, *op. cit.*). These typically attack Boletaceae (Hackman & Melander, 1979). Absence of phytophagous associates of *Betula*, *Salix* or *Alnus*, the components of the "twig layers", was predictable as no such Dipterons are known from Greenland.

For a group of sites so close to the littoral zone, the scarcity of flies belonging to the wrack-bed fauna seems remarkable. although remoteness from the open sea, and hence probably a reduced salinity, may result in a paucity of wrack-beds at Sandnes. Signs of the fly *Scathophaga litorea*, or one of its close Greenlandic congeners, were very scarce, and restricted to a few fragments of adults, yet this, along with *S. furcata* must have swarmed over the midden in search of prey in the form of other flies. In fact seaweed was only indicated by small numbers of *Fucellia* and just two single *Orygma*. As shown by Sadler (1989), there was also a very low incidence of the marine epizoote *Dynametra pumila (= Sertularia)* (cf. Buckland et al., 1993).

There was no evidence of mosquitoes at Sandnes but *Simulium* was obviously abundant, and hence presumably highly troublesome to the local human and animal inhabitants. The absence of the one bloodsucker and abundance of the other may be a result of sampling bias, or to the terrain being more favourable to the blackflies. These require running water, whilst mosquitoes normally breed in stagnant pools; both are present around Sandnes today (Buckland, *pers. comm.*).

Only two taxa from Sandnes could be regarded as humicoles, namely *Tipula arctica* and *Phaonia ?pallidisquama;* each represented by only one specimen. Both species however also breed in thick moss cushions, presence of which was inferred by Byrrhid beetles (Sadler 1992). In short, a truly humicolous fauna was apparently non-existant, possibly inferring rapid growth of the midden.

Conclusion. The Dipterous fauna of the Sandnes middens shows they were a totally artificial and alien habitat which nevertheless provided useful niches for a remarkably high proportion of the native Cyclorrhaphous fly fauna of that region. At least two species, *Telomerina flavipes* and *Melophagus ovinus*, were introduced by the Icelanders and became extinct when the colony came to an end in the 14th century. These flies, along with *Heleomyza* and *Simulium*, attest to the squalid living conditions and relative lack of creature comforts suffered by the human inhabitants. The extreme scarcity of immature stages of sun-loving carrion flies (exophilic necrophages) may indicate a very intensive utilisation of all meat-products in which nothing was wasted, although this appeared to characterise Norse dwellings and may have been a cultural feature. A comparison between the Dipterous faunas of the Sandnes and Qeqertasussuk middens (Böcher & Fredskild *lc.*) infers a very different life-style between the two cultures.

Table 34a Sandnes Diptera; Felt I(AU I-IV)

Taxon	AU I				AU III			AU IV				
	1070;	1158;	1204;	1277;	1052;	673;	856;	302;	736;	633;	783;	1041;
Simulium sp.	3;					26;				6;		
?Forcipomyia sp.			3;									
?*Bradysia* sp.						1;						
Heleomyza spp.	27;	11;	325;		2;	4;		6;	2;	42;	2;	13;
Neol. prominens												
?Copromyza sp.	1;											
Tel. flavipes	1;				1;				1;	3;		
Par. vulgaris			1;									
Ph. vittipennis												
Scat. ?stagnalis								2;		2;		6;
Scat. ?cribrata										1;		
T. quadrisetosa												

Table 34a (contd.)	AU I				AU III			AU IV				
Taxon	1070;	1158;	1204;	1277;	1052;	673;	856;	302;	736;	633;	783;	1041;
Phytomyza sp.					1;							2;
Agromyzid sp.												
Ph. terrae-novae										1;		
Scath. furcata	1;		1;		50;		2;		1;	3;		3;
S. litorea			1;									
Pegomya sp.									4;			
Botan. betarum			1;		7;							
B. ?profuga	3;		1;			1;	1;		3;	2;		
Fucellia sp.		1;				1;				1;		
Zaphne sp.											1;	
Delia fabricii		3;	6;					2;	1;	2;	2;	
D. ?platura	1;			1;								
Spil. cf. surda												
S. sp(b)												
Meloph. ovinus(*)	3;		2;			1;				1;		
Totals/sample	40;	15;	341;	1;	61;	34;	3;	10;	12;	64;	5;	24;

(* also 1 in Au 1, 1258. NB. Records of this species mainly from J.Sadler in this report

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Table 34b Sandnes Felt I(Au V-VI)					Au V				Au VI	Au ?	MNI	Sam
Taxon	369;	350;	591;	373;	372;	540;	399;	374;	367;	029;	1287;		
Simulium sp.			2;									37;	3
?Bradysia sp.												1;	1
?Forcipomyia sp.												3;	1
Megaselia sp.	1;											1;	1
Heleomyza spp.	6;	24;	25;	15;	5;	4;	13;	7;	15;	16;	34;	598;	21

Table 34b (contd.)	Au V									Au VI	Au?	MNI	Sam
Taxon	369;	350;	591;	373;	372;	540;	399;	374;	367;	029;	1287;		
Neol. prominens					1;				1;			2;	2
?Copromyza sp.												1;	1
Tel. flavipes	2;	3;	4;		2;	33;			1;	1;		52;	11
Allopio. vulgaris			?1;								2;	4;	3
Phil. vittipennis							1;					1;	1
Scat. ?stagnalis				18;	33;	1;	1;				1;	64;	8
Scat. ?cribrata	12;	9;	25;	3;		45;					1;	96;	7
Th. quadrisetosa											1;	1;	1
Phytomyza sp.												3;	2
Agromyzid sp.			1;			1;						2;	2
Ph. terrae-novae												1;	1
Scath. furcata	1;	2;	1;	1;		20;	1;				10;	97;	14
S. litorea												1;	1
Pegomya sp.						3;						7;	2
Botan. betarum			12;			2;						22;	4
B. ?profuga	1;	1;		1;	2;	1;				1;	2;	20;	13
Fucellia sp.				1;			1;			2;		7;	6
?Lasiomma sp.			1;								1;	2;	2
Zaphne sp.				1;								2;	2
Delia fabricii	3;	1;	5;	5;	4;	11;		1;		1;	15;	62;	15
D. ?platura						1;					8;	11;	4
Spil. cf. surda		1;					1;					2;	2
S. sp. (b)						2;	2;					4;	2
Mel. ovinus(*)												7;	4
Total MNI	26;	41;	77;	45;	47;	124;	20;	8;	17;	21;	74;	1112;	

Table 34c Sandnes	Felt II				Felt III			Felt V	MNI	Sam
Taxon	044;	877;	1046;	1238;	500;	236;	237/240;	510/298;		
Tipula arctica							1;		1;	1
Oryg. luctuosum								1;	1;	1
Heleomyza spp.	6;	12;	134;	569;	12;	11;	9;		753;	7
Tel. flavipes							8;		8;	1
Allo. vulgaris			1;						1;	1
Scat. ?stagnalis	1;		1;			3;	5;		10;	4
Call. uralensis				3;					3;	1
Scath. furcata			6;		2;	1;			9;	3
S. litorea			3;						3;	1
Botan. betarum							1;		1;	1
B. ?profuga					2;		4;		6;	2
Zaphne sp.			1;						1;	1
Delia fabricii				1;	2;		5;		8;	3
D. ?platura				1;					1;	1
Mel. ovinus(*)			1;						1;	1
Total MNI/sample	7;	12;	147;	574;	18;	15;	33;	1;		
Total MNI/Felt				740;			66;	1;	807	

Table 34d Sandnes	Felt VI							Felt VII		MNI	Sam
Taxon	989;	991;	992;	995;	998;	44SP;	45SP;	984;	985;		
Simulium sp.		1;		11;				2;	1;	15;	4
Orygma luctuosum						1;				1;	1
Heleomyza spp.	4;	1;			1;		5;			11;	4
Philygra sp.		1;								1;	1
Scath. furcata	3;						5;			8;	2

Table 34d (contd) Sandnes

Taxon	Felt VI 989;	991;	992;	995;	998;	44SP;	45SP;	Felt VII 984;	985;	MNI	Sam
Botan. betarum		1;								1;	1
Botan. ?profuga		3;	1;				2;			6;	3
Delia fabricii	3;	5;		1;	6;	1;	7;			23;	6
Ph. pallidisquama		1;								1;	1
Total MNI/sample	10;	13;	1;	12;	7;	2;	19;	2;	1;		
Total MNI/Felt							64;		3;	67	

Table 35 Complete List of Sandnes Diptera

Taxon	T;	Felt 1;	Felt 2;	Felt 3;	Felt 5;	Felt 6;	Felt 7;	MNI	Sam
Tip. arctica	h			1(1);				1;	1
?Forcipomyia	-	3(1);						3;	1
Simulium	g	37(3);				12(2);	3(2);	52;	7
?Bradysia	-	1(1);						1;	1
Megaselia	-	1(1);						1;	1
O. luctuosum	f				1(1);	1(1);		2;	2
Heleomyza	b	598(21);	721(4);	32(3);		11(4);		1362;	32
N. prominens	b	2(2);						2;	2
?*Copromyza*	-	1(1)						1;	1
T. flavipes	b	52(11);		8(1);				60;	12
A. vulgaris	c	5(3);	1(1);					6;	4
P. vittipennis	e	1(1);				1(1);		2;	2
S. stagnalis	e	64(8);	2(2);	8(2);				74;	12
S. cribrata	e	96(7);						96;	7
T. quadriset.	e	1(1);						1;	1
Agromyzid	d	2(2);						2;	2

Table 35 (contd.)

Taxon	T6;	Felt 1;	Felt 2;	Felt 3;	Felt 5;	Felt 6;	Felt 7;	MNI	Sam
Phytomyza	d	3(2);						3;	2
C. uralensis	c		3(1);					3;	1
P. terrae-nov.	c	1(1);						1;	1
S. furcata	a	97(14);	6(1);	3(2);		8(2);		114;	19
S. litorea	f	1(1);	3(1)					4;	2
Pegomya	d	7(2);						7;	2
B. betarum	d	22(4);		1(1);		1(1);		24;	6
B. profuga	d	20(13);		6(2);		6(3);		32;	18
Fucellia	f	7(6);						7;	6
?Lasiomma	d	2(2)						2;	2
Zaphne	e	2(2);	1(1);					3;	3
D. fabricii	d	62(15);	1(1);	7(2);		23(6);		93;	24
D. ?platura	d	11(4);	1(1);					12;	5
Spilogona a	e	2(2);						2;	2
Spilogona b	e	4(2);						4;	2
P. pallidisq.	h					1(1);		1;	1
Melophagus	i	7(4);	1(1);					8;	5
Total taxa 33		29	10	8	1	9	1		
Total MNI=		1112	740	66	1	65	3	1986	

NB. End column (Sam) gives number of samples in which taxon occurred. Felt 7 was a natural succession away from the farm site.

42 TUMERALIK (V.35) (Analysis on page 422)

Introduction This site is discussed in detail by Roussell (1941), and more recently by Christensen (1991). Table 36a lists the Dipterous taxa recovered from the four midden samples passed to me.

Table 36a Diptera of Tumeralik (V35)

Taxon	TG	a;	b;	c.	d;	MNI	Taxon	TG	a;	b;	c;	d;	MNI
Simulium sp.	g	-	2	3	-	5	*Botanophila* sp.	d	1			1	2
Neoleria prominens	b	-	-	-	1	1	*Fucellia* sp.	f				31	31
*Heleomyza sp**	b	752	231	32	7	1022	*Delia fabricii*	d		1			1
Telomerina flavipes	b	32	2	1	1	36							
Scatella ?stagnalis	e	-	-	-	1	1	Total taxa 9						
Scathophaga furcata	a	10	6	-	2	18		Total MNI=	795	242	36	44	1117

Key to samples *a* 35cm(1); *b* 35cm(2); *c* 45cm; *d* 135cm. * One *Heleomyza* puparium from 45cm sample was much larger than others and could belong to *H. serrata*; remaining specimens probably all *borealis*.

Table 36b Percentage Representation of Dipterous Trophic groups at Tumeralik

Samples;	Trophic Groups									MNI
	a	b	c	d	e	f	g	h	i	
35cm(1)	1	99								795
35cm(2)	2	96.8		0.4			0.8			242
45cm	3	89					8.0			36
TPI	4.5	20		2	2	72				44
								Total spp.		1117

Interpretation A very restricted fauna with *Heleomyza* and *Telomerina* constituting 95 per cent of the total Dipterous MNI of 1117 specimens.

As stated above, these species indicate an indoor assemblage when found in the complete absence of exophilic necrophages.

Of the remaining taxa, *Scathophaga furcata* probably infers sheep or cow-dung, and adult *Simulium* testify to the proximity of running water; adult female black-flies suck blood of mammals. *Delia fabricii* was represented by a single puparium, perhaps inferring a scarcity of *Poa pratensis* at the sampling site, although taphonomic considerations are not possible in the absence of detailed archaeological information.

The results from the study of these subfossil Diptera suggest a typical Norse medieval living room with copious human faeces, food scraps of animal origin, herbivore dung and perhaps some turf, used collectively for fuel. The human and animal occupants were evidently pestered by the attentions of black-flies breeding in adjacent streams, and it is interesting to note that T. McGovern (pers. comm.) remarked on the collossal populations of these flies still around Tumeralik especially which still bedevil human activity. Sample TP1 is unique amongst the Norse farms examined in this study in containing 70 per cent of *Fucellia*, inferring this deposit was mainly seaweed. This is very curious since, of the Western Settlement Norse farms studied here, this is the most remote from the shore (see map on page 238).

43 Farm site east of Tumeralik (V.36)

Interpretation. This site produced a single adult *Simulium* thorax.

6 THE ZOOGEOGRAPHY OF THE MUSCIDAE OF GREENLAND AND THE NORTH ATLANTIC

Introduction The North Atlantic area has traditionally been one of the most active regions in the world in terms of Dipterological research since such pioneers as Fabricius, Staeger and Holmgren first examined the fauna of their native Scandinavia, north to Spitsbergen and west to Greenland. Many workers of international calibre have followed their lead and a vast body of data has been assembled on species inhabiting this huge area. In view of this, it is perhaps surprising that no major North Atlantic review of any large Dipterous family has been produced. The present interest in the post-glacial colonisation of some of the North Atlantic islands highlights the potential value of such a study and it was for this reason that this study was undertaken.

The North Atlantic region has suffered repeated extensive glaciations (Nilsson 1984), all of which created *tabula rasa* in the lands which the glaciers actually covered. What species were the pioneer colonists of the areas newly exposed by the receding ice-sheets? In the case of remote islands, from whence came the new colonists? The modern fauna of Greenland is pivotal in these discussions; was it really colonised by a largely Palaearctic fauna and flora as many would have us believe?

Using the Muscidae, one of the largest Dipterous families represented in the region, this study seeks to shed light on some of these questions. An evaluation of the modern Muscid fauna of subarctic, Low Arctic and High Arctic regions helps towards an understanding of climatic conditions across Britain and northern Europe at the height of the last glaciation and of West Greenland during the Norse occupation of the Western Settlement. Furthermore, current distribution patterns afford clues to probable routes of colonisation of the North Atlantic islands.

The area covered in this survey extends from the Atlantic Palaearctic seaboard (Canary islands to Spitsbergen) to the eastern Nearctic (Labrador and north-east Quebec to Ellesmere Island. In Appendix 3, Check lists of the Muscidae recorded from this area are provided, giving the islands and territories from which they have been recorded, and their zoogeographical type(ie. Holarctic, Nearctic or Palaearctic). (For a discussion on these Zoogeograpohical regions, see page 302).

After defining the Arctic region, this study lists 82 Muscid species which appear to be mainly resident within it; these are termed "Arctic species". In his survey of the Arctic Diptera, the 34 species of Muscidae included by de Meijere (1910) comprised all species which had been recorded from the Arctic. Many of these were synonyms and others were of patently non-Arctic species.

Clearly a study of this magnitude will always be premature in that species must remain undiscovered and the real distribution will never be understood, nor will it ever remain static. However it is evident that with all its imperfections the compilation provides some useful data.

The following main sections are included:-

1 The Muscidae of the North Atlantic Region

2 Arctic Muscidae

3 The Muscidae of Greenland

4 The Zoogeography of the Muscidae of Greenland

5 Conclusions

Check Lists of the Muscidae of the North Atlantic Islands east of Greenland, and of the Muscidae of the coastal areas of Labrador, north-eastern Quebec, the Canadian Arctic Archipelago and Greenland, appear in Appendix 3.

Throughout this section the nomenclature of Palaearctic species follows Pont (1986), and for the Nearctic species that of Huckett (1965). Classification however is in accordance with Skidmore (1985) and Carvalho (1989).

1 The Muscidae of the North Atlantic Region.

In terms of Muscid research, the North Atlantic area probably leads the world. Consequently it is perhaps best suited to zoogeographical analysis and to investigations into faunal origins. In Appendix Three, Tables 41 and 42 list all of the Muscidae recorded from the area covered by this work, whilst Table 37 below gives numerical data on various countries and island groups within the region, indicating the percentage of holarctic species present in each.

Downes (1988) noted that in Canada the proportion of Holarctic insects in the fauna increases with latitude. Table 37 below shows that in the Western Palaearctic the percentage of Holarctic muscids in the best-worked countries are:- Spain (25), France (26), Germany (28), British Isles (31), Netherlands (36), Denmark (35), Ireland (37), Sweden (39), Norway (48) and Iceland (63). These data show a very clear increase with latitude and wholly support Downes' assertion. They also however testify to a marked westerly increase which is most marked on

Table 37 Summary of the Muscidae of the North Atlantic Area

Region	Rec.Sp.(Gen)	Pal.	Hol.	Nea.	Arctic Species			% Hol.
					Pal.	Hol.	Nea.	
Morocco	72(23)	51	21	---	---	---	---	29%
Canaries	60(18)	42	18	---	---	---	---	30%
Madeira	34(18)	19	15	---	---	---	---	44%
Azores	27(15)	14	13	---	---	---	---	48%
Portugal	41(16)	27	14	---	---	---	---	34%
Spain	178(34)	133	45	---	---	---	---	25%
France	296(41)	220	76	---	---	---	---	26%
Germany	255(40)	183	72	---	---	---	---	28%
Belgium	97(31)	61	36	---	---	---	---	37%
Netherlands	163(38)	104	59	---	---	---	---	36%
Denmark	219(38)	144	75	---	---	---	---	35%
British Isles	275(40)	191	84	---	---	---	---	31%
Ireland	160(33)	102	58	---	---	---	---	37%
Scotland	213	131	82	---	---	---	---	39%
Orkney	47	27	20	---	---	---	---	42%
Shetland	30	16	14	---	---	---	---	47%
Sweden	340(37)	207	133	---	2	11	---	39%
Norway	257(36)	134	123	---	?	?	---	48%
Faroes	22(11)	8	14	---	---	---	---	64%
Iceland	26(13)	9	16	1*	---	2	---	63%
Jan Mayen	2(1)	---	2	---	---	1	---	100%
Spitzbergen	5(2)*	---	5	---	---	4	---	100%
Greenland	37(9)	---	26	10*	6	7	---	70%
N.& E.Canada	168(22)	---	82	86	15	14	---	49%

NB. * 1 North and East Canada is here defined as the area north of a line from Cartwright (Labrador) through Coral Harbour (Southampton Island) to the south coast of Victoria Island.

* 2 One of these, *Musca domestica*, is a casual import to the island and has no zoogeographical significance. The other four species all belong to the genus *Spilogona*.

* 3 The single purely Nearctic species *Hydrotaea cristata* known from Iceland was clearly the result of casual importation and has no zoogeographical significance.

* 4 Note the uncertainty regarding the *Limnophora* species recorded from Greenland(see p. 293)

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the more remote islands (eg. Azores (48), Madeira (44) and Iceland (63).

Situated at the extreme western edge of the Palaearctic, Iceland is of particular zoogeographical interest. With an Holarctic component of 63 per cent, it is only exceeded in this respect by Jan Mayen and Spitzbergen in the Western Palaearctic. This again entirely supports Downes' thesis when one compares the Icelandic figure with the equally remote islands of Madeira (44%), Azores (48%), Jan Mayen (100%) and Spitsbergen (100%).

The following section defines Arctic species as those occurring mainly or entirely within the Arctic as delimited by the 10° July Mean Isotherm. Being the only European country of which a major part lies north of this isotherm Iceland is again of particular interest. Contrary to popular belief this is reflected in its insect fauna since Iceland has the largest percentage of Arctic muscids of any European country. Neither the British Isles nor the Faroes possess any Arctic muscid elements as defined here, and even for Scandinavia the percentage of these is much lower than in Iceland. The percentage representation of Arctic species in various regions of the North

Atlantic is as follows:- Scotland (0%), North and West Scandinavia (3%), Iceland (7.5%), North and East Canada (24.5%), Greenland (37%), Jan Mayen (50%) and Spitzbergen (80%). (It should be noted that the 10 degree C. July Mean isotherm just cuts the northernmost promontary of Norway.)

The Icelandic fauna is most probably of Scandinavian rather than of British origin. Assuming rapid transport, colonisation by ice-rafting from southern Scandinavia to Iceland, as has been proposed by Buckland (1988), would appear feasible. Such a route would presumably pass between Faroes and Iceland, and not further south, and would have occurred as a result of the late spring thaw when most Diptera would have been in the pupal stage.

The British fauna originated from western Europe via the wide land bridge which was not submerged beneath the English Channel and southern North Sea until the early Holocene (Dennis 1977).

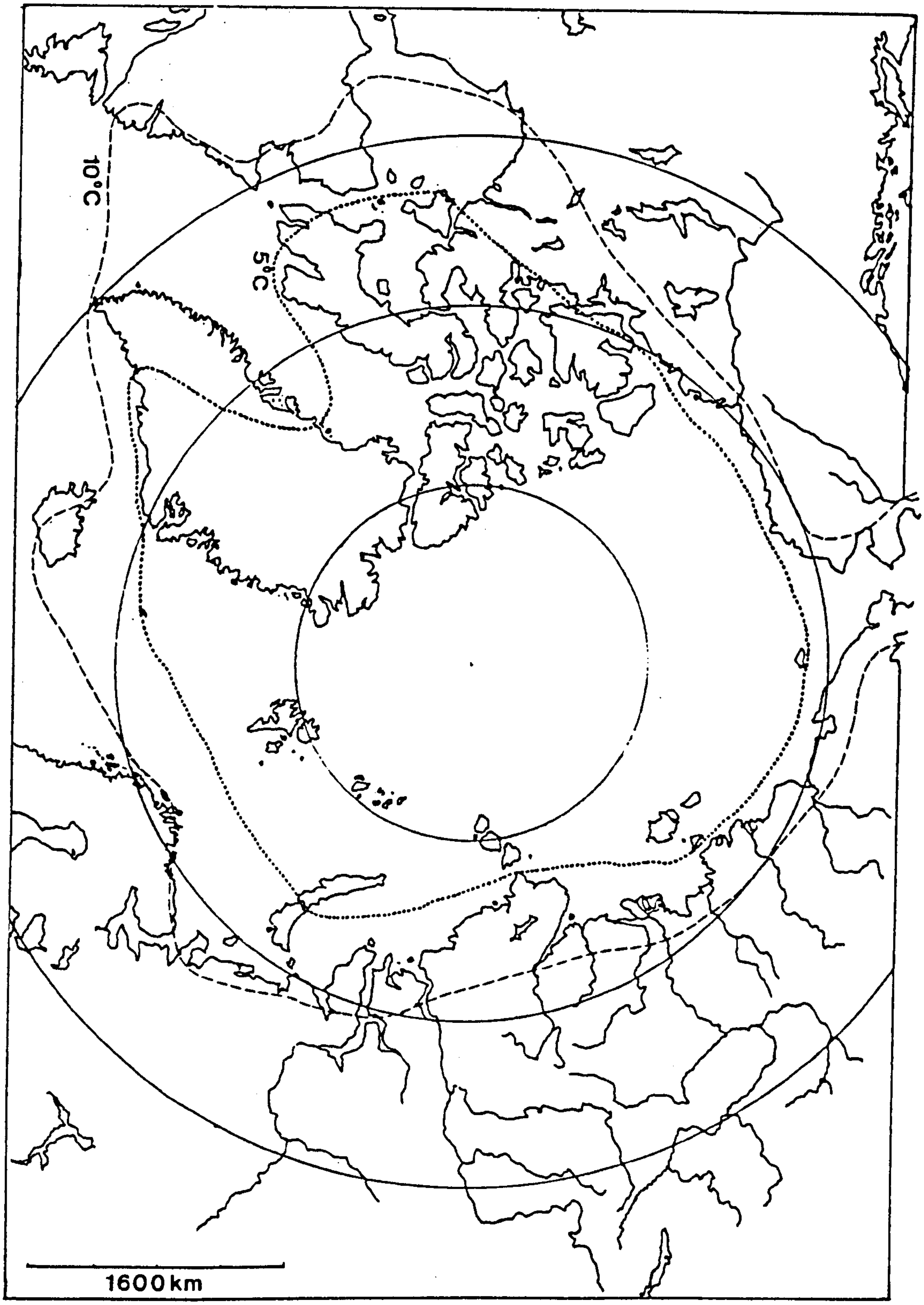
The question of the fauna of Greenland is covered in section three, but it is relevant to note here that no Nearctic Muscid has been recorded as a resident in Iceland. One truly Nearctic species, *Hydrotaea cristata* Malloch was recorded from Iceland by Messersmith (1982). This is very similar to the common *H. dentipes* which, though nearly ubiquitous in Iceland as elsewhere in its range, was surprisingly absent from his list. Like *H. dentipes*, *H. cristata* is a facultative synanthrope of the subgenus *Hydrotaeoides* with very similar habits and biology. There can be no doubt that it was casually transported to Iceland from North America, and its occurrence in Iceland has no zoogeographical significance. Another species, *Limnophora sinuata* Collin, originally described from Greenland, has been taken in Iceland and Faroes (Lyneborg 1968). This taxon however is the centre of much confusion and it is probable that it has a much wider range.

2 Arctic Muscidae

In considering the earliest colonisers of lands newly exposed by the receding ice-sheets in the North Atlantic area it is necessary to identify those species which are most resistant to the coldest conditions, and hence a list of Arctic species (pp. 288-291) has been prepared from Huckett (1965) for the Nearctic and from Hennig (1955-64) for the Palaearctic.

The problems of defining the Arctic region are amply discussed by Sage (1986) and I am following him here in accepting the southern limit of the Low Arctic as the 10°C July Mean Isotherm (at sea level). The High Arctic, as defined by Bliss (1977), comprises those areas with a July Mean below 5°C. at sea-level (see Map 4, page 283). Several authors (eg. Degerbøl (1939; Sage *(op. cit.)*, Downes 1964, Elias 1994, etc.) have discussed the particular problems of microclimates in Arctic regions, noting that temperatures often occur in dense cushions of vegetation which are greatly in excess of ambient values. Also, owing to the angle of incidence of the sun's rays the relationship between altitude and thermal values typical of lower latitudes no longer applies, enabling insects to live at higher altitudes than would otherwise be expected.

Degerbøl (1939) in his study of the Blosseville coast of East Greenland clearly demonstrated the changes occurring across the Low Arctic-High Arctic boundary in terms of climate, plant communities,



Map 4. Northern Hemisphere showing 5 and 10 degree C. July Mean Isotherms, forming boundaries of Low and High Arctic, and Low Arctic and Subarctic regions respectively.

etc. Subsequent work across the whole of northern Canada has made possible the production of detailed vegetational maps (Bliss (1977), etc.) which, along with climatic ones enable these disparate regions to be delineated. Allowing for special problems of microclimate alluded to above, the High Arctic has generally lower average temperatures and lower precipitation than the Low Arctic. Polar deserts typify the High Arctic, and these areas, suffering extreme cold and dessication, exacerbated by almost perpetual high winds, over long periods of time, are inimical to all but the hardiest of organisms. Areas of remarkable biotic richness do however occur, such as around Lake Hazen and other parts of northern Ellesmere Island (Chung 1989). The Low Arctic enjoys generally more benign conditions reflected in richer flora and fauna, but typically heavier precipitation and extreme fluctuations in temperature.

Stark biological changes mark the southern margins of the Low Arctic where open tundra characteristically replaces the subarctic forest scrub areas. Whilst some 25 genera of muscids just about reach the Low Arctic frontier from the lower latitudes, only perhaps a third extend far beyond it. Four of these reach the High Arctic but only *Drymeia* and *Spilogona* are widespread throughout the ice-free areas there.

Amongst the unexplained casualties on the doorstep of the Low Arctic is virtually the entire coprophilous fauna associated with the dung of Ungulates. In highboreal and subarctic regions, species which further south favour cow-dung apparently switch their attentions to reindeer, yet they do not follow these animals far into the Arctic proper and in the High Arctic the niche is entirely unoccupied

(R. Godfrey, *pers. comm.*). Downes (1964) noted however that the entire Arctic area is characterised by an abundance of unoccupied microhabitats.

The Arctic then is a region of spectacularly diminished faunas when compared with the very rich subarctic regions bordering them.

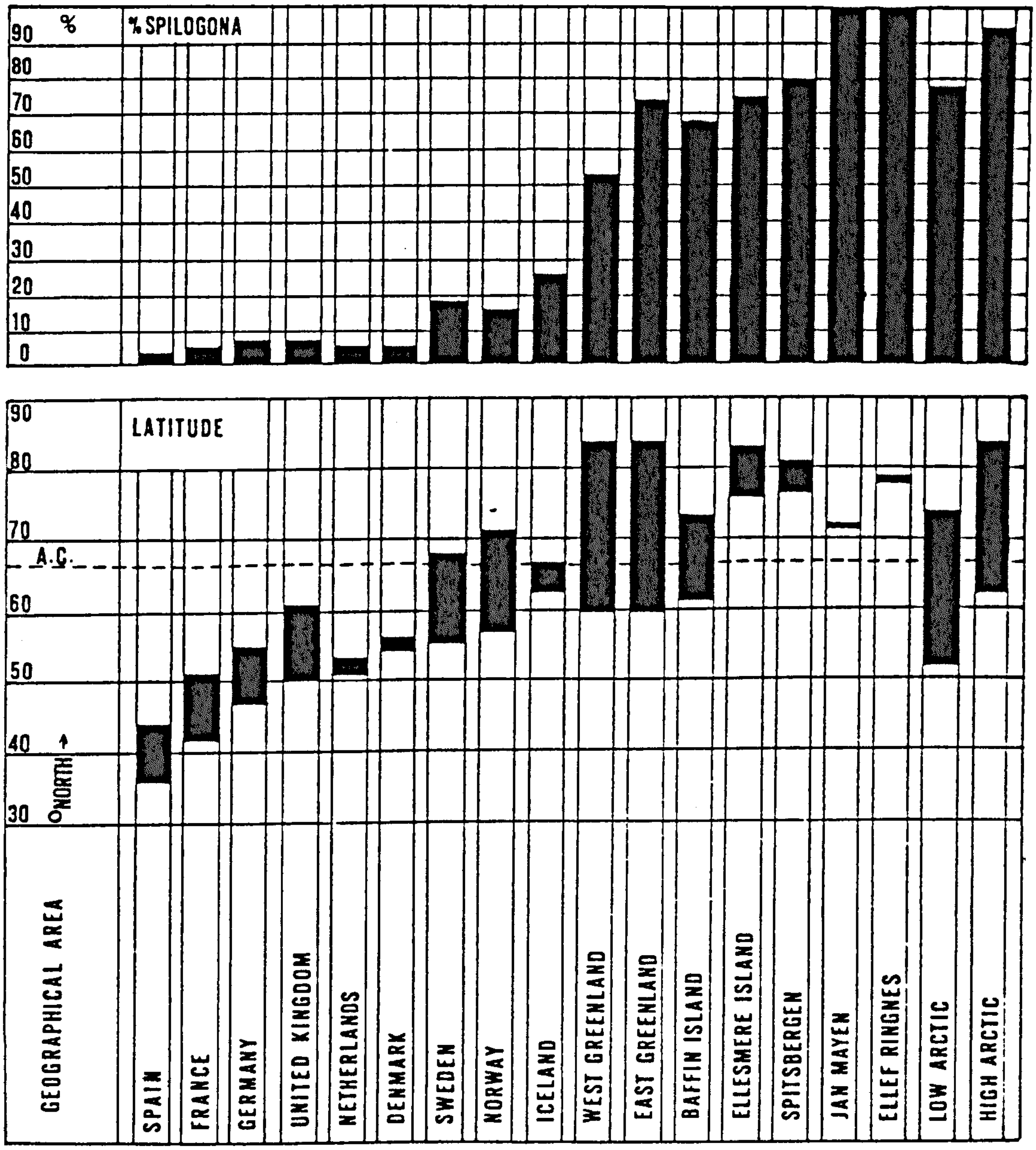
In this work, an Arctic species is defined as one whose distributional range lies mainly or entirely within the Arctic region. Those occurring also in alpine regions are not included. Many species found in both the Nearctic and Palaearctic regions have distributional ranges which reach the Low Arctic but appear not to extend into the High Arctic. Such species include *Mesembrina mystacea* and *meridiana*, *Neomyia cornicina*, *Eudasyphora cyanicolor*, *Morellia hortorum*, *Spilogona alpica*, *contractifrons*, *novaemaculata*, *obscuripennis*, *septemnotata*, *sjöstedti* and many others. Their main distribution areas however are outside the Arctic region proper so they are not here regarded as belonging to the true Arctic fauna. Probably many of the species listed below whose ranges closely follow the southern edge of the Low Arctic are also primarily subarctic in distribution.

By far the greatest land-mass within the Arctic is situated in the Nearctic and this is reflected in the global Arctic Muscid fauna. In the following list 82 species, belonging to 7 genera, are regarded as Arctic species. Of these 52 are only known from the Nearctic, 21 are Holarctic and only 9 are purely Palaearctic. Precisely half are known only from sites in the Low Arctic, the remainder reaching the High Arctic; four of these are only known from the High Arctic.

Text-figure 18 shows how, with increasing latitude, the relative importance of the Muscid genus *Spilogona* also grows, so that in the most barren lands of the High Arctic such as Ellef Ringnes and Jan Mayen, it is the only Muscid genus represented. Hennig (1964) observed that the vast majority of *Spilogona* species occur in the montane and boreal areas of the Nearctic and the Palaearctic regions. In the Neotropical region, on the other hand, the genus accounts for only one per cent of the total recorded Muscid fauna of 745 species (Pont 1972). Similarly in the Afrotropical region of the 870 described Muscid species, only two per cent belong to *Spilogona*. As far as is known (Skidmore 1985) all *Spilogona* larvae are obligative carnivores which prey on other small soft-bodied invertebrates. It is known that in warmer regions some such larvae can survive without feeding for months, and in Arctic areas *Spilogona* probably overwinter more than once. There is some evidence to suggest that the adults of some *Spilogona* may also be partially predatory (Skidmore *op. cit.*).

Unquestionably the major work covering the Muscidae of Arctic regions is that of Huckett (1965). In this huge compilation he includes 339 species belonging to this family from northern Canada, Alaska and Greenland, and provides copious records. A comparable work covering the Palaearctic Region has not been attempted but would doubtless result in the discovery of new species. Of the species included in Huckett no less than 168 (49.5 %) reach the Arctic Region as here defined.

The following abbreviations appear in the List of Arctic Muscidae (Table 42):- H, Holarctic species; N, Nearctic species; P, Palaearctic species. (*), species ranging from Low to High Arctic; *, species known only from High Arctic, (), species only in Low Arctic.



Text-Figure 18. The relationship between increasing latitude and the importance of the Genus *Spilogona* (Muscidae), shown as the percentage of the total Muscid fauna of various geographical areas. Thus, whilst only four per cent of the Muscid species in Spain belong to *Spilogona*, this is the only Genus known from Jan Mayen and Ellef Ringnes islands.

List of Arctic Muscidae

Azeliinae		
Drymeia cantabrigiensis	N ()	[Cambridge Bay (Victoria Island only)]
D. firthiana	N ()	[Firth River]
D. groenlandica	N (*)	[Herschel Isl-Sugluk-Holsteinborg-Lake Hazen; Greenland]
D. neoborealis	N (*)	[Pribiloffs-Chesterfield-Eureka]
D. pribiloffensis	N (*)	[Pribiloffs-Port Harrison-Mould Bay-Frobisher Bay]
D. segnis	H (*)	[N; Pribiloffs-Churchill-Payne Bay-Lake Hazen; Greenland], [P; Novaya Zemlya]
D. setibasis	N (*)	[Herschel Isl-Eskimo Point-Clyde Inlet]
Bebryx chillcotti	N ()	[Pribiloffs-Kidluit Bay-Chesterfield]
Mydaeinae		
Mydaea laevis	N ()	[Kidluit- Chesterfield]
Coenosiinae		
Spilogona aestuarium	N ()	[Nome; Reindeer Depot-Coral Harbour-Nutak]
S. albinepennis	N (*)	[Cambridge Bay-Spence Bay-Sugluk]
S. albisquama	H ()	[N; Rampart House-Churchill-Cartwright], [P; Lapland]
S. almquisti	H (*)	[N; Chesterfield-Clyde-Mould Bay-Alert; Greenland], [P; Taimyr-Chukchen Pen.-Novaya Zemlya-Wrangel Isl]
S. arcticola	N (*)	[Cambridge Bay-Coral Harb.-Clyde Inl.]
S. atrisquamula	N ()	[Reindeer Depot-Churchill]
S. barrowensis	N ()	[Point Barrow]
S. bathurstiana	N ()	[Teller-Kotzebue-Muskox Lake-Churchill]
S. bifimbriata	N ()	[Naknek; Firth River-Geillini Lake-Fort Chimo]
S. ciliatocosta	P ()	[Karskaya tundra]
S. coactilis	H ()	[Herschell Isl.]
S. confluens	N ()	[Reindeer Depot]

S. consortis	N () [Sawmill-Padlei]
S. contigua	N (*) [Point Barrow-Salmita Mines-Sugluk-Spence Bay-Coral Harbour
S. cordyluraeformis	P () [Karskaya tundra]
S. deflorata	N (*) [S. Alaska-Nutak-Lake Hazen; Greenland]
S. denudata	H (*) [N; Nome & Pt. Barrow-Port Harrison-Lake Hazen; Greenland], [P; Spitzbergen-Dikson/Yenesei]
S. dorsata	H (*) [N; Pt. Barrow-Geillini Lake-Indian House Lake- Lake Hazen; Greenland], [P; Jämtland-Spitzbergen- Taimyr]
S. dorsestriata	N () [Pt. Barrow]
S. empeliogaster	N () [Port Harrison-Indian House Lake-Nutak]
S. extensa	N (*) [Nem; Cambridge Bay-Clyde-Alert; Greenland]
S. fatima	N () [Salmita Mine-Churchill]
S. fimbriata	H (*) [N; Pt. Barrow], [P; Karskaya tundra-Kolyma]
S. firmididorsata	N () [Eskimo Point]
S. flavicornis	N () [Naknek-Reindeer Point]
S. humeralis	N (*) [Dawson-Firth River-Geillini Lake-Clyde]
S. hurdiana	N () [Point Barrow]
S. infuscata	N () [Bathurst Inlet-Churchill]
S. megastoma	H (*) [N; Pt. Barrow-Fort Chimo-Clyde; Greenland], [P; Iceland; Jan Mayen; Härjedalen-Spitzbergen- Taimyr]
S. melanosoma	N (*) [Anchorage-Pt. Barrow-Indian Hse. Lake-Eureka; Greenland]
S. minicalyptrata	N * [Clyde Inlet, Baffin Isl. only]
S. monacantha	N (*) [Watson Lake, S. Yukon-Bathurst Inlet-Indian House Lake-Eureka; Greenland]
S. mydaeiniformis	N (*) [Naknek; Firth River-Churchill-Spence Bay]
S. neglecta	N () [Naknek-Nome]
S. nitidicauda(=imitatrix)	H(*) [N; Bering Isl-Cartwright-Frobisher Bay], [P; Karskaya tundra]

S. nordenskjöldi	P (*) [Novaya Zemlya-Vajgach Isl.-Taimyr]
S. novaesiberae	P * [Kotelnyy Isl.(New Siberian Isl.)]
S. nutaka	N () [Padlei-Nutak-Hebron]
S. obscura	N (*) [Pt.Barrow-Churchill-Clyde]
S. obsoleta (=*hirticauda*)	H (*) [N; west coast of Alaska & Pt.Barrow-Port Harrison- Ellef Ringnes-Alert; Greenland],[P; West Taimyr-New Siberian Isl.]
S. opaca	H (*) [N; Savonoski-Mt.McKinley area-Umiat-Hebron-Clyde; Greenland]. [P; Iceland; Jämtland-Lapland-"Arctic Urals"(probably Kara)]
S. padlei	N () [Padlei]
S. princeps	N () [Umiat-Coral Harbour]
S. projecta	N (*) [Herschel Island-Chesterfield-Clyde]
S. pseudodispar	H (*) [N; Northern British Columbia-Dawson-Port Harrison-Clyde] [P; Lapland-Kola-Lena estuary]
S. pulvicrura	N () [Savonoski; Baker Lake-Fort Chimo]
S. robusta	N (*) [Pt.Barrow-Chesterfield-Clyde]
S. rostrata	N () [Fort Chimo-Hebron]
S. quinquelineata	H (*) [N; Naknek-Nome; Churchill-Gt.Whale River]. [P; Lapland-Spitsbergen-Latvia]
S. quinquesetosa	P () [Karskaya tundra-Taimyr]
S. sanctipauli	H (*) [N; Pribilloffs & Pt.Barrow-Payne Bay-Ellef Ringnes-Alert; Greenland]. [P; Taimyr-Wrangel and Kolyushin Islands.]
S. separata	N () [Bathurst Inlet]
S. seticaudalis	N () [Firth River]
S. seticosta	P () [Karskaya tundra]
S. sordidipennis	P * [Novaya Zemlya, Wrangel Isl.]
S. sospita	H (*) [N; Naknek-Barrow-Baker Lake]. [P; Chukchen pena., Kolyushin Island]
S. subnotata	N () [Nome-Kotzebue; Firth River-Bathurst Inlet]

S. tornensis	H (*) [N; W.coast Alaska & Firth River-Indian House Lake-Lake Hazen; Greenland]. [P; Lapland]
S. tundrae	H (*) [N; Nome & Pt.Barrow-Hebron-Clyde; Greenland].[P; Lapland-Taimyr-Kolyma-Wrangel Island]
S. tundrica	P () [Lapland-Kara-Kolyma estuary]
S. turbidipennis	N (*) [Naknek & Firth River-Port Harrison-Clyde]
S. wrangeli	P * [Wrangel Isl.]
S. zaitzevi (=*latilamina*)	H (*) [N; Nome-Point Barrow-Port Harrison-Nutak-Lake Hazen; Greenland].[P; Karskaya tundra-Taimyr-Ust Chaun]
Coenosia elegans	N () [Naknek-Nome-Kidluit Bay]
C. nigrifemorata	N () [Kotzebue-Point Barrow-Kidluit Bay]
Phaoniinae	
Helina longicornis	H () [N; Firth River-Churchill]. [P; Lapland]
Lophosceles hians	H () [N; Naknek-Kotzebue]. [P; Lapland]
L. minima	N (*) [Pribiloffs-Nome; Bathurst Inlet-Indian House Lake-Clyde]
Phaonia bidentata	N (*) [Chesterfield-Nain-Clyde; Greenland(HA)]
P. fausta	N () [Chesterfield]
P. imitatrix	N () [Firth River-Bernard Harbour]
P. pallidisquama	H (*) [N; Sugluk-Port Burwell-Frobisher Bay; Greenland(-HA)]. [P; Harjedalen-N.Norway]
P. tenebriana	N () [Firth River-Reindeer Depot]

NB. All of the above taxa, with authors, will be found in the lists in Appendix 3.

3 The Muscidae of Greenland

It is now over 200 years since the first Muscids were recorded from Greenland by Fabricius (1780) and collections from numerous expeditions to various parts of the island have resulted in the discovery of a relatively rich Muscid fauna. The most recent modern list was produced by Henricksen (1939), but the Muscidae was revised and supplemented by Huckett (1965).

The species list below gives distributional details for the 37 species of Muscidae currently known from Greenland. The European data is mainly from Hennig (1955-64) often quoting Ringdahl (1954-59). For North America the records from Huckett (1965) have been related to the distributional patterns given by Glen (1956). Where available, ecological and biological data for the species discussed has been included, although most of this is not from Greenland. Pont (1971) provides some useful ecological information on species taken by him in the Lake Tarraure region of Lule Lappmark (Sweden)

In this study, the whole of Greenland, since it lies north of the 10° July mean isotherm, is regarded as being within the Arctic. In accordance with Bliss (1977), the southern edge of the High Arctic bisects Greenland along a line running roughly diagonally from Tasiussaq north of Upernavik in the west (c. 73°50') to Kangerdlugssuaq (c. 68°) in the east.

In reviewing the Muscid fauna of Greenland it became evident that the family provides a valuable group to test Downes (1988) claim that the Greenlandic fauna is Nearctic rather than Palaearctic. The Muscidae is one of the largest insect families found in Greenland, the species are relatively well-known on a regional scale, and their members are amongst the most conspicuous Diptera occurring in high latitudes. Being mainly floricolous in adult habit, they are commonly found in quantities pollinating the flowers and are therefore conspicuous to non-entomological observers. The biology of some members of the genera reaching the High Arctic is known in outline, and something is known of even certain of the species concerned (Skidmore 1985). In other groups, Downes (1988) noted an increase in the relative proportion of hygrophilous species with increasing latitude, and this also applies in the Muscidae.

A discussion on the zoogeographical implications of the Muscid fauna of Greenland follows the systematic list. In this section the species are divided into the Arctic and non-Arctic species.

In the taxonomic list below, High Arctic sites are presented in bold type. Abbreviations are as follows:- S- Subarctic; LA- Low Arctic; HA- High Arctic. For North America the following categories from Glen (1956) are used:- A1- Broad low-arctic, A2- Western low-arctic, A3- Comprehensive arctic, CO3- Boreal and western, NW3 Alask-northwest Canada, SA1- General sub-arctic. It has been necessary to erect a further two categories not indicated by Glen, namely A3e- Eastern low-high arctic, A6- Eastern low-arctic. Palaearctic distributional types from Ringdahl are:- a- Arctic, alp- alpine, b- boreal, blp- boreoalpine, hb- highboreal, sa- subarctic. A very few species are coded Aa- Asia arctica, Ra- Regio arctica (Hennig, 1955-64)

Muscidae

Azeliinae

Hydrotaea anxia (Zett.) (=*bispinosa* Zett.) WG.61°13'-70°02'; EG.---- ----. [Nea; (A1)., Anchorage-Churchill-Indian Hse.Lake,n.-Reindeer Depot-Baker Lake-Coral Harbour-Hebron; Greenland LA] S-LA. [Pal; (hb-a). Härjedalen- north coast Norway-Mongolia-E.Siberia] S-LA. Subarctic to Low Arctic species. Biology; habits similar to *H. dentipes* and probably, like that species an eurytopic scavenger in larval state. Males seen swarming in hot sun on edge of dense birch scrub at Narssassuaq airfield on 12 July 1963 (Skidmore 1985); periodicity of adults at Fort Churchill (Webb & Graham, 1954 *Journ. econ. Ent.* 49; 495- 600). Puparial morphology very like *H.(Hydrotaeoides) dentipes* (F.), suggesting that the larva of *anxia* is also a facultative eurytopic carnivore; adult habits also very like *dentipes*, being unattracted to human perspiration, unlike many members of this genus (Skidmore 1985)

H.diabola (Harris) (=*bimaculata* Meigen) WG.--------. EG. *sine locus, Staeger*. [Nea; (NW3). Naknek-Nome-McKinley-Reindeer Depot] S-LA. [Pal. S.France-Rumania-Lapland-St.Petersburg-China-E.Siberia] Med-S. According to Lundbeck (1910) and Nielsen (1939) this early record quoted in Vanhöffen (1897 *Grönland Expedition, 1891-93*) was to be regarded as erroneous. Had it been correct however it could only have been a casual in Greenland where the single site was almost certainly in the High Arctic. It does however reach the Low Arctic in North America. Biology; see Skidmore (*op.cit.*)

Drymeia groenlandica (Lundbeck) WG.66°56'- 77°50'; EG.--------. [Nea; (A3). Herschel Isl.-Sugluk-Lake Hazen; Greenland L-HA] L-HA. Described from Greenland (*t.t.* Holsteinborg. *Lundbeck, 1910*), this is a nearctic Low to High Arctic species. Puparial morphology (Skidmore *op.cit.*)

D.segnis (Holmgren) WG.69°50'; EG.70°27'- 74°15'.[Nea; (A3). Pribiloffs. Firth River-Churchill-Payne Bay-Lake Hazen; Greenland L-HA] L-HA. [Pal; (Ra). Novaya Zemlya-W.Siberia] HA. Circumpolar species of Low to High Arctic. Biology; adults visit flowers of *Dryas integrifolius* (McAlpine 1965); puparial morphology (Skidmore,1985)

Muscinae

Musca domestica Linnaeus WG. Ivigtut; EG.--------. Cosmopolitan species transported through commerce throughout all regions including High Arctic but wholly eusynanthropic in higher latitudes. Casual import in Greenland. Biology (Skidmore 1985)

Mydaeinae

Graphomya maculata (Scopoli) WG.67°-68°10'; EG.--------. [Nea, widespread north to 10°July isotherm; Greenland LA] -LA. [Pal, widespread north to 10°July isotherm] -LA. Cosmopolitan species just extending into Low Arctic. NB. The Greenlandic records include *v.minor* Robineau-Desvoidy Biology; the larvae are obligative predators on the "rat-tailed maggots"of drone-flies; in Greenland evidently on the two *Helophilus* species. Carpenter, Hale & Roman (1938) found a female v. *minor* "on dung"; a most unusual attractant for this essentially floricolous fly. Further details of biology and morphology of immature stages in Skidmore 1985). *G.minor* is treated as a distinct species by many authors, including Pont (1986), but the common occurrence of them both together, and especially their presence in Greenland, strongly infer they are conspecific.

Coenosiinae

Spilogona almquistii (Holmgren) WG.70°25'-77°40'; EG.68°30'-74°25'. [Nea; (A3e). Baker Lake-Chesterfield-Mould Bay-Alert; Greenland L-HA] L-HA. [Pal; (a). Torneträsk mts.(Lapland)-Chukchen Pena.-Novaya Zemlya-Wrangel Isl.] L-HA. Circumpolar Low to High Arctic species. According to Collin (in Hennig, lc.) the Lapland specimens (v. *rostrata* Ringdahl) are not as dark as the Greenlandic ones.

S.alpica (Zetterstedt) WG.70°40'; EG.--------. [Nea; (A6). Port Harrison-Gt.Caribou Island-Fort Chimo; Greenland LA] S-LA [Pal. Alps; Scotland; Iceland; Jan Mayen; Jämtland-Kuusamo] Alps, S-HA. Holarctic boreoalpine to Low Arctic (reaching High Arctic on Jan Mayen). Pont (1971) found this only above the tree-line (700m) near L.Tarraure.

S.baltica (Ringdahl) WG.67°; EG.--------. [Nea;(A2). Matanuska- Nome-Chesterfield; Greenland LA] S-LA. [Pal. Dorset-Iceland-Rumania-C.Sweden-St.Petersburg]. Holarctic temperate to Low Arctic species. Biology; rather eurytopic in the British Isles. Pont (1971) took 2 on an island in L.Tarraure on 21 July 1962.

S.contractifrons (Zetterstedt) (=*arctica* Zett.) WG.60°-70°40; EG.66°17'. [Nea; (-SA1). S.Alaska-S.end Hudson Bay-Reindeer Depot-Padlei-Nagvak Fjord; Greenland LA] -LA. [Pal. Pyrenees-Iceland-Murmansk-Sverdlovsk-Kamchatka] [Ringdahl (1954-59) refers to *S.arctica* as a-s] Med-LA. Holarctic temperate to Low Arctic. The concensus view appears to be that *S.arctica* is merely a very dark, northern form of this common eurytopic holarctic species. Biology; the form *arctica* was found by Carpenter, Hale & Roman (1938) on willow scrub and seaweed on the shore at Utorquait, whilst Carpenter, Hale & Holm (1939) record it at an altitude of 3000 ft above sea level at Kangerdlugssuat. In Iceland Nielsen et al.(1954) found it reached the highest and coldest habitats. Pont (1971) found it in abundance from the birch forests and lakeside carrs to the 1700m summit of Mt.Antiluopta from 18 July to 10 August 1962. For further details and puparial morphology see (Skidmore lc.)

S.deflorata (Holmgren) WG.61°40'-77°50'. EG...... [Nea; (A3). Anchorage-S.Yukon-Churchill-Nutak-Firth River-Lake Hazen; Greenland L-HA] S-HA. Described from Greenland(*t. t.* "West Coast of Greenland"- *Holmgren 1872*) this is a Nearctic subarctic to High Arctic species.

S.denudata (Holmgren) WG.77°50'; EG.72°30-72°50'. [Nea; (A3). Nome-Pt.Barrow-Port Harrison-Lake Hazen; Greenland HA]. L-HA [Pal. Spitsbergen; Dikson area of Yenesei estuary] L-HA. Circumpolar Low to High Arctic species. Biology; found flying over dry tundra on 20 August (Collin 1923a).

S.dorsata (Zetterstedt) WG.64°25'-74°45'; EG.68°30'-74°15'. [Nea; (A3). Pt.Barrow-Geillini Bay-Nagvak Fjord-Mould Bay-Lake Hazen; Greenland L-HA] L-HA. [Pal; (a, Ra). Jämtland-Spitzbergen-Taimyr-Wrangel Isl.] L-HA. Circumpolar Low to High Arctic species. Biology; adults flying over dry tundra with ponds, over shingle of raised beach, marshy strips and rocky tundra by coast, on flowers of *Dryas octopetala, Silene acaulis* and *Saxifraga hirculus* from 19 July to 14 August on Spitsbergen (Collin 1923a); also over dry tundra at sea level, visiting flowers of *Silene acaulis* from 16 to 23 August on Spitsbergen (Collin 1923b). Pont (1971) took 2 females on delta sand-spit at L.Tarraure on 4 August 1962.

S. extensa (Malloch) WG.77°50'; EG.69°24'-73°35'. [Nea; (Ale). Cambridge Bay-Repulse Bay-Clyde-Alert; Greenland HA] HA. Described from Greenland (*t. t.* "West Coast of Greenland", *Malloch 1917*) this is a Nearctic Low to High Arctic species.

S. malaisei (Ringdahl) WG.61°-69°; EG.70°27'. [Nea; (C03). N.British Columbia; Rampart House-Firth River-Churchill-Hopedale-Frobisher Bay; Greenland L-HA] -HA. [Pal; (sa-a). Lapland] [a-sa] S. Holarctic subarctic to High Arctic species. Biology. Pont (1971) found this amongst sedge and *Salix* scrub on shore of L.Tarraure 4- 10 August 1962.

S. megastoma (Boheman) WG.--------; EG.69°24'-70°27'. [Nea; (A1). Pt.Barrow-Fort Chimo-Spence Bay-Clyde; Greenland HA] L-HA [Pal; (Ra). Iceland; Jan Mayen; Harjedalen mts.-Spitzbergen (Nordaustlandet)] S-HA. Circumpolar subarctic to High Arctic species. In mountains of northern Fennoscandia down to tree-line (Hennig lc.). In Iceland a member of the arctic barren ground and fell-field fauna found only in one area on north side of the Hofsjökull (Nielsen et al., lc.) Biology; found flying in sun over dry tundra near sea shore, 25 July-19 August on Spitsbergen (Collin 1923b) also on shingly raised beach on tundra visiting flowers of *Dryas octopetala, Silene acaulis* and *Cerastium alpinum* from 10 July to 14 August (Collin 1923a).

S. melanosoma Huckett WG.77°50'; EG.--------. [Nea; (A3). Anchorage -Pt.Barrow-Indian House Lake-Eureka; Greenland HA]. S-HA. Nearctic subarctic to High Arctic species. Biology; Skidmore (1985) describes the puparium from specimens collected at Hazen Camp (Ellesmere Island), by R.B.Madge on 13 July 1962(CNC).The external morphology is unusual for a *Spilogona* and suggests an adaptation to breeding in shallow water or mud.

S. micans (Ringdahl) WG.67°-77°50'; EG.--------. [Nea (A1). Savonoski-Churchill-Caribou Island-Firth River-Clyde; Greenland L-HA] S-HA. [Pal;(blp-sa). Alps; Iceland; Norway-Lapland] Alps- LA. Holarctic boreoalpine to High Arctic species. Lindroth et al.(1973) including this amongst the early arrivals on Surtsey, noted that it had only been found previously in northern Iceland. Biology; Lindroth et al.,(*op.cit.*) record it from sandy ground with *Salix* scrub and moist depressions with mire vegetation. Skidmore (1985) describes the puparium as of unspecialised form but evidently sabulicolous as sand particles were adhering to the cuticle; the specimen was collected by J.R.Vockeroth from a sandy beach by the Great Whale River (Quebec) on 16 July 1949 (CNC). Pont (1971) found this species on riverbank delta-spit by L.Tarraure amongst sedges and *Salix* scrub from 21 July-10 August 1962.

S.monacantha Collin WG.68°45'-70°40'; EG.74°20'. [Nea; (A3). S.Alaska-Churchill-Indian House Lake-Bathurst Inlet-Spence Bay- Lake Hazen; Greenland L-HA] S-HA. Described from Greenland(*t. t.* Umanáq, West Coast of Greenland. *Collin 1913*), this is a Nearctic subarctic to High Arctic species.

S.obsoleta (Malloch) (=*hirticauda* (Malloch)) WG. *sine locus*; EG.70°27'. [Nea; (A3). Pribiloffs; Pt. Barrow-Port Harrison-Mould Bay- Ellef Ringnes- Lake Hazen; Greenland HA] -HA. [Pal;(Aa). West Taimyr and New Siberian Islands]. L-HA. Described from "West Coast of Greenland". *Malloch 1917*). A circumpolar Low to High Arctic species. Biology; McAlpine (1965b) suggests this and *S.sanctipauli* may be the first Muscid colonisers of areas newly exposed by receding polar ice-sheets. This species favours marshy, low-lying areas where the adults visit flowers of *Papaver radicatum, Saxifraga oppositifolia, Saxifraga spp.,* and *Stellaria edwardsi.*

S.opaca Schnabl WG.64°45'-68°10'; EG....... [Nea;(A1). Savonoski-McKinley-Umiat-Hebron-Clyde; Greenland LA] S-HA. [Pal;(sa-a). Iceland; Jämtland-Lapland-W.Siberia] S-LA. Circumpolar subarctic to High Arctic species. Biology; Lindroth et al.(1973) say this occurs by streams, on *Salix* heaths and in mires and marshes. Ringdahl (1954-59) gives it as commonest above the treeline in Scandinavia.

S.sanctipauli (Malloch) WG.64°45'-78°30'; EG.69°24'-74°10'. [Nea; (A3). Pribiloffs-Pt.Barrow-Chesterfield-Payne Bay-Mould Bay-Ellef Ringnes-Lake Hazen; Greenland L-HA] L-HA. [Pal; (Ra). Norway-Taimyr-Kolyushin Isl-Wrangel Isl.] L-HA. Circumpolar Low to High Arctic species. McAlpine (1965b) found this on flowers of *Saxifraga caespitosa* and *S.flagellaris polysepala* in better drained areas on turfy talus slopes, thus complementing *S.obsoleta* in habitat preferences. He suggests that the two species are the Muscid pioneers in the High arctic.

S.semiglobosa (Ringdahl) WG.70°27'; EG.--------. [Nea; (A2). Valdez-Fort Chimo-Reindeer Depot-Spence

Bay; Greenland LA] S-LA. [Pal;(h). S.Sweden-Narvik-Lapland-W.Siberia] S-LA.Holarctic subarctic to Low Arctic species.

S. tornensis (Ringdahl) WG.--------; EG.70°27'-74°15'. [Nea; (A3). Savonoski-S.Yukon-Indian House Lake-Firth River-Spence Bay-Lake Hazen; Greenland HA] S-HA. [Pal;(sa-a). Lapland] S. Circumpolar subarctic to High Arctic species. Biology; not rare on stones above tree-line in Lapland (Ringdahl, 1954-59). Pont (1971) found 2 females on sedges on delta spit at Lale Tarraure on 4 and 10 August 1962.

S. trigonifera (Zetterstedt) WG.68°10'; EG.66°17'. [Nea; (SA1). S.Alaska-Cartwright-McKinley-Nagvak Fjord; Greenland LA]. S-LA. Described from Greenland (*t. t.* "Greenland", Zetterstedt 1838) this is a Nearctic subarctic to Low Arctic species

S. tundrae (Schnabl) WG.--------; EG.70°27'-73°35'. [Nea; (A3). Nome-Pt.Barrow-Hebron-Cambridge Bay-Lake Hazen; Greenland HA] L-HA. [Pal; (sa-a; Ra). Lapland-Taimyr-Kolyma-Wrangel Isl.] S-HA. Circumpolar subarctic to High Arctic species

S. zaitzevi Schnabl (=*latilamina* Collin) WG.--------; EG.68°30'-74°10'. [Nea; (A3). Nome-Point Barrow-Port Harrison-Nutak-Mould Bay-Lake Hazen; Greenland HA] L-HA. [Pal; (Asia arctica). Karskaya tundra-N.coast of Taimyr-Ust Chaun]. LA. Described by Collin (1930) under the synonym *latilamina* from Greenland (*t. t.* Hekla Havn, East Greenland) this is a circumpolar Low to High Arctic species

Limnophora groenlandica Malloch WG. "West coast of Greenland"; EG.--------. Only known from Greenland (*t. t.* West Coast of Greenland, Malloch 1920), and the diagnostic features are not given by Huckett (1965)

L. nigripes (Robineau-Desvoidy) WG. Sondre Strømfjord; EG.--------.[Nea. Widespread in U.S.A.- Firth River-Padlei-Fort Chimo] [-SA1]. -LA. [Pal. Mediterranean-Caucasus-Japan-N.Scotland-N.Lapland-Luga] -S. Holarctic warm temperate to low arctic. Biology; Skidmore (1985) describes the puparium and notes that, although nothing is known of the biology, it is certainly not essentially halophilous as has been stated by some authors. Pont (1971) found it on the shores of Lake Tarraure on 19 July 1962.

L.rotundata Collin WG, Tasiussaq; EG,--------, Only known from Greenland (*t.t.* Tasiussaq, Collin 1930), but Huckett (*op.cit.*) was unable to distinguish the species from *nigripes* despite "apparently valid differences" according to Collin's figures".

L.sinuata Collin (=*islandica* Lyneborg) WG, Orpigssuit; EG; Hekla Havn, [Nea, Only known from Greenland] LA, [Pal, Iceland; Faroes; Norway] S-LA, Described from Greenland (*t.t.* Orpigssuit and Hekla Havn, Collin 1930) this subarctic to High Arctic species is currently known only from these four areas, The genus however is highly complex and it is likely that this species will be found more widely, Biology; most *Limnophora* larvae are aquatic and this species will almost certainly prove to be so (Skidmore, *op.cit.*),

Lispe uliginosa Fallén WG, Qugssuk (*teste* Collin); Søndre Strømfjord (teste Huckett); EG,--------, [Nea, Churchill only (*teste* Huckett), apart from above], [Pal, S.France-Czech Republic-Kazakhstan-Kamchatka-N.Scotland-Finnmark-Irkutsk] Mediterranean- S, The occurrence of this species in North America is almost apocryphal, earlier records having almost all proved to belongs to the very similar *L.cotidiana* Snyder (1954), It is not known whether Collin checked the Qugssuk fly against Snyder's species, but the question appears merely academic since Huckett recognised the Churchill and Strømfjord specimens as belonging to *L.uliginosa* rather than *cotidiana*, These appear to be the only published records of true *uliginosa* from northern North America, and the species appears to be a Palaearctic one, *L.cotidiana* on the other hand occurs widely from Mexico to the southern edge of the Low Arctic in North America and from Ussuri area of south-eastern Siberia westwards to Tibet, Biology; Skidmore (1985) describes the puparium of *L.cotidiana* and discusses the biology of members of this species group(ie.the *L.uliginosa* gp.), He notes that like all members of the genus, so far as is known, the larvae are aquatic or semiaquatic obligative carnivores, but that *L.uliginosa* is peculiar in being highly tolerant of the acidic water in peat bogs.

Phaoniinae

Lophosceles frenatus (Holmgren) WG,61°30'- 68°42'; EG,--------, [Nea; (C03), Savonoski-Muir Inlet-Indian House Lake n.to Umiat-Padlei- Frobisher Lake; Greenland LA] S-LA, [Pal; (b1p-sa-a), Alps; Jämtland- N.Norway-Kola pena.] Alps- LA. Described from Greenland(*t. t.* "West Coast of Greenland, *Holmgren 1872*) this is an Holarctic boreo-alpine to Low Arctic species. Biology; found in abundance in hot sunshine on scrub birches beside the glacial river by Narssassuaq airfield on 12 July 1963 (PS.); only above treeline (700m) near Lake Tarraure, July (Pont 1971). Morphology of immature stages not known for any member of this genus but larvae almost certainly will be obligative carnivores like *Phaonia* (Skidmore 1985). Adults of all known species are sylvicolous, so the genus is unlikely to penetrate far into the arctic.

Phaonia bidentata Ringdahl WG.77°50'; EG.72°55- 74°15'. [Nea; (A6). Chesterfield-Nain-Clyde; Greenland HA] L-HA. Low to High Arctic nearctic species.

P. lugubris (Meigen) (=*morio* Meigen) WG.68°10'- 68°40'; EG.--------. [Nea;(A2). Naknek-Umiat-Kendall Island; Greenland LA] LA. [Pal. Alps; Dalarna-Lapland-Kola-Far East] Alps; S-LA. Disjunct Holarctic boreoalpine to Low Arctic. Note that in eastern Canada this appears to be replaced by the previous species which is unknown outside Canada. Biology unknown but see comments under *P. subfuscinervis* below. Commonly in birch forest to above tree-line(700m)at L.Tarraure, July (Pont 1971).

P. pallidisquama (Zetterstedt) WG.64°15'- 74°45'; EG.--------. [Nea;(A6). Sugluk-Port Burwell-Frobisher Bay; Greenland L-HA] L-HA. [Pal;(sa-a). Härjedalen-N.Norway] S-LA. Amphiatlantic subarctic to High Arctic species. Biology; Carpenter, Hale & Roman (1938) found this fly on moraine heath at Utorquait in Amerdloq; rather rare in mountains of N. and C. Scandinavia (Ringdahl, *1954-59*).

P. subfuscinervis (Zetterstedt) WG.66°56'-74°45'; EG.70°27'. [Nea;(A1). S.Alaska-McKinley- Reindeer Depot-Knob Lake-Fort Chimo; Greenland L-HA] S-HA. [Pal;(sa-a). Cairngorms (Scotland); Dalarna-Lapland-?Far East] S. Circumpolar sub-arctic to High Arctic species. Biology; Skidmore (1985) shows that the genus *Phaonia* is broadly divisible into the major subgenera (ie. *Phaonia* sensu stricto and *Rohrella*. The former are essentially humicolous in the larval stage and the adults are usually strongly floricolous, often having their mouthparts adapted for that purpose. In contrast *Rohrella* species are much more strongly associated with woodland where the larvae of most species are associated with decaying timber habitats. The adults are seldom strongly floricolous. The four species known from Greenland all belong to *Phaonia* s.str. and are typical of areas beyond the tree line in mountainous or highboreal areas. Pont (1971) found this in the Lake Tarraure birch forests on 21 July 1962.

4 The Zoogeography of the Muscidae of Greenland

The concept of Zoogeographical regions was proposed, rather surprisingly in view of avian dispersal powers, by the ornithologist P.L. Sclater in 1858. Amongst the 6 regions which he recognised were the Palaearctic ("Europe, North Africa and northern Asia") and the Nearctic ("North America above the tropics, from about 20°N to about 83°N"). He recognised similarities between these and proposed the term Holarctic to include both. Wallace (1876) modified Sclater's original map but left Greenland in the Nearctic and, whilst apathy towards these innovations inevitably prevailed, and indeed even today many workers never use either term, the idea that Greenland was biogeographically a part of the Nearctic was accepted by such authors as the British Lepidopterist Kirby (1896). Generally the view in the New World never wavered as successive revisions of Torre-Bueno (1989) have shown. About the turn of the century however, as most of the insects described first from Greenland were turning up in Europe, a claim that the Greenlandic fauna was European, and hence Palaearctic, was made by the Danish Dipterist Lundbeck (1898), amongst others. Territorial claims on Greenland became common currency, primarily in Scandinavia and in the ensuing biogeographical war over Greenland a major battle was won with small arms and considerable intellectual dexterity by Lindroth (1957). He suggested the western Palaearctic boundary should be re-drawn down the Davis Strait, thereby annexing Greenland. His small arms consisted of several beetles with mobility problems, an array of conveniently-placed temporary islands across the North Atlantic and hot spots in the icecaps where beleagured insects awaited the return of better times. Such was Lindroth's military achievement that he clearly converted the American ornithologist Vaurie to his view. When in 1959 he wrote the Passeriniformes volume of *The Birds of the Palaearctic Fauna,* Vaurie states "In the west the region covered in this book extends to eastern Greenland." But in the introduction to his volume on the Non-Passeriniformes, published in 1965 his "Limits.. extend in the west from Greenland (Western Greenland, which was not covered in the first [volume] is included in the present one).."

The typical view now was exemplified by Thompson (1964) who stated "Greenland, although geographically part of the Nearctic Region, is, on the evidence of plants, insects and birds, part of the Palaearctic". Lindroth had won a major battle but not the war. Downes (1988), in his masterly discussion on the origins of the insect fauna of the North Atlantic islands, concludes that the Greenlandic fauna is of Nearctic, not Palaearctic origin. His arsenal was formidable, drawing from the vast amount of Canadian Arctic climatological and biological data assembled in the past 30 years, major advances in our understanding of post-glacial history, and in Plate-tectonics. There were no possibilities either for Lindroth's island-hoppers or his glacial refugia. Coope (1986) and others (*cf.*Buckland et al., 1988), with the concept of surface drifting in the "terminal spasms of the Last Glaciation" around 10000Bp even accomodated the beetles with transportation problems.

The Arctic Muscids of Greenland

Owing to the location of Greenland, wholly within the Arctic region and remote from other land-masses save Ellesmere Island in the extreme north-west, the Greenlandic fauna is inevitably very restricted compared with the nearest subarctic continental areas in Labrador. It has however a highly interesting fauna.

Degerbøl (1937) recognised that High Arctic faunal elements as diverse as Musk-ox and the native butterflies had reached Greenland from Ellesmere Island and had been unable to complete the circuit down the east coast and up the west. Downes (1988) revealed a near-complete harmony in the High Arctic Lepidopterous fauna of Greenland and Ellesmere Island, and likewise concluded that this was the colonisation route which had been taken by these insects just as it had by the first wave of Inuit (eskimoes).

Thanks to the intensive studies at Lake Hazen at 81°49'N, 71°18'W in northern Ellesmere Island by the Entomology Research Institute of the Canada Department of Agriculture, a valuable baseline for studies in the Canadian High Arctic insect fauna has been established. The details given in Table 38 below show several interesting features regarding Greenland's 18 Arctic Muscids (ie. 2 *Drymeia*, 2 *Phaonia* and 14 *Spilogona.*). The inescapable conclusion from the analysis (Table 41) is that the Arctic Muscid fauna of Greenland is wholly Nearctic and that it entered via Ellesmere Island, as proposed for other groups by Degerbol (*op. cit.*) and Downes (*op. cit.*), where a minimum distance of 25 miles separates the two islands.

Four of the 18 Arctic species have not been recorded in West Greenland but occur in the east, whilst one of these (ie. *Spilogona* *megastoma*), also occurs in Iceland. It is unnecessary to conjecture that it entered from Iceland; indeed it may have reached Iceland from Greenland.

Table 38 The Zoogeography of the Arctic Muscids of Greenland.

Species	Hol.	Nea.	Pal.	Ell.	Baf.	WGr.	EGr.	Ice.	Spt.	NSc.	Sib.	Ala.
Drymeia groenlandica		x		x	x	x						x
D. segnis	x			x	x	x	x				x	x
Spilogona almquistii	x			x	x	x	x				x	
S. deflorata		x			x	x						x
S. denudata	x			x	x	x	x		x		x	x
S. dorsata	x			x	x	x	x		x		x	x
S. extensa		x		x	x	x	x					
S. obsoleta (=hirticauda)	x			x	x	x	x				x	x
S. megastoma	x				x		x	x	x	x	x	x
S. melanosoma		x		x	x	x						x
S. monacantha		x		x	x	x	x					x
S. opaca	x				x	x		x		x	x	x
S. sanctipauli	x			x	x	x	x				x	x
S. tornensis	x			x	x		x			x		x
S. tundrae	x			x	x		x			x	x	x
S. zaitzevi (=latilamina)	x			x	x		x				x	x
Phaonia bidentata		x			x	x	x					
P. pallidisquama	x				x	x				x		
18 species	12	6		13	18	14	13	2	3	5	10	14

a) 13 have been recorded in Ellesmere Island where three localities had been surveyed by the Canadian research teams (ie, Eureka, Hazen Camp and Alert, in the mid-west, north-central, and extreme north-east cape respectively).

b) the other five have been recorded from the north-western coast of Baffin Island and may well occur undetected in the unsurveyed southern half of Ellesmere Island. In fact all 18 are known today from Baffin Island, showing total harmony with Greenland,.

c) 12 of the species(ie.67%) have a circumpolar range, the remaining six being Nearctic. None of them is otherwise purely Palaearctic.

d) only two of the Greenlandic High Arctic species (11%) occur in Iceland, whilst in the entire west-European seaboard and islands only seven or 39% are known. Eastwards across Arctic Siberia the number rises to ten (55%) and in Alaska reaches 13(or 78%).

The non-arctic species

Whilst Greenland's High Arctic Muscid species exhibit complete harmony with the islands to the west, what of the origins of the non-Arctic species occurring in Greenland? These elements are listed in Table 39 below.

The details given in Table 39 show that in the non-Arctic elements, allowing for a number of anomalies, there is also a closer harmony between Greenland and adjacent parts of Canada than with areas to the east.

How did the non-Arctic Muscid fauna reach Greenland? The presence of closest harmony with eastern Canada suggests that it originated from that source, but many of the species are clearly unable to survive normal High Arctic conditions. This perhaps precludes their having entered Greenland via the Ellesmere Island route which would be so simple for their more hardy relatives. However, it appears that a period warmer than the present occurred around 5000 Bp when mean July temperatures across the Canadian Arctic were some 3°C warmer than at

Table 39 The Zoogeography of the non-Arctic Muscids of Greenland

Species	Hol	Nea	Pal	Lab	Baf	WGr	EGr	Ice	Far	Bri	Sca	Sib	Ala
Hydrotaea anxia	x			x		x					x		
H. diabolus	x						x			x	x	?	x
Musca domestica	x			x		x		x	x	x	x	x	
Graphomya maculata	x			x		x		x		x	x	x	x
Spilogona alpica	x^3			x		x				x	x^4		
S. baltica	x^5					x		x		x	x		x
S. contractifrons	x			x		x	x	x		x	x	x	x
S. malaisei	x			x	x	x	x				x		x
S. micans	x				x	x	x				x		x
S. semiglobosa	x			x		x					x	x	x
S. trigonifera		x		x		x	x						x
Limnoph. groenlandica	?				x								
L. nigripes	x			x		x				x	x	x	
L. rotundata		?				x							
L. sinuata		?				x	x	x	x				
Lispe uliginosa	x					x					x		
Lophosceles frenatus	x			x	x	x					x		x
Phaonia lugubris	x^1					x				x	x	x	x
P. subfuscinervis	x			x^2		x	x			x	x		x
19 Species	?16	?3	-	11	5	19	8	6	2	9	15	7	12

Notes.

1. This is known in Nearctic only from Hudson Bay west to Alaska.

2. Locality (Fort Chimo)in north-east Quebec.

4. This known in Nearctic only east of Hudson Bay so probably amphi-Atlantic.

5. Also occurs on Jan Mayen.

6. This is known in Nearctic only from Hudson Bay to Alaska

7. It is uncertain whether this species occurs in the Palaearctic.

The species concerned in Table 6 may be grouped as follows:-

a) One cosmopolitan eusynanthrope clearly introduced by man (ie. *Musca domestica*). This could not survive in Greenland unaided by man.

b) One species probably recorded in error(ie. *Hydrotaea diabolus*).

c) 12 species whose main ranges lie to the south of the Arctic though some reach the High Arctic(ie. *Hydrotaea anxia, Lophosceles frenatus, Phaonia lugubris* and *subfuscinervis, Graphomya maculata, Spilogona alpica, baltica, contractifrons, maläisei, micans, opaca, semiglobosa* and *trigonifera* and *Limnophora nigripes*. Two of these, *P. lugubris* and *S. baltica*, are known in Canada only west of Hudson Bay but the remaining ten are found in parts of eastern Canada immediately to the west of West Greenland.

d) *Lispe uliginosa* may be a casual import from Europe as the only positively authenticated specimens in Huckett (1965) are from sites having strong trade connections with Europe. If the Qugssuk specimen is correct it raises the possibility of the species having been a Viking import to the Western Settlement nearby which had outlived the colony. Skidmore (above) has shown that at least two Cyclorrhaphous flies (*Telomerina flavipes* and *Melophagus ovinus*) accompanied the Vikings to Greenland and shared their fate.

e) Some uncertainty surrounds the taxonomy of two species:- *Limnophora groenlandica* is only known from the female type specimen from the "West coast of Greenland". Huckett (*op. cit.*) was unable to distinguish it from the widespread Holarctic *L. uniseta* Stein, which also occurs on the Labrador coast and at Clyde on the east coast of Baffin Island. *L. rotundata* is only known from Collin's Tasiussaq male specimen. Huckett (1965) accepts that Collin's figures show valid differences, but he was unable to distinguish the species from *L. nigripes*. This may infer that both of Collin's "species" are junior synonyms of the holarctic *uniseta* and *nigripes* respectively. (NB. It is pertinent to note here the oft-repeated assertion that there are no truly endemic species in the Greenlandic fauna. These two Muscids, if indeed they are valid species, and *Atheta groenlandica*, remain to be recognised outside

Greenland.)

f) *Limnophora sinuata* was described from males from Orpigssuit and Hekla Havn. Pont (1986) synonymises this taxon with *L.islandica* Lyneborg, and gives the distributional range as Greenland, Iceland, Faroes and Norway. It is therefore the only member of the Greenlandic Muscid fauna which is otherwise only known from the Palaearctic. As stated above however this genus is the subject of much taxonomic confusion and it is likely that all of the above three species, if indeed all are valid, occur elsewhere.

Ten of the 12 category "c" species above (83%) occur on the Labrador coast, Baffin Island and (or) the north-eastern coast of Quebec. Two further species are not currently known from the eastern parts of Canada; of these *Phaonia lugubris* is a boreoalpine-subarctic fly for which the nearest known localities to West Greenland are Padlei(N.W.T., at 62° west of Hudson Bay), and the Cairngorms in Scotland. *S.baltica* is known from the same area of Canada but no further east, whilst the closest locality to the east of Greenland is in Iceland.

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present (Elias 1994). With the 4.7° July mean at Thule (in extreme north west Greenland close to Ellesmere Island) prevailing in the early 1950s (Barfod *et al.*, 1962) a further rise of 3°C would probably have been adequate for the entire Greenlandic Muscid fauna to have made that crossing, assuming no other major barrier prevented their moving northwards from the southern parts of the Low Arctic. Those Greenlandic High Arctic species currently unknown in Ellesmere Island but present on Baffin Island could certainly have reached the Kennedy and Robeson Channels. A major problem in even the mildest parts of Greenland is the shorter term instability which bedevils the climate. Dagerbøl (1937) observed that in the late 1930s summers were getting warmer in East Greenland. On the other hand, Barfod *et al.* (*op.cit.*) give the following details of July averages for the period 1957- 59, showing that it was getting colder:-

Prins Christian Sund +8.1°- +7.6°; Scoresbysund (August) +3.9- +2.1°;
Egedesminde +7.9- +5.9. ..., etc.

A more southerly route for the non-arctic species into Greenland would seem probable and would obviate the necessity of invoking a much warmer phase. Northern Baffin Island, where the Davis Strait narrows to some 200 miles, still has a High Arctic climate and the prevailing winds blow southwards. Further south, in the Labrador Sea, the shortest crossing to Greenland is some 500 miles, but the prevailing winds blow towards Greenland. So, aerial plankton, including flies, would be blown southwards from Baffin Island and eastwards from Labrador. A surface-drift crossing seems improbable since the Labrador current flows southwards.

Apart from species which were casually introduced by man, the main dispersal mechanism then which led to the Dipterous colonisation of Greenland by non-Arctic Muscids was probably aerial drift across the Labrador Sea.

5 Conclusions

The data provided above on North Atlantic Muscidae appears to reveal a number of facts relevant to the discussion of post-glacial colonisation of these areas.

The pioneer Muscid colonists of newly exposed land resulting from the retreat of ice-sheets throughout the Northern Hemisphere were probably all members of the genus *Spilogona*. The distribution of these flies today shows that the genus forms an expanding proportion of the muscid fauna with increasing latitude. In the most barren High Arctic islands representing the absolute frontiers for sustainable life such as Ellef Ringnes, Jan Mayen, New Siberian Islands and Wrangel Island, the genus exists alone. The fact that it is not the remoteness of these islands alone which accounts for the sole presence of *Spilogona* is emphasised by the total absence of the genus in such similarly remote, but much more southerly islands as the Azores, Madeira and the Canaries. As noted by Hennig (1955-64) *Spilogona* is the characteristic genus of colder regions of the Northern Hemisphere.

As observed by many workers, including most recently Downes (1988), the fauna of Greenland is a Nearctic one exhibiting a very clear division between a pure, High Arctic fauna in the north and a low boreal to subarctic one in the south. The former almost certainly entered via the Kennedy and Robeson Channels from Ellesmere Island, whilst the latter probably mainly resulted from aerial planktonic drift from the Labrador coast. There is no case on Muscid grounds for any claim that Greenland has a Palaearctic fauna. Indeed it is clear that the Denmark Straits, and not the Davis Straits, form the Nearctic / Palaearctic boundary.

The Muscidae then conform almost perfectly to the findings of Downes (*op. cit.*), which were based upon a survey of most elements of the Greenlandic fauna. That the Coleoptera, in stark contrast, do not conform to Downes' "rules was convincingly demonstrated by Böcher (1988). The submission of Bergersen (in press) that Greenland forms a separate Zoogeographical region finds very dubious support amongst the Muscids. Rather do they provide concrete evidence for the view that Greenland is a part of the Nearctic region.

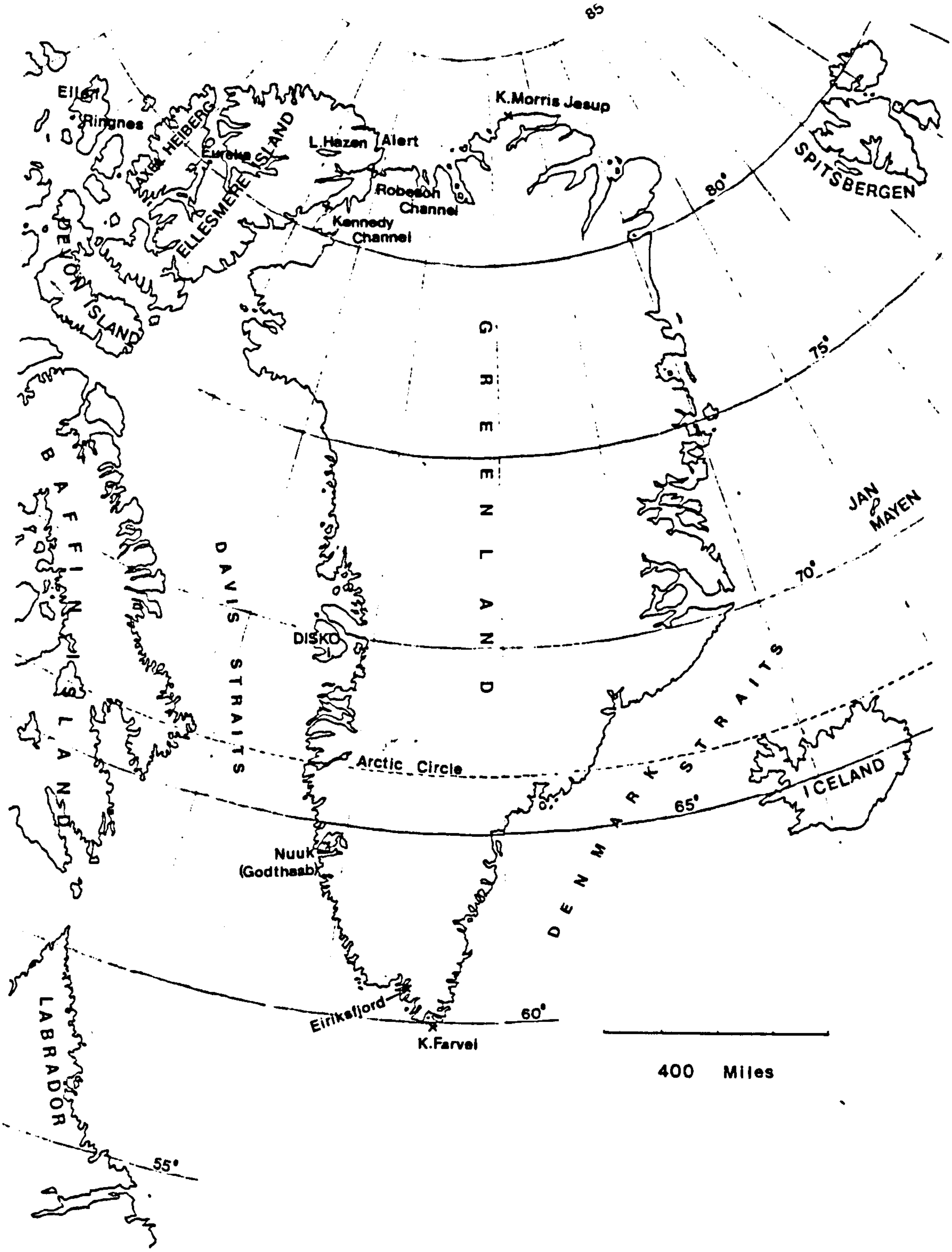
Iceland and the islands to the east (Faroes, Shetland, Orkney and the Hebrides) have faunas of West European origin, with no unequivocal

Nearctic influence. The Icelandic and Faroese faunas probably resulted from surface drift from Scandinavia, assuming a rapid transport of habitat material containing the puparia *in situ*.

The British fauna of course crossed via the wide land-bridge from north-western Europe, before that access was broken by rising sea-level during the early Holocene.

Whilst neither the British Isles nor the Faroes contain any Arctic elements as here understood in their muscid faunas, this is not true of Iceland. Contrary to common assertions, Iceland in fact has a relatively richer Arctic muscid fauna than Scandinavia (7.5% compared to 3%). This could be predicted if the Icelandic fauna emanated from Scandinavia when the climate there was more Arctic than today. It is interesting to note in this connection that whilst the 10°C July Mean isotherm just skirts the northern coast of Fennoscandia it bisects Iceland approximately from Breiðafjörður to Ingólfshöfdi.

Downes (1985) and others, noted that in other floral and faunal groups the proportion of Holarctic species increases northwards. This is also clearly demonstrated by the North Atlantic Muscidae, but the proportion also increases in a westerly direction up to and including Greenland.



Map of North Atlantic area showing various islands etc.

referred to in the Zoogeographical section.