Studies on the morphology and taxonomy of the immature stages of calliphoridae, with analysis of phylogenetic relationships within the family, and between it and other groups in the cyclorrhapha (diptera)

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Studies on the Morphology and Taxonomy of the Immature Stages of Calliphoridae, with Analysis of Phylogenetic Relationships within the Family, and between it and other Groups in the Cyclorrhapha (Diptera)

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A B S T R A C T

The present study deals with the taxonomy and morphology of the immature stages of the Diptera family Calliphoridae (blowflies).

The eggs were studied, using both the light and the scanning electron microscopes, and structural features were found that enable specific identification.

The larvae and puparia of some sixty species were studied, and a large number of new characters were found that enable the separation of species reliably. In addition, various anatomical details, especially of the cephalopharyngeal skeleton, have been elucidated.

The cephalopharyngeal skeletons of various related families were studied and compared with the Calliphorid structure.

Descriptions of the larvae of sixty species are presented, and keys to various groups, especially those of medical or veterinary importance, are given.

A discussion of the evolution and phylogeny of the Calliphoridae and related families is presented, based on the above-mentioned morphological studies and other evidence.

A N N E M E

(TO MY MOTHER)

... though there are animals which have no attractiveness for the senses, yet for the eye of science, for the student who is naturally of a philosophic spirit and can discern the causes of things, Nature which fashioned them provides joys which cannot be measured.

Aristotle

De Partibus Animalium

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CHAPTER ONE

INTRODUCTION

1.1 The Value of Anatomical and Taxonomic Studies on Calliphorid Larvae

There are three main reasons for conducting anatomical and taxonomic studies on the larvae of Calliphoridae. Firstly, such studies contribute a great deal to our understanding of the functional anatomy and morphology of these larvae, and to a clearer understanding of how they are adapted to their particular way of life. Secondly, comparative studies on many species can contribute greatly to the systematics of the group, by clarifying affinities and giving a stronger foundation for phylogenetic reconstructions; often, particular problems, such as deciding whether two forms are, in reality, one species or two, can only be solved by a detailed study of the immature stages. In other words, larval studies will result in an improvement of an already existing classification based on adult morphology.

The third, and perhaps practically the most important, reason is the value of such studies in species identification. The usual method of identifying the species of a larval Calliphorid is to rear it out to the adult stage which can then be identified easily. However, larvae (and eggs) are often presented to the specialist either preserved in alcohol or in a moribund condition, and in many cases

live, and seemingly healthy, larvae fail to develop. In some cases, facilities for rearing may not be available, or very large numbers of specimens may need to be dealt with. For these reasons it is very desirable to be able to identify the larvae to species. Regarding the puparia, these are often found empty (i.e. after the emergence of the adult) in various situations; in such cases any attempt at identification must, of course, be made from the puparium alone.

The identification of the immature stages of Calliphoridae may find practical applicability in the following fields of human endeavour:

a) Ecological Research. As natural agents of decomposition, blowfly maggots are of interest to the ecologist and others who are involved in studies of the processes of decay and the recycling of nutrients within ecosystems. Much of what is known of the bionomics of blowflies has been summarised by Norris (1965).

b) Medicine. Many species of blowfly larvae may act as parasites (either obligate or facultative) and invade the living tissues of Man and domestic and wild animals, while others may suck the blood of their hosts. These larvae may cause permanent injury or even death of the host. Myiasis in the Old World has been comprehensively dealt with by Zumpt (1965).

c) Forensic Science. Calliphorid larvae are often found in human cadavers and, in murder cases, may be of use in attempts to determine the minimum time of death on the basis of the stage of

development of the larvae. Other information, such as place and manner of death may be gleaned from examination of these larvae. This subject has recently been reviewed by Erzinclioglu (1983).

d) Archaeology. Due to their very tough and durable nature Calliphorid (and other Diptera) puparia are often found in archaeological deposits, perfectly preserved after hundreds, or even thousands, of years. Species identification in this field contributes much to the reconstruction of events in ancient times. The use of examining puparia from archaeological deposits has been discussed by Phipps (1983).

e) Palaeontology. Associations of fly maggots and vertebrate remains in a fossilised condition are not commonly reported in the literature, but it is probable that this is due to the fact that the material is not recognised, rather than an actual lack of such associations. When such associations are reported, they have contributed some information to the palaeoecological reconstruction of the remains. The subject is reviewed by Gautier (1974).

f) Hygiene. Meat intended for human consumption is sometimes found to be infested with blowfly maggots. In these situations species identification is important in order that preventive measures may be taken against the fly. In areas where adult flies act as mechanical transmitters of disease by settling on human foods, larval identifications from various pabula in the vicinity

(e.g. dung, carrion etc.) may assist in controlling the population of the pest species. A comprehensive treatment of the subject is given by Oldroyd (1973).

In a recent report by the NERC Working Party on the Role of Taxonomy in Ecological Research (1976), it was pointed out that basic research on cyclorrhaphous larvae was needed. However, the Working Party also stated that the ecological importance of cyclorrhaphous larvae is 'medium', whereas the larvae of Lepidoptera and Coleoptera, as well as such groups as the Aculeate Hymenoptera and the Mammalia are of a 'high' ecological importance. This view is without doubt erroneous. The diversity of larval habits and the number of species of the Cyclorrhapha is very great and their impact (as decomposers, parasites, parasitoids, predators, leaf-miners etc.) on the terrestrial environment is profound, and much greater than, e.g. the Mammalia, at least in Britain.

1.2 The Aims and Scope of the Present Work

In this thesis the family name Calliphoridae is used in the restricted sense, to exclude the Sarcophagidae and the Rhinophoridae, but including the Ameniinae and the Rhiniinae. In all, sixty species of Calliphoridae (as here defined) have been studied during the course of this work. However, the genera Calliphora, Lucilia, Chrysomya and the subfamily Phormiinae have received special attention.

In addition, representative species from those families in the 'Calliphorid'-line of the Calypterates have been studied; in other

words, the 'Tachinidae' in the old, wide sense to include the following families: Tachinidae sensu stricto, Sarcophagidae, Oestridae, Gasterophilidae, Hypodermatidae and Cuterebridae. Examples from these groups have been studied in order to compare their structures with those of the Calliphoridae and in order to attempt to arrive at an understanding of the evolution of the group. The 'Muscid'-line (i.e. Muscidae, Anthomyiidae and Fanniidae) will not be dealt with.

The scope of the present work is, therefore, as follows:

a) A discussion of the general anatomy of the immature stages of the Calliphoridae in order to provide a basis for the taxonomic work that follows. Also, various structures whose form or function is in dispute are re-examined and discussed and new interpretations offerred, and the form of certain imperfectly understood structures is clarified.

b) Descriptions of sixty species of Calliphoridae at the immature stages are given, and keys to certain groups in certain regions are provided where feasible.

c) An anatomical comparison is made of the cephalopharyngeal skeleton of the the various families of the 'Tachinidae' sensu lato.

d) A phylogenetic reconstruction is tentatively proposed. This is based on the comparative morphological studies carried out during the course of this study.

1.3 Previous Work

The literature on the immature stages of Calliphoridae will be reviewed and referred to at the appropriate points in the thesis, but a general summary is given here.

Weismann (1864) was probably the first to investigate the anatomy of immature stages. Lowne (1890) published a very full account of the anatomy of the larva of Calliphora vicina (as C.erythrocephala), which, although containing some misleading statements, nevertheless remains the standard work on the subject. Other workers, especially Cook (1949), Ludwig (1949), Miller (1932) and Roberts (1969, 1971), have contributed greatly to the field of larval anatomy and embryology.

The literature on the comparative anatomy and systematics of Calliphorid larvae, although extensive, is scattered and of varying quality. Most descriptions appeared during the first half of the Twentieth Century and were usually the results of work on problems of a medical or veterinary nature. The result of this was that species were described singly or in unrelated groups, and no systematic and comparative treatments of the subject were attempted. Furthermore, most of the work was carried out in tropical and subtropical areas, and temperate (especially northern) species were largely ignored. An added obstacle in the way of attempting systematic 'revisions' was the difficulty in obtaining reliably named material, the difficulty in rearing many of the species (e.g. parasitic or termitophilous species) and the inadequacy of collections in museums and other institutions. This meant that the, often very detailed, descriptions published in

the past lacked a solid taxonomic basis, resulting in reliance on unreliable characters, and potentially useful characters were often overlooked. Therefore, it is not possible to compare newly-described species with published descriptions of other species meaningfully, since these latter require to be redescribed on the basis of a strong morphological foundation which was lacking when these species were first described.

This work could not have been attempted without the pioneer works of the following authors whose writings first stimulated my interest in the subject: Austen, Banks, Cuthbertson, Froggatt, Fuller, Hall, James, Keilin, Knipling, Miller, Patton, Roubaud, Schumann, Smart, Tao, Thompson, Townsend and Zumpt. In addition, Hennig's (1948, 1950 and 1952) monumental review of the larvae of Diptera deserves special mention.

Although attempts at comprehensive treatments have been made in other groups of cyclorrhaphous larvae, e.g. Drosophilidae (Okada, 1968), Sciomyzidae (Knutson, 1963) and Muscidae (Skidmore, 1973), no such attempts have previously been made in the Calliphoridae. It is hoped that the many questions posed by this thesis will encourage others to take up the study of this interesting group.

1.4 Species Studied

The following is a full list of the species of immature Calliphoridae studied during the course of this work:

Calliphora vicina Robineau-Desvoidy

Calliphora vomitoria (Linnaeus)

Calliphora uralensis Villeneuve

Calliphora alpina (Zetterstedt)

Calliphora subalpina Ringdahl

Calliphora loewi Enderlein

Calliphora lata Coquillett

Calliphora croceipalpis Jaennicke

Calliphora terraenovae Macquart

Calliphora stygia (Fabricius)

Calliphora augur (Fabricius)

Calliphora ochracea Schiner

Calliphora livida Hall

Calliphora hortona (Walker)

Calliphora quadrimaculata (Swederus)

Cynomya mortuorum (Linnaeus)

Cynomyopsis cadaverina (Robineau-Desvoidy)

Triceratopyga calliphoroides Rohdendorf

Eucalliphora latifrons (Hough)

Aldrichina grahami (Aldrich)

Lucilia sericata (Meigen)

Lucilia caesar (Linnaeus)

Lucilia ampullacea Villeneuve

Lucilia cuprina (Wiedemann)

Lucilia bufonivora Moniez

Lucilia porphyrina (Walker)

Lucilia caeruleiviridis Macquart

Lucilia pallescens Shannon

Hemipyrellia fernandica (Macquart)

Hemipyrellia ligurriens (Wiedemann)

Chrysomya putoria (Wiedemann)

Chrysomya chloropyga (Wiedemann)

Chrysomya marginalis (Wiedemann)

Chrysomya megacephala (Fabricius)

Chrysomya pinguis (Walker)

Chrysomya bezziana Villeneuve

Chrysomya albiceps (Wiedemann)

Chrysomya rufifacies (Macquart)

Chrysomya varipes (Macquart)

Chrysomya incisuralis (Macquart)

Chrysomya saffranea (Bigot)

Cochliomyia hominivorax Coquerel

Cochliomyia macellaria (Fabricius)

Phormia regina (Meigen)

Phormia terraenovae Robineau-Desvoidy

Boreellus atriceps (Zetterstedt)

Protocalliphora azurea (Fallen)

Protocalliphora avium Shannon and Dobroscky

Protocalliphora sialia Shannon and Dobroscky

Pollenia rudis (Fabricius)

Amenia imperialis Robineau-Desvoidy

Amenia leonina (Fabricius)

Stomorhina cribrata Bigot

Tricyclea deemingi Zumpt

Auchmeromyia luteola (Fabricius)

Elephantoloemus indicus Austen

Booponus intonsus Aldrich

Cordylobia anthropophaga (Blanchard)

Cordylobia ruandae Fain

Cordylobia rodhaini Gedoelst

CHAPTER TWO

MATERIALS AND METHODS

2.1 Sources of Material

Specimens of many British species were obtained by setting up carrion traps at various localities in County Durham, England. All British species of Calliphora (except C. uralensis), Cynomya mortuorum and Lucilia caesar were obtained in this way. Calliphora uralensis was obtained from a gannet (Sula bassana (L.)) carcase from Ailsa Craig, Scotland. All stages of Protocalliphora azurea were obtained by searching the nests of swallows (Hirundo rustica L.) starlings (Sturnus vulgaris L.), blackbirds (Turdus merula L.) and nuthatches (Sitta europaea L.) in various localities in County Durham.

Specimens of other British and non-British species were received as loans or gifts from many individuals and institutions throughout the world. Most of this material was received preserved after having been obtained from positively identified cultures or individual females, although in some cases live cultures were received. The sources of all these specimens are listed in the Acknowledgements.

2.2 Culture Methods

Pure cultures were kept in cages at 20°-25°C, constantly supplied with water and sugar; newly emerged specimens were given a

protein meal by placing liver in the cage and all species readily oviposited on this medium. Rearing was done on mice carcasses placed in glass dishes with some peat as pupation medium. Pupating individuals were removed to a clean cage for emergence.

2.3 General Laboratory Methods

Eggs and larvae were fixed and preserved in acetic alcohol (3 parts 90% ethanol:1 part glacial acetic acid); fixation in alcohol alone is undesirable as the larvae contract and become difficult to dissect. Eggs and first and second instar larvae were examined whole under a stereomicroscope (mag. X10-X60), then slide-mounted whole in Berlese's Fluid and examined under a compound microscope (mag. X32-X320). Third instar larvae were examined whole under a stereo-microscope; for examination under the compound microscope dissected parts of the larvae were slide-mounted. For stereomicroscope examination a strong light is needed to see details of the spinulation, and fibre-optic illumination was found to be particularly useful. No clearing by KOH or any other substance was done, as some parts of the various sclerites are easily destroyed in this way. Whole puparia were preserved in acetic alcohol, but empty puparia were preserved dry. Puparia were examined whole under the stereomicroscope; parts of puparia were then slide-mounted as above.

Measurements were made with a micrometer eyepiece and graticule.

2.4 Sectioning Methods

For general purposes, eggs and larvae were fixed in Bouin's Fluid for 24 hours and then embedded in wax. Sections were then made using an ordinary microtome. The sections (at a thickness of 8 μ) were then mounted on slides and stained with Ehrlich's haematoxylin and eosin.

Attempts at sectioning the cephalopharyngeal skeleton using the above method gave unsatisfactory results, due to the fact that the hard skeleton was pulled through the soft tissues by the microtome blade when it was struck by the latter, rather than being neatly sliced. For sections through the skeleton, therefore, a cryostat was used. The method adopted was as follows: Live larvae were dropped into a container of isopentane which was then lowered into a canister of liquid nitrogen and held there for about 30 seconds. The larvae were then immersed in the liquid nitrogen and left there for about 15 minutes. Sections were then made using a cryostat, and then stained and mounted as above. Good results were obtained using this method, due to the fact that the frozen specimen is of a uniform hardness throughout.

2.5 Scanning Electron Microscopy

Eggs and larvae were prepared for the SEM as follows: Specimens were placed in 50% alcohol for a day and then removed to 60%, 70%, 80%, 90% and, finally absolute alcohol, being kept for a day at each concentration; the absolute alcohol being changed twice on the day.

The specimens were then transferred to a mixture of 1 part absolute alcohol and 1 part acetone for a day, followed by pure acetone (two changes); the specimens could then be kept indefinitely in acetone.

Empty puparia were simply washed in absolute alcohol, then transferred directly to acetone which was changed twice.

All specimens (except empty puparia) were dried using a Polaron Critical Point Dryer. Puparia were dried in air. The specimens were then gold-coated and examined with a Cambridge Stereoscan 600.

2.6 Illustration

Both line drawings and photographs are used to illustrate this thesis. Line drawings were used to illustrate three-dimensional structures, like the cephalopharyngeal skeleton, that cannot be satisfactorily shown in a photograph since parts of the structure will, of necessity, be out of focus. Also, the limits of the various sclerites of the skeleton are very difficult to make out in a photograph. Drawings were made with the aid of a camera lucida.

Scanning electron micrographs were taken using a Minolta camera. Photographs of sections and slide preparations were taken using an ultraphot. Photographs were used as the form of illustration when:

a) Evidence is presented to resolve a disputed point.

b) A structure is too complex to be satisfactorily rendered in a drawing.

c) The degree of pigmentation of a structure is important.

CHAPTER THREE

THE MORPHOLOGY OF THE EGGS

...I began to believe that all worms found in meat were derived directly from the droppings of flies, and not from the putrefaction of the meat, and I was still more confirmed in this belief by having observed that, before the meat grew wormy, flies had hovered over it, of the same kind that later bred in it.

Francesco Redi

Experiments on the Generation of Insects

3.1 The Literature on Calliphorid Eggs

The above quotation from a book published in Italy in 1668 is the first known reference in history to blowfly eggs. Since that time much has been published on the egg-laying habits of blowflies (e.g. Portchinski, 1874; Osten Sacken, 1887; later work on blowfly oviposition has been well summarised by Norris, 1965 and Nuorteva, 1977).

The first detailed account of Calliphorid egg morphology was that of Weismann (1864). Davies (1948) described the chorionic structure of Lucilia sericata, and Wigglesworth and Beament (1950, 1960) published accounts of the chorionic structure of Calliphora vicina (as C. erythrocephala), but their interpretations were disputed by Hinton (1960). Further works by Hinton (1961, 1962, 1963),

Anderson (1960) and Wigglesworth and Salpeter (1962) finally produced a clear picture of chorionic structure.

However, relatively little work has been carried out on the comparative morphology and systematics of blowfly eggs. Moreover, most of the descriptions so far published are a matter of measurements of length and width, and a few comments on colour and shape. The first descriptions of diagnostic use were made by Laake, Cushing and Parish (1936) who compared the morphology of Cochliomyia hominivorax (as C. americana) with that of C. macellaria, using the light microscope. Later, Hinton (1981) published descriptions and S.E. micrographs of several species, but his concern was primarily with plastron function and his descriptions are of little diagnostic use. The first to examine eggs under the S.E.M. with a taxonomic viewpoint was Kitching (1976) who published very useful descriptions and S.E. micrographs of six species of Australian Chrysomya. O'Flynn and Moorhouse (1980) described, and published S.E. micrographs, of Lucilia cuprina and two species of Australian Calliphora.

Other relevant references will be referred to at the appropriate points below.

3.2 General Morphology of Calliphorid Eggs

A typical Calliphorid egg (Fig.188) may be described briefly as follows: White or yellowish in colour. Cylindrical over most of its length, but tapering at the anterior end and somewhat blunt at its posterior end. The anterior end terminates in a disc-like area, the micropylar plate. The micropyle perforates the centre of the plate.

The whole egg is slightly curved; on the concave dorsal surface a hatching strip (or median area) is present, which broadens out at the anterior end and also, although to a lesser extent, at the posterior end. The median area is delimited on either side by a slightly raised hatching pleat.

Muirhead-Thomson (1937), working on Muscids and Anthomyiids, termed this type of egg the muscine-type to distinguish it from the phaoniine-type egg which he characterised by the possession of two large flanges, one on each side of the hatching strip. He also described a Myiospila-type egg in which the two flanges diverge and project anteriorly, and in which the anterior part of the egg projects forward as an apicomedian process. Much has been made in the literature of this classification, and eggs have been described as muscine etc. on the basis of this classification. (Skidmore, 1973; Ferrar, 1979). However, since the 'flanges' of the phaoniine and Myiospila-type eggs are simply enlarged hatching pleats and many intermediate forms occur, it is felt that this classification is misleading, as many eggs cannot be fitted into any one of these categories. The muscine and phaoniine eggs merely represent extremes of the same condition and not different 'types'. This may be seen by comparing figures

3.3 Taxonomic Value of Egg Characters

In this section the various characters of actual or potential taxonomic value are discussed and evaluated. Comments on the possible adaptive significance of the various character states will also be made, and suggestions for future work proposed. The discussion is based on a study of 22 species.

3.3.1 Colour

The colour of eggs is typically white or creamy-white, although larger eggs appear to be yellowish. According to published descriptions almost all Calliphorid eggs are of this colour, although Zumpt (1965) describes the egg of Booponus intonsus as a 'dull greyish white'. Ferrar (1978) states that the ovarian eggs and more advanced follicles in specimens of Euphumosia papua are brown; he also states that the material was 'not particularly well preserved' and that 'this is not necessarily the colour in life'.

3.3.2 Size and Shape

The length of Calliphorid eggs ranges from 1.00-1.80mm and the width from 0.20-0.50mm. The dimensions of the species studied are listed in Table I . A minimum of 20 eggs was measured for each species. The size of an egg can serve only as a very rough guide in identification, although certain species seem to have larger eggs than average. In a few species, e.g. Auchmeromyia luteola and Cynomya mortuorum the width of the egg in relation to its length is unusually great, giving the egg a more robust appearance. This feature is best presented as a Shape Factor, which is calculated by dividing the width by the length (Table I). It will be seen that this figure for the above two species is appreciably greater than for the other species. On the other hand, in Chrysomya bezziana, the size factor is unusually low, this species being narrow in relation to its length.

The robustness (or otherwise) of an egg may be related to the

Species	Measure-ments	Median Area Index	Shape Factor	Volume
Calliphora vicina	1.37-1.50 0.38-0.44	0.08-0.12	0.28-0.33	0.10-0.20
Calliphora vomitoria	1.25-1.50 0.38-0.44	0.09-0.11	0.29-0.30	0.09-0.15
Calliphora uralensis	1.37-1.44 0.38-0.44	0.11-0.12	0.28-0.31	0.10-0.14
Calliphora alpina	1.31-1.55 0.38-0.40	0.18-0.19	0.26-0.29	0.09-0.13
Calliphora subalpina	1.72-1.79 0.44-0.50	0.08-0.09	0.26-0.29	0.17-0.23
Calliphora loewi	1.50-1.63 0.44-0.50	0.10-0.11	0.29-0.31	0.15-0.22
Calliphora stygia	1.30-1.35 0.35-0.38	0.19-0.20	0.27-0.28	0.08-0.10
Calliphora ochracea	1.45-1.53 0.38-0.40	0.11-0.12	0.25-0.26	0.10-0.13
Calliphora quadri-maculata	1.70-1.75 0.40-0.43	0.19-0.20	0.24-0.25	0.14-0.16
Calliphora hortona	1.00-1.08 0.28-0.30	0.20-0.22	0.22-0.28	0.04-0.05
Calliphora terrae-novae	1.25-1.38 0.25-0.28	0.08-0.15	0.20-0.21	0.04-0.06
Cynomya mortuorum	1.63-1.75 0.50-0.69	0.05-0.07	0.31-0.39	0.21-0.44
Triceratopyga calliphoroides	1.42-1.48 0.33-0.38	0.12-0.13	0.23-0.26	0.08-0.11
Lucilia sericata	1.13-1.25 0.25-0.31	0.24-0.28	0.22-0.25	0.04-0.06
Lucilia caesar	1.25-1.30 0.25-0.28	0.25-0.28	0.20-0.22	0.04-0.05
Hemipyrellia ligurriens	1.24-1.37 0.34-0.37	0.15-0.16	0.26-0.27	0 08-0.10

Species	Measure-ments	Median Area Index	Shape Factor	Volume
Auchmeromyia luteola	1.43-1.48 0.50-0.55	0.06-0.07	0.35-0.37	0.19-0.24
Phormia terraenovae	1.00-1.06 0.25-0.32	0.09-0.11	0.25-0.30	0.04-0.06
Phormia regina	1.19-1.25 0.31-0.38	0.10-0.11	0.26-0.30	0.06-0.09
Protocalliphora azurea	1.19-1.25 0.31-0.34	0.14-0.15	0.26-0.27	0.06-0.08
Chrysomya bezziana	1.08-1.18 0.20-0.25	0.52-0.60	0.19-0.21	0.02-0.04
Chrysomya putoria	1.31-1.37 0.28-0.38	0.28-0.36	0.21-0.28	0.04-0.06

threat of dessication. Thus Au. luteola is known to lay its eggs in dry dusty soil or sand in many parts of Africa where the temperature is high (Zumpt, 1965). Under such conditions an egg with a greater volume in relation to its surface area would lose water at a slower rate than other eggs. On the other hand, Ch. bezziana lays its eggs in open wounds of animals and men, which situations are unlikely to dry out; its lack of 'robustness' is, therefore, not a disadvantage.

It is, however, difficult to see what advantage Cy. mortuorum may have in laying such a robust egg. This species lives in cool, wet (often coastal) areas and should have no particular problems of dehydration; however, Nuorteva (1972) states that it is active mainly on sunny days. It is also possible that a larger egg would better withstand low temperatures.

From the length and breadth measurements of the eggs, their volumes may be calculated. Since the volume of a sphere may be calculated as follows:

$$V = 4/3\ \pi r^3$$

a modification of this formula will enable the computation of the volume of an egg. Since only two of the radii of an egg are equal (the breadths) and one is unequal to the either of the other two (the length), the following formula will give the volume of the egg:

$$V = 4/3\ \pi\left(\frac{b}{2}\right)^2\left(\frac{L}{2}\right)$$

Where V = volume, b = breadth and L = length. All volumes, which are of some diagnostic value, are listed in Table I

3.3.3 Chorionic Structure

As is well known, the surface of the chorion is covered with a network of hexagonal reticulations, (Fig. 39) which are a reflection of the shapes of the follicular cells. I have not found any characters in the shape of these hexagons that permit species identifications, but further work, including careful measurements, may prove useful; there does seem to be a tendency for some species to have larger reticulations than others (compare Figs. 2 and 4). All that can be said for the time being is that the reticulations are much fainter in certain species (e.g. Calliphora hortona) than in others. (Compare Figs. 2 and 7) Au. luteola (Fig. 24) possesses very well-developed reticulations. The shape of the reticulations has, however, been used diagnostically in other groups e.g. Muscidae (Hinton, 1981; O'Flynn and Moorhouse, 1980) and Rhinophoridae (Bedding, 1973)). The character is probably of value at the family level.

In some species, e.g. Au. luteola (Fig. 24) the chorion is grooved (or ridged) as is the case in many Muscidae (see Fig. 37). Zumpt (1965) describes the egg of Cordylobia anthropophaga as having 'longitudinal grooves and also a fine hexagonal reticulation on the surface'. Zumpt states that this species, like Au. luteola, oviposits in dry sand and avoids moist soil. It is possible, therefore, that these ridges are an actual thickening of the chorion that may curtail water loss. It is also possible that the ridges may strengthen the eggs against knocking and rubbing in the dry, loose soil in which they are laid and to which they are not firmly stuck.

The detailed structure of the chorion has been studied by Hinton (1960, 1981). It is essentially composed of a thick outer layer and a thin inner layer connected by a series of vertical columns (Fig. 31). According to Hinton these columns delimit air spaces. In sectioned material roughly every sixth air space is larger than the others and the outer layer above it is ridged. This air space corresponds to Hinton's canal of the hexagonal system. Sections of the chorion of five species were studied during the course of this work: Calliphora vicina, Lucilia sericata, Phormia terraenovae, Cynomya mortuorum and Chrysomya bezziana. No features of diagnostic value could be found, however.

3.3.4 Micropyle and Micropylar Plate

The micropyle is an anteriorly situated pore which admits the entry of spermatozoa during fertilisation. It varies in diameter from 8-40 µ according to species, but most species fall in the range of 8-12 µ . Auchmeromyia luteola is an exception with a micropyle diameter of about 40 µ (Fig. 23).

Typically, the micropyle is situated on a dome-like structure which is surrounded by a depressed area of the chorion. This whole area is termed the micropylar plate (Fig. 8). The chorion of the plate is usually smooth i.e. with only faint reticulations, but, as with the reticulations on the rest of the chorion, this feature varies (rather subtly) between species (compare Figs. 2 and 8). In Auchmeromyia there does not seem to be a well-defined plate, and the area around the micropyle is normally reticulated (Fig. 23).

3.3.5 Median Area

This feature provides some of the most useful diagnostic characters of the egg. The median area is delimited on either side by the hatching pleats and, in most known Calliphorid eggs it has a peculiar structure that enables it to function when submerged, as a plastron, or physical gill; its structure and function have been described in detail by Hinton (1960, 1981). However, in Pollenia rudis the median area is similar in structure to the rest of the chorion, the plastron being restricted to the inner sides of the hatching pleats (Richards and Morrison, 1972). In all known Calliphorid eggs the median area is situated dorsally; the statement by Tawfik and El-Husseini (1971) that it is ventral is incorrect. (The terms dorsal, anterior etc. when applied to eggs are all in relation to the body axis of the ovipositing female.)

Probably the most useful taxonomic feature afforded by the median area is its shape. Anteriorly the structure is usually one of two basic shapes. It either ends abruptly before the micropylar plate as is the case in e.g. Calliphora vicina and Calliphora alpina (Figs. 1 and 4), or it bifurcates forming a U- or V-shape anteriorly as in Calliphora vomitoria and Lucilia sericata (Figs. 2 and 16). In Chrysomya putoria (Fig. 21) the very narrow median area bifurcates anteriorly giving rise to two narrow bands one on either side of the micropylar plate forming a very distinctive Y- shape which is very similar to Kitching's (1976) S.E. micrographs of Ch. megacephala. In Chrysomya bezziana the wide median area bifurcates sending a wide band around either side of the micropylar plate. These bands curve down

ventrally on either side, but do not meet (Figs. 19 and 20). Fig. 36 shows a section through the ventral part of the chorion lying between the two lateral bands. The shape of the median area in Ch. bezziana is very similar to Laake, Cushing and Parish's (1936) light microscpe description of Cochliomyia hominivorax.

The length of the median area along the body of the egg is also of great diagnostic value. In many species, e.g. Calliphora vicina, it extends over most of the length of the egg (Fig. 39), while in others, e.g. Protocalliphora azurea, it extends over one third to a half of the way down the egg (Fig. 26). In some species the median area ends abruptly about a half or two-thirds the way down the egg, only to reappear again after a short distance. This feature is present in Chrysomya putoria (Fig. 22) and Calliphora ochracea (Fig. 11). According to Dr Lewis Davies (pers. comm.), the median area is broken in some specimens of Lucilia sericata and Lucilia caesar.

The shape and thickness of the part of the chorion lying between the two arms of the median area (in species where it is bifurcated) is also of diagnostic use. This 'lip' may be pointed as in Calliphora uralensis (Fig. 3) or rounded as in Chrysomya bezziana (Fig. 20). Intermediate forms occur, as in Calliphora vomitoria (Fig. 2) and Lucilia sericata (Fig. 16) where the lip is roughly V-shaped, but does not have a pointed tip.

The width of the median area is, to some extent, useful in separating species. Along most of its length, the median area is usually between 30-40 μ in width, but the greatest interspecific variation occurs at the anterior wide end of the median area. In this connection, the median area index, calculated by dividing the greatest

width of the median area by the greatest width of the egg is of some value. The results are listed in Table I . These figures may be of use as a rough guide in identification, but they cannot be taken to show differences in the extent of the respiratory surfaces of the different species. This is because only the greatest width is measured, and in some species with very narrow median areas, the median area may widen out anteriorly giving a figure that does not reflect the true extent of the respiratory surface (e.g. Chrysomya putoria Fig. 21). A measure of surface area would be more meaningful in this context.

The structure of the meshwork of the median area seems to be of potential value in taxonomy, although this character was not fully explored during this study. The structure and respiratory function of this area has been described in detail by Hinton (1960, 1981). For the purposes of identification, three different types were observed. Firstly, Hinton's type, which possesses a surface network layer (Fig. 28); this is typical of species of Calliphora and Lucilia. The network may be rather dense, as in Lucilia sericata (Fig. 16), or more open as in most species of Calliphora (e.g. Calliphora loewi Fig. 6). Secondly, a Protocalliphora-type, found in Protocalliphora azurea (Fig. 27), which seems to lack the network layer and in which the aeropyles appear to lie on the surface; the general impression is of a spongy appearance. Thirdly, bezziana-type, characteristic of Chrysomya bezziana (Fig. 20); this has a 'furry' appearance under the light microscope, but appears somewhat 'scaly' under the S.E.M. The structure of this type of respiratory surface was rather difficult to elucidate. Transmission election microscopy should prove useful in this field.

The structure of the median area must be seen in the context of respiratory and dehydration problems (Hinton, 1981). Therefore, one must assume that species with narrow median areas must be subject to dessication in nature, for example, Lucilia sericata, which favours high temperatures for oviposition, has, on average, a narrower median area and a more closed structure, than Calliphora species that are active at lower temperatures. The parasitic Chrysomya bezziana and Cochliomyia hominivorax, with their wide median areas, oviposit in wounds that are unlikely to dry out. Protocalliphora azurea, with its short median area and rather closed structure is found in the dry habitat of birds' nests.

However, Davies (1948) found that water loss in Lucilia sericata occurred over the whole surface of the egg. Anderson (1960), on the other hand, found that if the plastron was blocked, eggs of Calliphora vicina died through lack of oxygen; this must mean that water exchange can also take place across this surface as the water molecule is smaller than the oxygen molecule (Hinton, 1981).

Finally, the narrow respiratory surfaces of Chrysomya putoria and Chrysomya megacephala present something of a problem. These two species live in the humid parts of Africa and Asia respectively and should have no water loss problems. However, it is possible that, during the rainy season, the high temperatures in these areas may mean that the water covering the eggs may be deficient in oxygen; the plastron would thus work in reverse, resulting in loss of oxygen to the ambient water (Hinton, 1981). In temperate areas, where rain water is rich in oxygen, this problem would not arise.

3.3.6 Hatching Pleats

The hatching pleats delimit the median area on either side. They are usually double structures, with an outer layer continuous with the chorion, and inner layer continuous with the median area respiratory surface (see Fig. 7). (However, see 3.3.5 for comments on Pollenia rudis.) The surface of attachment of these two layers forms the line of weakness which splits apart during hatching. This line may be seen as a faint grey line in Fig. 33 (T.S. of Lucilia sericata egg). Figs. 4 and 29 show the two layers splitting apart. Hinton (1960, 1981) has described this mechanism.

The value of the hatching pleats in species identification lies in their relative thickness. In some species e.g. Triceratopyga calliphoroides (Fig. 14), and Chrysomya bezziana (Fig. 19) the pleats are little more than small folds on the surface of the egg, whereas in Calliphora subalpina (Fig. 5) , Cynomya mortuorum (Fig. 13) and Protocalliphora azurea (Fig. 25) the pleats are thick, well-developed structures. The pleats of Pollenia rudis are produced into large flange-like structures (Richards and Morrison, 1972). In T.S. the thick hatching pleats appear curved, as in Phormia terraenovae (Fig. 35) and Cynomya mortuorum (Fig. 34), while the thinner pleats appear straighter (Calliphora vicina Fig. 32 and Lucilia sericata Fig. 33).

3.3.7 Plastron Craters

Hinton (1981) published S.E. micrographs of two Muscid species,

Musca sorbens from Egypt and Musca vetustissima, the Australian bushfly. In addition to the plastron between the batching pleats, there were present in these two species isolated areas in the chorion (outside the pleats) that possessed a plastron network structure and which were surrounded by raised areas of the chorion. He termed these structures plastron 'craters'.

In only one of the species studied during the course of this work were plastron craters found (see Fig. 11 of Calliphora ochracea). As was noted above (3.3.5) the median area of this species is 'broken' along its length. It would seem, therefore, that these two features are devices to minimise water loss, C.ochracea being a species of dry habitats, as are M. sorbens and M. vetustissima.

3.3.8 Examination and Identification of Eggs

This study was based mainly on S.E.M. work, but once the various character states were elucidated, it was found that most features may be seen using the light microscope. However, it was found that the stereomicroscope was not very useful; the compound microscope, on the other hand, could be used to examine most of the diagnostic features used in identification.

Initially, slide preparations were made of the eggs, but it was found that this method distorted the eggs, making identification difficult. The best method was found to be to place the eggs on a slide with a drop of liquid (water, not alcohol which tends to evaporate quickly, drying the eggs), and to examine under low power, without a coverslip. Adjusting the light and focus as necessary will

reveal most features. The only features I could not see using this method are the structure of the respiratory surface, and the plastron craters of C. ochracea.

The following keys are to be seen as interim ones, and should be used tentatively.

3.3.8.1 Tentative Key to the Eggs of British Genera of Carrion-Breeding Calliphoridae and all Species of British Calliphora

1. Median area ending more or less in a straight line anteriorly 2
   - Median area bifurcated anteriorly 5

2. Hatching pleats thick, well-developed (Figs. 5 and 13) 3
   - Hatching pleats thin, weakly developed (Figs. 1 and 4) 4

3. Size factor high, 0.31-0.39 Cynomya mortuorum
   - Size factor low, 0.26-0.28 Calliphora subalpina

4. Median area 70-75 μ wide at widest point Calliphora alpina
   - Median area 40-45 μ wide at widest point Calliphora vicina

5. Egg about 1mm long or very slightly longer Phormia terraenovae
   - Egg well above 1mm long 6

6. 'Lip' forming distinct pointed V-shape (Figs. 3 and 6). 7

- 'Lip' with more rounded edge (Figs. 2 and 16) 8

7. Egg long, about 1.50-1.63 mm in length Calliphora loewi

- Egg shorter, about 1.37-1.44mm in length Calliphora uralensis

8. Median area index low, 0.09-0.11; size factor high, 0.29-0.30; Hatching pleats thick (Fig. 2) Calliphora vomitoria

- Median area index higher, 0.24-0.28; size factor lower, 0.22-0.25; hatching pleats thin (Fig. 15) Lucilia spp.

CHAPTER FOUR

MORPHOLOGY OF THE LARVAE AND PUPARIA

The dead flies should be besprinkled and soaked with honey-water, and then placed on a copper-plate exposed to the tepid heat of ashes; afterwards, very minute worms, only visible through the microscope, will appear, which little by little grow wings on the back and assume the shape of very small flies, that slowly attain perfect size.

Athanasius Kircher

The Twelfth Book of the Subterranean World

4.1 Introduction: Literature Review

The first to unravel the life-history of blowflies and to describe scientifically their immature stages was the great scholar and physician Francesco Redi (1668). In his book, Esperienze intorno alla generazione degli insetti, he showed beyond doubt that maggots found in carrion were the offspring of blowflies and that they were not spontaneously generated by the putrefaction of the meat. He concluded that "the flesh of dead animals cannot engender worms unless the eggs of the living be deposited therein". Redi's main contribution to immature stage morphology was the distinction between the larvae and puparia of Lucilia and Sarcophaga (Sarcophagidae).

In the year following the publication of Redi's Esperienze, 1669, Jan Swammerdam presented his studies on insect metamorphosis in

his book, Historia insectorum generalis, which included work on the morphology of fly puparia. It is often forgotten that it was Swammerdam who first observed that the puparium is, in fact, the hardened skin of the final instar larva.

The first detailed description of a Calliphorid larva was that of Weismann (1864), who described the anatomy and morphology of Calliphora vomitoria (as Musca vomitoria). This work was of great importance in understanding the structure of the larvae of Calliphoridae, but was of little use in a taxonomic sense. Brauer (1883) was the first to carry out a study on the comparative morphology of Diptera larvae and his work was thus the first serious attempt to use larval characters in the taxonomy of flies. Lowne (1890-92) presented an extensive monograph on 'The Blowfly', Calliphora erythrocephala (= C.vicina); this work is still the classic reference on the subject, but it contains many errors, especially in some of the illustrations of larval morphology. These illustrations were described by Hennig (1952) as "schlecht und einzeln nicht angefuhrt". Since Lowne's book is still a widely used reference, the above-mentioned errors will be discussed in some detail below.

The first half of the twentieth century saw the publication of a large number of papers containing descriptions of the larvae and puparia of isolated species of blowflies. As pointed out in the Introduction this 'piecemeal' description of larvae resulted in the reliance on unreliable characters for identification, since the workers in question seldom had access to large numbers of reliably named specimens with which to work out useful specific characters. The characters used in the present work were worked out by the examination

of large numbers of specimens derived from cultures of British and non-British species. In this way, it was possible to identify those characters that vary intraspecifically and to distinguish them from those useful characters that vary interspecifically. Inevitably, a number of characters were found to be useful only when used in combination with others characters. In the sections below, the basic structure of a Calliphorid larva will be described and the taxonomic value of each character in turn will be discussed. It is hoped that this morphological foundation will form a basis for detailed descriptions of further species in the future.

Most of the descriptive work that appeared up until 1951 is reviewed in Hennig's monograph on Diptera larvae (1948-52) (although Hennig missed the major work of Hall (1948) on North American blowflies). The most important authors who contributed descriptions of Calliphorid larvae are listed on page 7, and their work (and that of other authors) will be referred to at the appropriate points in the thesis. After the appearance of Hennig's book several further descriptions of various species have appeared, as well as two major references: Schumann (1954) describes the larvae of several central European species of of medical importance, and Zumpt (1965) monographs the species known to cause myiasis in the Old World.

In addition, the work of Hewitt (1914) on Musca domestica (Muscidae) and that of Snodgrass (1924) on Rhagoletis pomonella (Tephritidae), although not on Calliphorid larvae, are useful references on the morphology of Cyclorrhaphous larvae.

This chapter will deal with all taxonomically useful structures that I am aware of other than the cephalopharyngeal skeleton, which will be dealt with in the next chapter.

4.2 Morphology of the Larvae

The following survey of structural features refers to the third instar unless otherwise stated.

4.2.1 Colour

The colour of Calliphorid larvae is almost always a creamy white or yellowish-white. Some heavily spined species may appear grey (e.g. Protocalliphora azurea) or brownish (e.g. Chrysomya albiceps) to the naked eye, but the colour of the cuticle is actually the usual whitish colour in these species.

Occasionally, some actively feeding specimens may appear darker due to the fact that the gut contents may be seen through the cuticle. Dr L. Davies (pers. comm.) has noted that the larvae of Lucilia species possess a pinkish tinge, and it is interesting to note that Redi (1668) used this character to distinguish between Lucilia and Sarcophaga larvae.

Most larvae have a somewhat shiny cuticle. However, Davies (unpublished data) has noted that the cuticle of Calliphora alpina is dull. S.E. micrographs show that the surface of the cuticle of this species is 'granulated' in appearance, being covered with regular low-dome-like structures some 5 μ across and 1 μ high (Fig. 105). The cuticle of other species is smooth, lacking these domes.

Although colour characters may be useful in separating species, it is the sort of character that can only be understood by first-hand experience, as the differences are rather subtle and very difficult to

describe; moreover, colour terms often mean different things to different people. In addition, specimens may become discoloured when badly preserved. For these reasons, colour is not used as a character in the descriptions or keys.

4.2.2 Size and Shape

The length of a fully grown third instar larva is of the order of 10-18mm and its greatest width is of the order of 2.5-3.5mm. Younger third instars and earlier instars are, of course, much smaller, and all measurements taken are shown in Table II . Where unlimited specimens of a species were available (e.g. culture-derived specimens) at least twenty specimens of each instar were measured. In cases where less than twenty specimens were available all available specimens were measured.

Size is a variable character, although it is useful as a general guide. However, it must be remembered that the size of a larva (or any organism) is a function of its age and the quality of its diet. Certain preservatives, e.g. alcohol, will cause larvae to contract; this will, of course, give a misleading idea of size. Only relaxed larvae should be measured.

The shape of a typical third instar Calliphorid larva may be described as a long cone-shape (Fig. 194), being wider posteriorly and gradually narrowing anteriorly. The widest part is usually in the middle of the posterior third of the body. However, bloodsucking larvae like Protocalliphora azurea and Auchmeromyia luteola often are barrel-shaped, being thickest more or less at the centre. The earlier

TABLE II

Measurements of larvae and puparia in mm. Lengths (above) and greatest widths (below).

Species	1st Instar	2nd Instar	3rd Instar	Puparium
Calliphora vicina	2.5-3.25 0.5-0.63	3.5-5.75 0.75-1.00	8.88-13.75 1.75-2.88	7.12-8.37 3.00-3.62
C. vomitoria	3.25-3.63 0.5-0.63	3.13-7.25 0.63-1.13	15.12-16.88 2.87-3.13	8.25-8.63 3.50-3.75
C. uralensis	1.87-3.38 0.25-0.63	3.12-4.75 0.49-1.00	9.75-16.38 1.87-3.13	7.49-8.13 3.00-3.50
C. alpina	2.25-3.00 0.37-0.63	5.75-6.50 1.25-1.31	12.00-13.50 2.62-3.25	7.49-8.25 3.24-3.50
C. subalpina	1.37-1.63 0.49-0.62	4.75-5.37 0.87-1.13	11.87-12.88 1.90-2.88	7.49-8.00 2.24-2.50
C. loewi	1.87-2.5 0.37-0.5	2.62-5.25 0.62-0.88	11.00-11.75 2.50-2.88	8.12-8.37 2.74-3.25
C. lata	- -	- -	13.38-15.37 2.50-2.88	- -
C. quadrimaculata	- -	- -	6.75-19.63 1.63-2.88	10.25-10.75 3.63-4.00
C. hortona	2.88-3.13 0.50-0.63	3.63-5.25 0.63-1.00	12.25-13.50 2.50-2.63	6.75-7.25 2.63-2.88
C. terraenovae	2.5-3.5 0.5-0.63	3.00-5.70 0.75-1.10	15.00-16.25 2.75-3.13	- -
C. livida	- -	- -	12.50-16.63 2.25-3.38	- -
C. stygia	- -	2.50-5.50 0.57-0.62	14.75-16.50 2.75-3.00	- -
C. augur	3.75-4.00 0.63-0.75	2.75-5.25 0.63-0.75	11.63-16.63 1.63-3.13	8.25-8.81 3.63-3.75
C. ochracea	- -	- -	15.00-17.50 2.50-2.75	- -
C. croceipalpis	2.50-2.63 0.38-0.44	5.63-6.00 0.75-0.88	11.50-16.63 1.50-3.75	- -
Cynomya mortuorum	1.87-2.13 0.37-0.39	2.74-3.75 0.62-0.75	13.12-14.00 3.00-3.50	8.49-9.75 3.31-3.62

Species	1st Instar	2nd Instar	3rd Instar	Puparium
Cynomyopsis	-	-	13.38-16.50	-
cadaverina	-	-	3.00-3.50	-
Triceratopyga	2.00-3.25	-	13.13-15.88	-
calliphoroides	0.38-0.50	-	2.50-2.88	-
Eucalliphora	1.13-1.50	-	11.13-11.75	-
latifrons	0.25-0.38	-	2.25-2.75	-
Aldrichina grahami	-	-	15.00-16.50	8.75-9.25
	-	-	2.88-3.13	3.13-3.25
Lucilia sericata	2.50-3.00	5.50-6.25	11.63-14.00	7.75-7.88
	0.44-0.50	1.00-1.25	2.00-2.38	3.13-3.25
L. caesar	2.50-2.75	4.38-5.00	12.50-14.38	8.5-9.88
	0.25-0.28	0.38-0.50	2.75-2.88	3.00-3.50
L. ampullacea	3.50-3.75	5.00-8.13	12.25-12.88	-
	0.38-0.41	0.50-0.63	2.25-2.5	-
L. cuprina	1.63-1.75	1.88-3.75	10.00-10.38	-
	0.25-0.34	0.31-0.50	2.00-2.38	-
L. porphyrina	-	-	10.63-11.25	-
	-	-	1.50-1.75	-
L. bufonivora	-	5.63-6.25	9.88-10.00	-
	-	0.75-0.875	2.00-2.50	-
L. caeruleiviridis	-	-	11.88-12.25	-
	-	-	2.00-2.25	-
L. pallescens	-	-	6.88-12.13	-
	-	-	1.13-2.00	-
Hemipyrellia	1.38-2.88	7.38-7.50	8.25-12.5	8.50-8.75
ligurriens	0.38-0.50	1.25-1.50	1.75-2.50	3.75-4.00
Hemipyrellia	-	-	9.88-10.50	6.25-6.5
fernandica	-	-	2.25-2.50	2.56-2.75
Pollenia rudis	-	-	9.38-10.00	5.00-6.88
	-	-	2.63-2.88	1.75-3.00
Chrysomya bezziana	-	-	10.75-12.37	-
	-	-	2.75-3.00	-

Species	1st Instar	2nd Instar	3rd Instar	Puparium
Chrysomya chloropyga	-	-	7.50-13.88	-
	-	-	1.63-3.13	-
Ch. putoria	1.81-3.00	4.87-5.37	11.50-13.38	7.56-7.88
	0.38-0.50	0.88-1.13	2.13-2.75	2.63-2.94
Ch. albiceps	-	4.00-4.25	4.50-6.50	5.25-6.50
	-	0.62-0.75	2.75-3.00	1.50-3.75
Ch. rufifacies	-	3.62-3.94	10.62-11.25	-
	-	0.62-0.69	1.75-2.25	-
Ch. incisuralis	-	-	13.38	-
	-	-	4.38	-
Ch. varipes	-	-	8.75-10.00	6.13-6.38
	-	-	1.88-2.25	2.13-2.25
Ch. marginalis	-	-	15.00-15.88	-
	-	-	3.38-4.25	-
Ch. megacephala	-	6.88-9.00	14.62-17.75	-
	-	1.00-1.75	2.99-3.88	-
Ch. semimetallica	-	-	9.80-10.50	-
	-	-	2.25-2.50	-
Ch. suffranea	-	-	10.25-11.13	-
	-	-	2.25-2.75	-
Ch. pinguis	-	4.12-4.38	15.25-15.50	8.37-9.25
	-	0.75-0.88	2.88-3.25	3.63-3.88
Cochliomyia hominivorax	-	-	15.00-15.81	-
	-	-	3.00-3.13	-
Co. macellaria	1.63-2.50	4.13-4.38	13.88-14.75	7.75-7.88
	0.38-0.50	1.00-1.13	2.25-2.75	3.25-3.28
Phormia regina	1.20-2.50	5.38-5.63	6.25-13.75	8.37-9.50
	0.38-0.50	0.5-0.63	1.13-2.75	2.25-3.50
Ph. terraenovae	1.37-2.63	3.25-5.75	10.62-11.87	8.37-9.13
	0.38-0.62	0.50-1.00	2.25-2.50	2.50-3.38
Boreellus atriceps	-	-	4.13-8.38	7.25-7.75
	-	-	1.00-1.75	3.13-3.25

Species	1st Instar	2nd Instar	3rd Instar	Puparium
Protocalliphora azurea	1.50-2.13 0.41-0.50	3.25-5.25 1.13-1.63	9.25-12.25 2.69-4.13	7.37-8.25 3.50-4.12
P. sialia	- -	- -	12.38-12.50 4.25-4.50	- -
P. avium	- -	- -	11.13-11.38 3.62-3.88	8.75-9.25 3.75-4.13
Amenia imperialis	- -	6.37 0.88	- -	- -
Amenia leonina	3.56-4.00 0.62-0.74	7.12 1.24	- -	- -
Stomorhina cribrata	- -	- -	- -	6.88 2.75
Tricyclea deemingi	- -	- -	4.13-4.50 1.00-1.50	- -
Auchmeromyia luteola	- -	- -	8.63-11.25 2.75-3.88	7.38-7.63 3.38-3.63
Elephantoloemus indicus	- -	2.63-2.88 1.75-2.00	3.25-8.25 1.88-3.75	- -
Booponus intonsus	- -	- -	3.50-4.88 1.90-2.25	- -
Cordylobia rodhaini	- -	- -	13.63-14.38 6.75-7.38	- -
Cor. ruandae	- -	- -	9.50-11.50 3.38-4.00	- -
Cor. anthropophaga	- -	4.00-5.00 0.94-1.88	9.63-13.00 3.50-4.75	- -

instars are more uniformly cylindrical, although they also tend to taper at the anterior end. An exception is the second instar of the cutaneous parasite Cordylobia anthropophaga in which the anterior half of the body is considerably thicker than the posterior half.

The shape of a larva as described above is as seen in dead and relaxed specimens. In life, however, the larval body has a natural curvature, as seen in Fig. 192 . This curvature is shared with most other Cyclorrhaphous larvae, but it is not very obvious in, e.g. the bloodsucking species mentioned above.

The shape of a larva is often a feature of some taxonomic value. It is best expressed as a Shape Factor (SF) calculated by dividing the greatest width of the larva by its length. Larvae that are thicker in relation to their length give a higher value than others (see Table III). Thus Calliphora vicina gives a value of 0.20-0.21, while the barrel-shaped Protocalliphora azurea gives a value of 0.26-0.34.

4.2.3 Segmentation

A typical Calliphorid larva has twelve visible segments, one cephalic, three thoracic and eight abdominal segments (Fig. 194). However, the number of segments in the third instar has been a matter of debate in the past. Weismann (1864) and Brauer (1883) counted twelve segments, but the latter author considered that the last segment actually represents two fused segments. Much earlier, Newport (1839) stated that the larva of Calliphora vomitoria (as Musca vomitoria) had fourteen segments. Schiner (1863) stated that Diptera larvae normally possess thirteen segments. (As far as the number of visible segments goes, this statement is certainly true of the Nematocera, but not the Brachycera or Cyclorrhapha). Lowne (1890) believed that sixteen segments were present in C. vicina. Hewitt

TABLE III

Third Instar and Puparium Shape Factors (SF)

$$\text{Shape Factor} = \frac{\text{Greatest Width}}{\text{Length}}$$

Species	3rd Instar SF	Puparium SF
Calliphora vicina	0.19-0.21	0.42-0.43
C. vomitoria	0.18-0.19	0.42-0.43
C. uralensis	0.19	0.40-0.43
C. alpina	0.21-0.24	0.43
C. subalpina	0.16-0.22	0.29-0.31
C. loewi	0.22-0.26	0.33-0.39
C. lata	0.18-0.19	-
C. quadrimaculata	0.14-0.24	0.35-0.37
C. hortona	0.19-0.20	0.38-0.40
C. terraenovae	0.18-0.19	-
C. livida	0.18-0.20	-
C. stygia	0.18-0.19	-
C. augur	0.14-0.19	0.42-0.44
C. ochracea	0.15-0.16	-
C.croceipalpis	0.13-0.22	-
Cynomya mortuorum	0.23-0.25	0.37-0.39
Cynomyopsis cadaverina	0.21-0.22	-
Triceratopyga calliphoroides	0.18-0.19	-
Eucalliphora latifrons	0.20-0.23	-
Aldrichina grahami	0.18--0.19	0.34-0.35
Lucilia sericata	0.17-0.18	0.40-0.41
L. caesar	0.20-0.22	0.35-0.36
L. ampullacea	0.18-0.19	-

Species	3rd Instar SF	Puparium SF
Lucilia cuprina	0.20–0.23	–
L. porphyrina	0.14–0.16	–
L. bufonivora	0.20–0.25	–
L. caeruleiviridis	0.16–0.18	–
L. pallescens	0.16–0.17	–
Hemipyrellia ligurriens	0.20–0.21	0.44–0.45
H. fernandica	0.10–0.23	0.40–0.42
Pollenia rudis	0.28–0.29	0.35–0.44
Chrysomya bezziana	0.24–0.25	–
Ch. chloropyga	0.21–0.23	–
Ch. putoria	0.18–0.20	0.34–0.37
Ch. albiceps	0.46–0.61	0.28–0.57
Ch. rufifacies	0.16–0.20	–
Ch. incisuralis	0.33	–
Ch. varipes	0.21–0.23	0.34–0.35
Ch. marginalis	0.22–0.28	–
Ch. megacephala	0.20–0.22	–
Ch. semimetallica	0.22–0.24	–
Ch. saffranea	0.21–0.25	–
Ch. pinguis	0.18–0.20	0.41–0.43
Cochliomyia hominivorax	0.19–0.20	–
Co. macellaria	0.16–0.19	0.41–0.42
Phormia regina	0.18–0.20	0.27–0.36
Ph. terraenovae	0.21–0.22	0.30–0.37

Species	3rd Instar SF	Puparium SF
Boreellus atriceps	0.21-0.24	0.41-0.43
Protocalliphora azurea	0.30-0.34	0.47-0.49
Pr. sialia	0.36-0.43	-
Pr. avium	0.32-0.34	0.42-0.44
Stomorhina cribrata	0.39	-
Tricyclea deemingi	0.24-0.33	-
Auchmeromyia luteola	0.31-0.34	0.45-0.47
Elephantoloemus indicus	0.45-0.58	-
Booponus intonsus	0.46-0.54	-
Cordylobia rodhaini	0.49-0.51	-
Cor. anthropophaga	0.34-0.36	-
Cor. ruandae	0.36-0.37	-

(1910), working on Musca domestica (Muscidae), counted thirteen segments, taking as his criterion the arrangement of the somatic musculature. The cause of this difference in opinion is not only the possible dual nature of the last segment, but also the possibility that the second (or first thoracic) segment is in fact two segments, comprising anteriorly the so-called Newport's segment and posteriorly the 'third' segment. In this thesis Weismann's system (twelve segments) is followed, as it is practically the most convenient system on which to base the taxonomy of these larvae.

However, a few words need to be said about the criteria used in delimiting the segments. Each segment (except the first and last) is delimited by a definite ring-like crease anteriorly and posteriorly; the first and last segments being delimited by a crease posteriorly and anteriorly respectively. The anterior and posterior margins of each segment are often ringed by a band of spines (see Fig. 194), but these bands are not always complete.

In the case of the first thoracic segment there is present, approximately mid-segmentally, a wide spinal band which is incomplete dorsally (Fig. 198). No crease or fold accompanies this band, however. It is the presence of this band that has caused authors to disagree as to whether this segment is, in fact, a complex of two. Lowne (1890) gives a misleading illustration (p.34) of this segment; he shows the mid-segmental spinal band as being complete, whereas it is never complete in any of the species studied by me. On the other hand, Tao (1927) states that the first thoracic segment cannot be divided into two on the basis of external features, since the "complete fold and spinose annulus which ordinarily indicate the separation of the segments are absent between the second and third segments". This statement is incorrect; as noted above, the fold is absent, but the

spinal band, though incomplete, is present.

Regarding the dual nature of the last segment, there is present a crease ventrally and approximately mid-segmentally, but no spines are ever present on either side of it. Lowne (1890) illustrates this crease as reaching dorsally to meet the posterior rim of the segment (p.34), whereas it is always incomplete in the material studied by me.

The dual nature of the second and twelfth segments is not externally apparent in the early instars.

4.2.4 Processes, Papillae and Surface Structures

In this section, all surface structures (except the spines, hairs and spiracles) will be described and their taxonomic value discussed.

4.2.4.1 The Cephalic Segment

Although the misleading statement 'acephalous' is often used to describe Cyclorrhaphous larvae (e.g. Richards and Davies, 1977), these larvae do, in fact, have a highly specialised head. In the third instar Calliphoridae it is divided into two (right and left) cephalic lobes (Fig. 111) each bearing five papillae, only two of which are visible on slide-mounted specimens under low power. The more dorsally situated of these papillae is generally considered to be the homologue of the antenna (Ludwig, 1949; Roberts, 1971; Hartley, 1963). It is composed of two parts: a basal, roughly cylindrical part, and a much smaller, conical, apical part (Fig. 190). The more ventral papilla is

considered to be a maxillary palp homologue. It is roughly cylindrical and bears several minute tubercles on its apical surface (Fig. 190). The cuticle around the palp has a reticulate appearance, and situated amongst these reticulations are two much smaller papillae (S, in Fig. 190), the larger of which is situated closer to the palp than the smaller one, which is situated more dorsally. The latter is often difficult to see, even under high power; I term these the lower and upper supra-maxillary papillae respectively. The fifth papilla is situated at the edge of the oral cavity and is said to be sensory in function (Roberts, 1971). I term this the oral papilla. It is bulbous in form and possesses a single minute tubercle apically. Associated with it are two or three small processes (Figs. 111 and 190).

These papillae are of limited taxonomic value. However, in some species, e.g. Protocalliphora azurea the antennae and palps are very much reduced. In others, e.g. Cynomya mortuorum, the palps are quite as large as the antennae. In some species of Chrysomya e.g. Ch. regalis the upper supra-maxillary papilla is separated from the lower one while in all species of Calliphora examined the papillae were touching. The antennae are particularly well-developed in the termitophilous species, Tricyclea deemingi (Fig. 298).

The function of the antennae (and possibly the palps) is olfactory (Bolwig, 1946), and not optical as thought by Hewitt (1914).

The ventral surface of the cephalic segment is covered with a series of oral ridges (or pseudo-tracheae) that are presumed to channel food towards the mouth (Fig. 112). In cross-section each ridge appears as a T-like structure (Fig. 116). These ridges are very uniform in structure throughout the Calliphoridae and thus they are of

no taxonomic value, but they have been used diagnostically at the family level within the Cyclorrhapha (Teskey, 1981).

Ventral to the oral cavity is the lower lip (Fig. 116), whose dorsal surface is covered with anteriorly pointing spinules. A tongue-like structure, covered with long, thin spines anteriorly and shorter, more robust spines posteriorly is present as an evagination of the posterior part of the lower lip (Figs. 116 & 117). The lower lip and tongue-like organ have revealed no features of diagnostic use.

4.2.4.2 The Twelfth Segment

The third instar twelfth segment possesses a wealth of characters of taxonomic value (Fig. 197). It is composed of a circular ridge that encompasses the larger part of its posterior surface, and an anal protuberance ventrally. The posterior spiracles (see below) lie in the area delimited by the ridge.

The ridge itself bears seven pairs of papillae on its margins; these are designated P_1 - P_7 as in Fig. 197 . Lowne (1890) makes the erroneous statement that only six pairs of papillae are present; from his description it appears that he missed papillae P_7 which are very small and often difficult to see. Papillae P_6 are somewhat larger, but still very small, while all the others are large and usually easy to see. All these papillae are conical in shape (Figs.108-110) and often bear fine tubercles on their surfaces, but this feature can only be seen with the SEM. In addition, papillae P_5 often have an annulated appearance in life, but this feature is not very obvious in preserved material (Fig. 110).

The papillae differ between species in two ways: relative size, and distance between one another. They are relatively large in species like Phormia terraenovae (Fig. 97), and Chrysomya albiceps (Fig. 98); in the latter species they are rather broad and flattened. The other extreme may be seen in Protocalliphora azurea where the papillae are so reduced as to be almost absent (Fig. 99). In the descriptions the size of a papilla has been indicated by comparing the width of its base with the distance between it and another papilla. Another useful feature furnished by these papillae is the position of P_2 in relation to P_1 and P_3; in some species it is closer to P_3 and in others it is approximately equidistant between P_1 and P_3.

The function of these papillae does not seem to have been investigated. Brindle (1957) used the size and number of anal papillae of Tipula larvae (Tipulidae) to classify the species of this genus into ecological groups. He found that those species possessing larger and more numerous papillae lived in wetter habitats than did those that possessed smaller and fewer papillae, and he proposed that these papillae may have an osmoregulatory function. Dr J.C. Coulson (pers. comm.) has suggested that they are more likely to be respiratory in function. Be that as it may, the decrease in size of the posterior papillae in Calliphoridae also seems to be correlated with dryer habitats. Thus, Protocalliphora azurea, which lives in the warm, dry habitat of birds' nests, possesses very much reduced papillae, whereas species that live in carcasses in cold, wet environments, e.g. Boreellus atriceps (Fig. 96), possess well-developed papillae.

In the area delimited by the ridge, there lie, ventral to the

posterior spiracles, two circular, wrinkled areas of the cuticle (Fig. 197); they have revealed no features of taxonomic use. The whole area delimited by the ridge, however, does vary between species; it is sunk well below the level of the ridge in some species, e.g. Boreellus atriceps (Fig. 96), while in other species, e.g. most species of Calliphora, the area is at most only slightly concave. In Protocalliphora (Fig. 99) it is even somewhat convex, or raised; in this genus the ridge is hardly discernible.

The ventral part of the posterior segment is composed of the anal protuberance, which consists of the anal lobes and the anus (Fig. 197). Not much interspecific variation occurs in the structure of this part of the segment, although the protuberance does appear to be more pronounced (i.e. it takes up a greater proportion of the segment) in species with a low Shape Factor (see 4.2.2) than in others. The anus is delimited by two fleshy lips (Fig. 101) and, in most species studied, exhibited no features of diagnostic use. However, in the termitophilous Tricyclea deemingi, a heavily sclerotised anal plate is found (Fig. 297). This is the only Calliphorid seen by me that possesses this structure; the anal plate, as well as anal tubercles, are almost always present in Muscidae (Skidmore, 1973; Ferrar, 1979).

In the early instars the above-mentioned papillae are also present, but are much less developed. They were not found to be of diagnostic use in these stages.

Finally, the posterior spiracles and the spinulation of the twelfth segment are of great systematic value; these are discussed below.

4.2.4.3 The Thoracic and Remaining Abdominal Segments

In most Calliphorid larvae the only surface structures present on these segments are small papillae resembling the oral papillae on the cephalic segment (see 4.2.4.1), but rather smaller. They are situated laterally and ventrally (and about mid-segmentally on all the segments from the second thoracic to the seventh abdominal inclusive. There are about ten per segment and they vary somewhat in size, the more ventral ones tending to be larger.

Sinton (1921) used these papillae to differentiate between Lucilia sericata and Chrysomya megacephala (as Pycnosoma dux) on the basis of the number of papillae per segment and their positions on the segment. For example, he illustrates Ch. megacephala with four papillae situated at each side (eight in total) on the second thoracic segment. He also shows L. sericata as possessing an additional pair (ten in total) situated ventrally on the equivalent segment. In general, he showed L. sericata as possessing more ventral papillae than Ch. megacephala.

I attempted to repeat Sinton's work using the same two species. The method I employed was as follows: The larva was cut open mid-dorsally from end to end, the body contents were removed, and skin was washed in clean water. it was then mounted flat (external surface upwards) on a slide, using Berlese's Fluid as mounting medium, and covered with a large coverslip. The preparation was examined under a compound microscope at magnifications of up to X320.

Using this method I was unable to distinguish between the two species. The number of papillae on the second thoracic segment varied

between six and ten in both species, and no difference in size could be noted between the species. Two further species, Calliphora vicina and Calliphora vomitoria, were examined by the above method. Again, it was not possible to distinguish between these two species, or between them and the first two species.

There are two possible reasons why these results differ from Sinton's. Firstly, Sinton boiled his specimens in 10% KOH for one minute and then allowed them to soak for a further 5 or 10 minutes; he then dehydrated, cleared and mounted them in Canada balsam. This method, especially the KOH treatment, may have obliterated some of the papillae; no KOH treatment was done in the present study. Secondly, Sinton's specimens were derived from a few cases of myiasis in India and persia and were thus only a few in number; it is possible, therefore, that his specimens, falling as they do within the natural range of variation, simply happened to show the numbers he illustrates. In this study, thirty specimens of each species were examined by the above method.

I was not able to find any trace of these papillae in the early instars.

The third instars of some species of Chrysomya possess long processes on all but the first thoracic segment. There are typically fourteen per segment, situated dorsally, laterally and ventrally. The dorsal and lateral ones are always much longer than the ventral ones. The processes of each side are numbered 1-7 and arranged as shown in Fig. 195 . In addition, there is present in some species a small process, 4a, which is situated ventral, and slightly anterior, to

process 4. Each process is an outgrowth of the segment and is topped with a tuft of spines (Fig. 115).

Processes 1 and 4a are of great diagnostic value in the species examined. The stalks of the processes are usually devoid of spines, but spines are present on process 1 in Chrysomya sufifacies. This is an excellent character with which to distinguish this species from Ch. albiceps whose process 1 is devoid of spines (compare Figs. 114 & 115). In Ch. incisuralis all processes possess spines on their stalks.

All known 'hairy' maggots of this type are predatory upon other larvae (Patton and Evans, 1929). It is said that the processes aid the larva to support itself while attacking its prey.

The second instars of 'hairy' maggots also possess these processes. The first instars, however, possess only very small tubercles in the equivalent positions.

Finally, it is interesting to note that, in all known hairy maggots, the posterior papillae of the twelfth segment are always well-developed.

4.2.5 Spinulation

The arrangement and structure of the spines of Calliphorid larvae are of great systematic importance. The spines are present in general bands (the spinal-welts of authors) at the anterior and posterior margins of the segments. As a general rule segments 2-12 possess anterior bands, while only segments 6 or 7-12 possess posterior bands. The spines forming the anterior bands point backwards, while those forming the posterior bands point forwards. Not

all the bands form complete rings round the segments; those anterior bands present on posterior segments (9-12) and those posterior bands present on anterior segments (6-9) tend to be incomplete dorsally. Furthermore, the more posteriorly situated an anterior band is, the more incomplete it tends to become. Similarly, the more anteriorly situated a posterior band is, the more incomplete it too becomes. The result of this is that there are more backward-pointing spines on the anterior half of the larva, but more forward-pointing spines on the posterior half. The dorsal incompleteness of certain bands is often of use in specific identification.

In addition to the bands proper, there is present in many species a rather short band situated immediately anterior to the anterior bands (Fig. 196) one on either side. This feature is particularly well-developed in species of Chrysomya, although it is present in other genera. I term it the pleural band.

The posterior band of segment twelve in the third instar deserves special mention, as the spinal arrangement here is often very useful in the separation of species. This 'band' is characteristically composed of two semi-circles of spines, one above and one below the anus (Fig. 205). The diagnostic value of this lies in the extent to which the two semi-circles converge on one another to form a complete circle of spines surrounding the anus. This spinal arrangement is a very reliable guide to the identification of many species. Another useful feature is the patch of spines immediately dorsal to the anus (Fig. 206). This may consist of many, heavily-pigmented spines or a few weakly-pigmented ones, or may be absent altogether.

The anterior bands situated on the more posterior segments

(usually segment 6 onwards posteriorly) are divided ventrally to form bands that may be described as having an inverted Y-shape (Fig.193). This feature varies a great deal intraspecifically and could not be used for diagnostic purposes.

Not all species have their spines localised in bands. Some species, e.g. Cordylobia, Protocalliphora and Elephantoloemus species, possess spines that are uniformly distributed over the entire body surface. In other species, e.g. Booponus intonsus, the whole surface is not covered, but the spines seem to be distributed randomly. In those species in which the spines are localised in bands, that part of the cuticle in which they are situated is almost always somewhat thickened (Fig. 100).

On the second segment (or first thoracic segment) there is present, in addition to the usual anterior band, a second, much wider, dorsally incomplete band, situated approximately mid-segmentally (see 4.2.3.: Newport's segment). The width of this second band in relation to the width of the spineless area between it and the anterior band is of diagnostic value in some species.

The structure and degree of pigmentation of the spines themselves are of great systematic value. Each spine consists of a broad base and a tooth, the pigmentation being greatest in, either the tooth itself, or the area where the base and the tooth join; this feature is thus of diagnostic use (compare e.g. Figs. 41 and 42). A cross-section through the spines of Lucilia sericata shows that the pigment is located only peripherally in the base, but that it is distributed throughout the body of the tooth (Fig. 77). The degree of pigmentation (i.e. how dark-coloured the spine is) is also a feature

of diagnostic use, but it is not easy to describe in words; however, a comparison of e.g. Figs. 48 & 49 will show clearly the difference in pigmentation. (It must be noted that the colour of the spines is a dark brown to a light orange colour. This, of course, appears black or grey in the photographs.)

The form of the spines themselves is an excellent diagnostic character, but which has hitherto hardly been exploited in the taxonomy of the Calliphoridae and most other Cyclorrhapha. The spines may be small with pointed tips, or large with rounded tips (compare e.g. Figs. 40 & 41). Intermediate forms also occur. In many species, e.g. Chrysomya pinguis (Fig. 62) and Cochliomyia hominovorax (Fig. 65) each spine may possess two or three teeth. The spines of many species may be quite long, e.g. Protocalliphora azurea (Fig. 67) and Amenia imperialis dubitalis (Fig. 70). Many species possess spines that are strikingly different from the usual form, e.g. the scale-like spines of Chrysomya albiceps (Fig. 71) and the long hair-like spines on the first segment of Protocalliphora (Fig. 68). In the latter genus the first segment is adapted as a sucker, and these long spines presumably enable the larva to obtain a grip on the host's skin. The spines at the apex of the above-mentioned body processes of the hairy maggots are also distinctive (Fig. 115).

The spines on any one individual are never uniform in shape. In general, the anterior spines of the anterior bands, and the posterior spines of the posterior bands are much more robust than those situated more posteriorly or anteriorly respectively. In many species, especially of Phormia, the posterior spines of the anterior bands are of somewhat different type, being much smaller and narrower (Fig. 69). The spines on the ventral part of the anterior band of

seg. 2 are always more robust.

The arrangement of the spines within the bands is often a useful specific character. In many species, especially those with large spines, the spines are located alternately in the rows (Fig. 48) but there are always areas on the bands where this arrangement breaks down. In other species, no pattern at all is discernible, although in some the spines are often in neat (non-alternate) rows in large areas of the bands (Fig. 52), whereas in others the spines appear to be arranged totally haphazardly (Fig. 50). The bands are usually from about seven to twelve spines broad, with those species possessing large spines having fewer spines per band.

The above remarks refer to all larval instars, although the spines of the first and second instars are smaller and never have more than one tooth.

Apart from the spines, there are present on the twelfth segment in the first and second instars a circle of fine hairs situated around the posterior spiracles. These hairs were found to be an excellent character for distinguishing between the early instars of Calliphora and Lucilia, being considerably longer and more robust in the former genus (Figs. 73 & 74). In practical terms, Calliphora hairs may be seen under low power, but those of Lucilia cannot.

4.2.6 The Tracheal System

A great deal of information on the respiratory systems of Diptera was presented by Keilin (1944). Whitten (1955, 1960) established the systematic value of the internal respiratory systems

of Diptera larvae at the family level.

An attempt was made to find diagnostic features in the internal tracheal system that would serve to distinguish between the genera Calliphora and Lucilia. The method adopted was as follows: Larvae were aetherised and then pinned at the extreme anterior and posterior ends onto a dissecting dish and covered with insect saline. The integument was then cut open and pinned back and the tracheal system examined. The species examined were third instar C. vicina and L. sericata; five specimens of each species were dissected.

Two features of possible diagnostic use were noted. The junction of the lateral branch from the dorsal cervical anastomosis (Fig. 199) appeared to be situated closer to the lateral trunk in Calliphora than in Lucilia. The tenth anastomosis, immediately behind the posterior spiracles, appears shorter in Calliphora than in Lucilia (Fig. 199).

Another feature of the internal tracheal system, first noted by Laake, Cushing and Parish (1936) and confirmed by the present study, is that the posterior parts of the lateral trunks are darkly pigmented in Cochliomyia hominivorax, but are the normal tracheal colour in Cochliomyia macellaria.

However, the features of greatest taxonomic value are the structure of the anterior and posterior spiracles which are visible externally. The anterior spiracles are situated on the second segment in the second and third instars, but were long thought to be absent in the first instar. However, Kitching (1976) was able to detect them in this instar as simple holes in species of Australian Lucilia and Chrysomya using the SEM. I have not been able to find them in Calliphora vicina using this technique.

In the later instars the anterior spiracle, which is the anterior extremity of the lateral trunk, can be seen as a multi-lobed structure (Fig. 200). It has a granular appearance, is yellow or orange in colour and lacks the spiral thickenings of the tracheal trunk. The body of the spiracle is termed the felt chamber. Froggatt (1918) stated that the part of the chamber closest to the lobes is lighter-coloured than the rest of the chamber in some species and that this feature enabled specific separation of certain species. While this feature does occur, it is very variable intraspecifically and I have not found it reliable for identification.

The thickness of the chamber and the general arrangement of the lobes (e.g. tree-like, fan-like), have been considered to be of diagnostic use in certain groups of Calypterate larvae (e.g. Ferrar, 1979), but in the Calliphoridae it was found that these features were very variable within one species. An exception is the genus Amenia, where the chamber is very narrow and the arrangement of the numerous lobes may be said to be 'tree-like' in appearance (Fig. 293).

The number of lobes, however, is of great systematic use, each species having a limited range, rather than a definite fixed number (see Table IV). This feature is of particular use at the specific, rather than the generic, level. Thus, in the genus Calliphora, Calliphora loewi possesses 5-8 lobes (usually 5 or 6), whereas Calliphora vomitoria possesses 9-12 lobes (usually 10 or 11) in the third instar. The number of lobes may be different in the two spiracles in an individual; also, the number is often, but not always, greater in the third instar than in the second. The lobes of the spiracle are, in fact, double structures, as may be seen in Fig. 107. In the species

TABLE IV

(AS) Number of lobes of anterior spiracles of 2nd and 3rd Instars
(PSD) Posterior spiracle greatest diameter of 3rd Instar and Puparium (in mm)

Species	2nd Instar AS	3rd Instar AS	3rd Instar PSD	Puparium PSD
Calliphora vicina	8–10	8–11	0.23–0.30	0.20–0.25
C. vomitoria	9–11	9–12	0.33–0.38	0.31–0.33
C. uralensis	9–11	9–11	0.33–0.35	0.28–0.33
C. alpina	5–8	5–8	0.18–0.20	0.20–0.21
C. subalpina	5–8	5–8	0.20–0.23	0.17–0.20
C. loewi	5–6	5–8	0.17–0.19	0.15–0.18
C. lata	–	10–12	0.25–0.30	–
C. quadrimaculata	–	12–13	0.23–0.29	–
C. hortona	6–7	6–7	0.23–0.30	0.20–0.23
C. terraenovae	8–9	8–9	0.23–0.28	–
C. livida	–	10–11	0.28–0.30	–
C. stygia	10–11	11–12	0.31–0.35	–
C. augur	9–10	9–10	0.22–0.3	0.22–0.28
C. ochracea	–	9–10	0.23–0.30	–
C. croceipalpis	8–10	9–10	0.23–0.30	–
Cynomya mortuorum	8–10	8–10	0.22–0.25	0.17–0.23
Cynomyopsis cadaverina	–	6–7	0.25–0.28	–
Triceratopyga calliphoroides	–	7–8	0.23–0.25	–
Eucalliphora latifrons	–	7–8	0.23–0.30	–
Aldrichina grahami	–	9–11	0.22–0.25	–
Lucilia sericata	7–9	7–9	0.25–0.28	0.20–0.22
L. caesar	8–9	9–10	0.20–0.25	0.20–0.23

Species	2nd Instar AS	3rd Instar AS	3rd Instar PSD	Puparium PSD
Lucilia ampullacea	7-8	7-8	0.23-0.26	-
L. cuprina	4-5	4-5	0.20-0.23	-
L. porphyrina	7-8	7-8	0.25-0.26	-
L. bufonivora	4-6	4-6	0.26-0.28	-
L. caeruleiviridis	-	7-9	0.25-0.26	-
L. pallescens	-	6-7	0.20-0.23	0.20-0.23
Hemipyrellia ligurriens	7-8	7-9	0.20-0.22	0.23-0.25
H. fernandica	-	7-8	0.23-0.25	0.25-0.26
Chrysomya bezziana	4-6	4-6	0.43-0.45	-
Ch. chloropyga	-	11-13	0.40-0.43	-
Ch. putoria	12-13	12-13	0.40-0.43	0.35-0.40
Ch. albiceps	8-10	11-12	0.43-0.45	0.43-0.45
Ch. rufifacies	11-12	11-12	0.33-0.35	0.30-0.35
Ch. incisuralis	-	10-11	0.45-0.48	-
Ch. varipes	-	8-9	0.25-0.30	0.25-0.28
Ch. marginalis	-	11-13	0.55-0.63	0.55-0.60
Ch. megacephala	12-13	12-13	0.53-0.60	-
Ch. semimetallica	-	11-13	0.40-0.45	-
Ch. saffranea	-	12-13	0.25-0.43	-
Ch. pinguis	12-13	12-13	0.40-0.43	-
Cochliomyia hominivorax	-	8-9	0.40-0.42	-
Co. macellaria	8-10	8-10	0.40-0.45	0.40-0.43

Species	2nd Instar AS	3rd Instar AS	3rd Instar PSD	Puparium PSD
Pollenia rudis	-	4-5	0.25-0.28	0.25-0.26
Phormia regina	9-11	9-11	0.35-0.38	0.36-0.38
Ph. terraenovae	9-11	9-11	0.36-0.38	0.32-0.40
Boreellus atriceps	-	9-11	0.36-0.38	0.33-0.36
Protocalliphora azurea	8	8	0.20-0.23	0.20-0.23
P. sialia	-	8-10	0.24-0.25	-
P. avium	-	8-10	0.27-0.28	-
Amenia imperialis	Numerous	-	-	-
Amenia leonina	Numerous	-	-	-
Tricyclea deemingi	-	10	0.20-0.25	-
Auchmeromyia luteola	-	3-5	0.15-0.20	0.15-0.20
Elephantoloemus indicus	9	9-10	0.10-0.18	-
Booponus intonsus	-	9-10	0.18-0.20	-
Cordylobia rodhaini	-	6-9	0.35-0.38	-
Cor. anthropophaga	-	5-7	0.22-0.27	-
Cor. ruandae	-	5-7	0.20-0.25	-

descriptions the number of lobes refers to the number of each complete lobe, not to its components.

The posterior spiracles, situated on the twelfth segment, are in the first instar simple, kidney-shaped structures, (Fig.201), whereas in the second and third instars they are much more elaborate. In the latter instars the spiracle consists of an outer heavily sclerotised ring, the peritreme, which surrounds the spiracular apertures. In the second instar the peritreme is incomplete at the ventral end, and there are two apertures (Fig. 202). In the third instar (Fig. 204) the peritreme is complete and a 'button' is present at the ventral end; this is the ecdysial scar of the second instar spiracle (Keilin, 1944). Three apertures are present in the third instar.

Each aperture possesses a superficial series of interlocking teeth, whereas deeper inside the strucutre there is a network of anastomosing bands (Fig. 204). The number of these bands is often a useful identification feature, some species, e.g. Calliphora vomitoria (Fig. 90), having many more such bands than others, e.g. Protocalliphora azurea (Fig. 92).

Another important feature of the apertures is the angle at which they are inclined with respect to each other. In most Calliphoridae, they are inclined only at a slight angle to one another (Fig. 204). In some species, however, e.g. Pollenia rudis, they are inclined at a much wider angle, often at a right angle (Fig. 95). In other species, e.g. Auchmeromyia luteola (Fig. 106), the apertures are effectively parallel.

In many illustrations published in the past, e.g. Hall (1948) and Zumpt (1965), the apertures are given a broader (i.e. wider in

relation to length) appearance in some species than in others, thus implying that this character is of diagnostic use. In fact, this feature is particularly misleading, not only because of natural intraspecific variation, but also because these apertures are capable of opening and closing, and hence the appearance of an aperture would depend at any given time on its degree of closure.

In most Calliphorid larvae the apertures are more or less straight, but in species of Cordylobia, especially C. rodhaini, the apertures are sinuous (Fig. 302). In species of Protocalliphora, the middle aperture is often at least slightly twisted at its dorsal end. It is interesting to note that both these genera are parasitic; in particular, the extremely tortuous apertures in C. rodhaini closely resemble those of the parasitic Gasterophilidae.

In spite of the traditional reliance placed on the thickness and degree of sclerotisation of the peritreme, the present study has shown that these characters are of limited taxonomic use, since they were found to vary in one species to such an extent as to render this character useless for specific identification. However, it is true that there is a tendency for some species to have more heavily sclerotised spiracles than others; nevertheless, reliability in identification must not be placed on this character, particularly when dealing with carrion-breeding species. However, the peritremes of the parasitic genera Auchmeromyia, Cordylobia and Booponus are always very weakly sclerotised.

Another structure subject to such variation is the internal peritremal projection (Fig. 204). Both Hall (1948) and Schumann (1954) illustrate this structure in C. vicina; in these illustrations no deep

peritremal projections are shown, although these do occur in many specimens of this species. This may be misleading as this structure has been used diagnosticaly in certain Calliphorid species. For example, Zumpt (1965), in his key to the Lucilia larvae known to cause myiasis, states that the presence of an inner peritremal projection in L. sericata distinguishes it from L. cuprina. Having examined many culture-derived specimens of both these species, I find that they are inseparable on this basis, as many specimens of L. sericata lack a peritremal projection.

In many descriptions the pigmentation of the 'button' area is used as a diagnostic feature. This is a rather difficult character since some species, e.g. Phormia terraenovae, consistently lack pigmentation in this area, while other species vary a good deal in this character; compare Figs. 90 and 91.

Another feature, while of no systematic value, but nevertheless worth mentioning, is the three-dimensionality of the peritreme. Most illustrations (including those in the present work) tend to give the impression that the peritreme is simply a band of colour having no thickness or depth. In fact, the peritreme is very much a three-dimensional structure as may be seen by dissection.

A feature of some taxonomic importance is the so-called 'sun-ray' structure, first described by Froggatt (1918). It is composed of four foci in the third instar (Fig. 204) which are presumed to strengthen the spiracle. The elements of this structure situated on the inner (relative to the mid-line body axis) side of the inner aperture and the outer sides of the middle and outer apertures have been termed by Froggatt 'blister-structures', while giving the

name 'intermediate structure' to the large element lying between the middle and inner apertures.

The filaments of this structure give the appearance of light rays, (Fig. 204), but careful focussing will show them to be much thicker bands, as may be seen easily with the SEM (Fig. 94). These bands branch dichotomously and their apical tips end on the peritreme. At the point of origin these bands usually number about four to six.

The first to use the sun-ray structure in systematics was Huff (1925), who compared its structure in several families of Cyclorrhapha. In the Calliphoridae, the sizes of the intermediate and outermost blister structures were found to be of diagnostic use, especially in the genus Chrysomya. In this genus these two elements were found to be consistently shorter than in others. In species of other genera, e.g. Auchmeromyia luteola and Protocalliphora azurea, all four foci of the sun-ray structure are absent, or extremely reduced (Figs. 106 and 92). Again, it is worth noting that these two species are parasitic.

A feature hitherto overlooked is the group of filaments emanating from the 'button'. These filaments are often more numerous and more easily discernible in certain genera, e.g. Cynomya and Triceratopyga, than in others, e.g. Calliphora. It is presumed that these filaments, like the sun-ray structure, strengthen the spiracle.

The sun-ray structure is also present in the early instars, there being two foci in the first instar and three foci in the second. It has not been found to be of diagnostic use in these instars.

The most recent publication dealing mainly with the sun-ray structure is a paper by Khole (1977). This paper contains many errors

and it is necessary to correct them in order to avoid future confusion.

Quite apart from the confusingly bad grammar of the paper, five separate errors can be identified. Firstly, the illustrations of the sun-ray structure bear little resemblance to the real structure. Secondly, Khole states that the sun-ray structure is absent from the first instar and, in Lucilia cuprina from the second instar. Thirdly, he states that it is absent from the third instar of Chrysomya megacephala. From my own observations I can state that the structure is present in all instars of both these species. Fourthly, he states that the sun-ray structure disappears after pupariation, whereas it actually becomes more prominent in the puparium. Fifthly, he attacks and misquotes Huff (1925), by saying that he (Huff) claimed that the function of the sun-ray structure in Calliphoridae is similar to the function of the interspiracular bristles in Drosophila i.e. to prevent sinking of the spiracles below the surface of the medium. What Huff actually says is "the small size of the 'sun-ray' structures would indicate that they do not, in the species which he [i.e. the author] has examined, serve the same function as the interspiracular bristles of the Drosophila larvae". In fact, Huff is saying the exact opposite of what Khole claimed he was saying. Finally, on a matter of opinion, Khole states that Huff "treated 'sun-ray' structures as homologous to such 'interspiracular bristles'[i.e. of Drosophila] without much justification". In fact, Huff only suggested the possibility of such a homology, and he did present "much justification" for this point of view. This point will be discussed in a later chapter.

One of the most useful features of the third instar posterior spiracles is the spiracle distance factor (SDF), first proposed by van Emden (1965) for Muscidae larvae. This value is calculated by dividing the distance between the spiracles by the greatest diameter of one spiracle. SDFs were calculated for a large number of specimens and it was found that each species had fixed ranges which in some species, e.g. Calliphora vicina, was amazingly narrow. Species with low values have large spiracles set close together, whereas those with high values had smaller spiracles set farther apart. (See Table V)

Finally, the actual measurement of the greatest diameter of the spiracle of the fully grown third instar is also very constant in each species and is often a very reliable guide in identification. (See Table IV)

4.3 Morphology of the Puparia

4.3.1 Pupariation

During the process of pupariation, the third instar cuticle contracts, darkens and hardens, to form a protective covering for the pupa. The puparium thus formed shows many of the features of the third instar, the most obvious of which are the spines and the, now non-functional, larval spiracles. The spines, like the rest of the puparium, become much darker, although their structural details remain discernible. The features of the spinal bands enabling specific identification remain, of course, as they were in the larva.

Contraction causes some changes at the anterior and posterior ends of the puparium. Anteriorly, the first segment contracts strongly

TABLE V

Third Instar and Puparium Spiracle Distance Factors

$$\text{Spiracle Distance Factor (SDF)} = \frac{\text{Distance between posterior spiracles}}{\text{Greatest diameter of one spiracle}}$$

Species	3rd Instar SDF	Puparium SDF
Calliphora vicina	1-1.2	0.77-1.11
C. vomitoria	0.69-0.80	0.61-0.74
C. uralensis	0.64-0.92	0.48-0.52
C. alpina	1.29-1.88	1.55-1.58
C. subalpina	1-1.13	0.6-0.63
C. loewi	1.29-1.67	1.43-1.47
C. lata	0.6-0.8	-
C. quadrimaculata	1.0-1.2	0.77-1.0
C. hortona	1.1-1.2	0.8-1.0
C. terraenovae	0.69-0.75	0.50-0.53
C. livida	0.8-1.1	0.58-0.67
C. stygia	0.75-0.84	-
C. augur	0.86-1.1	0.86-1.1
C. ochracea	0.95-1.2	-
C. croceipalpis	1-1.2	-
Cynomya mortuorum	1.75-1.88	0.97-1.38
Cynomyopsis cadaverina	1-1.2	-
Triceratopyga calliphoroides	1.1-1.3	-
Eucalliphora latifrons	1.12-1.14	-
Aldrichina grahami	0.93-1.18	1-1.38
Lucilia sericata	1-1.18	0.56-0.70

Species	3rd Instar SDF	Puparium SDF
Lucilia caesar	0.69-0.83	0.48-0.75
L. ampullacea	0.50-1.58	-
L. cuprina	0.67-0.75	-
L. porphyrina	0.47-0.50	-
L. bufonivora	1.6-1.8	-
L. caeruleiviridis	0.6-1.20	-
L. pallescens	0.88-1.11	-
Hemipyrellia ligurriens	0.92-1.00	0.63-0.75
H. fernandica	0.85-0.95	0.60-0.65
Chrysomya bezziana	0.11-0.13	-
Ch. chloropyga	0.31-0.35	-
Ch. putoria	0.44-0.57	0.63-0.75
Ch. albiceps	0.22-0.24	0.20-0.29
Ch. rufifacies	0.36-0.59	-
Ch. incisuralis	0.5	-
Ch. varipes	0.47-0.79	0.41-0.50
Ch. marginalis	0.39-0.41	-
Ch. megacephala	0.27-0.35	-
Ch. semimetallica	0.48-0.55	-
Ch. saffranea	0.18-0.90	-
Ch. pinguis	0.29-0.38	0.37-0.43
Cochliomyia hominivorax	0.18-0.25	-
Co. macellaria	0.46-0.53	0.55-0.82

Species	3rd Instar SDF	Puparium SDF
Pollenia rudis	0.92-1.2	0.83-0.86
Phormia regina	0.58-0.67	0.67
Ph. terraenovae	0.45-0.67	0.5-0.71
Protocalliphora azurea	2.1-3	2.50-2.56
P. sialia	2.2-2.5	-
P. avium	1.75-1.9	1.9-2.5
Stomorhina cribrata	-	1.2
Tricyclea deemingi	1.2-1.5	-
Auchmeromyia luteola	4.0-5.3	4.5-5.63
Elephantoloemus indicus	0.57-0.73	-
Boreellus atriceps	0.47-0.88	1-1.18
Booponus intonsus	1.8-2.2	-
Cordylobia rodhaini	0.30-0.5	-
C. anthropophaga	0.36-0.67	-
C. ruandae	0.30-0.55	-

into the second, which later becomes the first visible segment of the puparium. The second segment is easily recognised by the presence of the larval anterior spiracles at its anterior margin. The features of the spiracles themselves, which are usually lighter in colour (an orange-brown) than the rest of the puparium, remain discernible and are useful in identification. However, care must be taken when examining these structures in the puparium, as the lobes become very brittle and are liable to break off. When counting the lobes, therefore, it is important to attempt to detect any 'breaks' showing missing lobes.

At the posterior end contraction results in the almost complete obliteration of the posterior papillae in those species in which the papillae are not well-developed. However, in species in which they are well-developed, e.g. Boreellus atriceps, the papillae remain almost unchanged; the same applies to the body processes of 'hairy' maggots.

The posterior larval spiracles become very heavily sclerotised and their structure remains discernible. Also, the spiracle distance factor remains of diagnostic value. In most species, e.g. Calliphora vomitoria, pupariation results in a decrease in the SDF (i.e. the spiracles come closer together), but in some species, e.g. Chrysomya albiceps the SDF increases. In some species, e.g. Calliphora loewi, the SDF remains within the same range as in the third instar, but with even narrower limits.

4.3.2 Colour

As with the larvae, colour is usually not a reliable

identification feature in puparia. The colour ranges from reddish-brown to almost black and, while specific differences do occur, they are often difficult to describe. Among the species of Calliphora, C. vicina and C. vomitoria tend to be consistently darker and shinier than the other British species of the genus. However, in some species colour is a reliable guide to identification, e.g. Phormia terraenovae whose puparium is almost black.

4.3.3 Surface Sculpture

During the process of contraction, the cuticle undergoes a great amount of folding and circumferential (i.e. transverse to long axis) creasing, e.g. in Calliphora vomitoria (Fig. 104). In a few species, however, the creasing is less regular, forming a reticulate pattern as in Auchmeromyia luteola (Fig. 102), and this feature is, therefore, often of diagnostic use.

The area of cuticle surrounding the posterior larval spiracles seems to be less subject to wrinkling in most species, e.g. Boreellus atriceps, while in other species, e.g. Cordylobia anthropophaga (Fig. 103) this area is subjected to heavy folding.

In species of Protocalliphora very little folding seems to occur at any part of the cuticle, and contraction is kept to a minimum.

4.3.4 Size and Shape

In all the species studied, the puparium is shorter but broader than the third instar larva; this is the natural consequence of

contraction. As with larvae, size is useful as a general guide, but with puparia there is the added advantage that preservatives do not cause them to contract.

At least twenty puparia of each species were measured, whenever an unlimited number was available. In other species, where less than twenty specimens were available, all specimens were measured. All measurements are given in Table II.

The shape of a puparium is typically barrel-shaped, being broadest more or less at the centre. The ventral side in most species is somewhat flatter than the more convex dorsal surface.

The puparial measurements and the Shape Factor (measured in the same way as the larval equivalent; see 4.2.2) are very useful in the identification of puparia. All factors calculated are given in Table III.

4.3.5 Pupal Respiratory Apparatus

As noted above, the larval spiracles become non-functional in the pupal stage. The functional pupal respiratory apparatus is represented externally by a pair of respiratory horns situated dorsolaterally at the posterior margin of the fifth segment (the apparent fourth in the puparium; see 4.3.1) (Fig. 189). These horns form the sclerotised outer covering of a tube, known as the felt chamber, which leads to an internal prothoracic spiracle and a tracheal branch (Fig. 203).

It is interesting to note that, while respiratory horns are present in many Calypterates, most Acalypterates do not possess them. In these groups only the internal spiracle is present, but the

air-filled space between the pupal cuticle and the puparium is large, thus enabling the pupa to respire (Keilin, 1944).

During pupariation two small round areas on the fifth segment do not harden and darken like the rest of the cuticle, and it is at these points that the horn pierces the cuticles. According to Keilin (1944) (referring to Phoridae pupae), the horns sometimes miss the aperture and come to lie between the pupa and the puparium. He also states that if only one horn does this the pupa will still develop normally and an adult will eventually emerge, but if both horns come to lie internally the pupa will be unable to respire and dies.

When the respiratory horns are in the process of developing, the pupa is at a rather vulnerable stage, since the horns may be damaged or broken off quite easily. Prof. K. Bowler (pers. comm.) tells me that shaking the medium in which larvae are pupating causes a significant increase in their mortality; it is possible that this is due to damage to the respiratory connections. Even after full development and sclerotisation the horns are liable to be broken (see Fig. 89).

The respiratory horns vary in length from about 0.02-0.05 times the greatest width of the puparium. The structure of the horns is of great diagnostic use, in spite of the fact that they exhibit a certain amount of intraspecific variation. The spiracular papillae present mainly on the posterior side of the horn are few and large in certain species, e.g. Calliphora vomitoria (Fig. 79), and small and numerous in others, e.g. Calliphora uralensis (Fig. 80). Some species have very smooth horns, e.g. Chrysomya megacephala (Fig. 87) and Lucilia sericata (Fig. 85). In Phormia terraenovae rather fine papillae are

present (Fig. 86), while in Calliphora loewi (Fig. 83) the papillae are present as rather irregular bands of thickening. The robustness of the horns differs markedly between species, as may be seen by comparing Calliphora vicina (Fig. 78) with Lucilia sericata (Fig. 85). In Cynomya mortuorum the horn bears two or three large tubercles (Fig. 84); the papillae are situated both on these tubercles and the main body of the horn.

The internal structure of the horns was not studied in detail, but in the broken horn of Calliphora augur (Fig. 88) may be seen a rather spongy structure.

The respiratory horns of all six British species of Calliphora are shown in Figs. 78-83. Their structure is a reliable identification guide, but it is interesting to note that the horns of C. alpina and C. subalpina, once placed in the distinct genus Acrophaga, resemble one another more closely than any other pair of Calliphora species. Of all the characters studied in these two species, the shape of the respiratory horn is the only one that is shared between them and not by any other species, and is the only immature feature that can be described as an 'Acrophaga' character.

4.3.6 Adult Eclosion

At the time of adult emergence from the puparium, the anterior end or operculum of the puparium breaks into two parts along two lines of cleavage. The first, which may be termed the true 'cyclorrhaphous' line occurs at the boundary of segments 4 and 5, while the second line of weakness extends from the anterior end of the puparium to the first

line (Fig. 191). This second line always runs in such a way that the dorsal 'cap' bears the larval anterior spiracles. The third instar cephalophoryngeal skeleton is to be found adhering to the ventral 'cap'.

This method of eclosion seems to be the rule in most Cyclorrhapha, although in many Acalypterates the second line is absent, the cap breaking off in one part. It is interesting to note that in those Diptera families of disputed systematic postion (i.e. the Higher Brachycera and the Cyclorrhapha Aschiza) the lines of cleavage are more complex than in the Cyclorrhapha Schizophora. Thus, in some Pipunculidae the 'cap' fractures into five parts (Clausen, 1940). In many Phoridae a second line of fracture exists as in Calliphorideae, but it is dorsal, running between the respiratory horns (Disney, 1983). The horns themselves lie on the caps, whereas in Calliphoridae they always to remain on the main body of the puparium.

It is a matter of common knowledge that the fully expanded Calliphorid adult is appreciably longer and stouter than the puparium from which it emerged. And yet this is not always so among the Cyclorrhapha. For example, Skidmore (1967) states that, in Heleomyzidae, the adult fly is approximately as long as its puparium (excluding the wings) and less stout. It is possible that this is connected with the fact that these species do not possess external respiratory horns and the pupa is, therefore, much smaller than the puparium (see 4.3.5).

CHAPTER FIVE

THE CEPHALOPHARYNGEAL SKELETON

The larvae of the Bluebottle hatch within two days in the warm weather. Whether inside my apparatus, in direct contact with the piece of meat, or outside, on the edge of a slit that enables them to enter, they set to work at once. They do not eat, in the strict sense of the word, that is to say, they do not tear their food, do not chew it by means of implements of mastication. Their mouth-parts do not lend themselves to this sort of work. These mouth-parts are two horny spikes, sliding one upon the other, with curved ends that do not face, thus excluding the possibility of any function such as seizing or grinding.

Jean Henri Fabre

The Life of the Fly

5.1 Introduction

The literature on the cephalopharyngeal skeleton is, like that on larval morphology generally, scattered throughout the literature. However, a number of works deal with the skeleton in detail, and a few are largely or mainly devoted to this structure alone. Weismann (1864) was the first to give a description of the Calliphorid skeleton. Lowne's (1890-92) work dealt with the skeleton in some detail, but his structural interpretations were faulty and will be discussed below. Snodgrass (1924), working on the larva of Rhagoletis pomonella (Tephritidae) made an important contribution to knowledge of the structure and function of the skeleton, but he also made a few minor

mis-interpretations. Miller (1932) presented what is probably the best account of the functional morphology of the Calliphorid skeleton, and some of his findings that were supposedly refuted by later workers are upheld in the present work. Ludwig (1949) studied the structure and embryology of the Calliphorid larval head, including the skeleton. Roberts (1969, 1971) investigated the functional morphology of various Calypterate larvae, including Calliphoridae, and related it to their feeding habits.

As noted at various points above, the descriptions of larval Calliphorid species were made usually on a piecemeal basis, and many of these descriptions included a figure of the skeleton, almost always in lateral view. This meant that those sclerites that were best studied from the ventral or dorsal aspect were ignored. In spite of the large number of illustrations that have been published, there is an almost total lack of critical discussion of the taxonomic value of the various sclerites (except where a more or less major deviation from the 'normal' condition occurs, such as the loss of a sclerite).

The aim of this chapter is, therefore, to describe the basic structure of the skeletons of the three larval instars and to discuss the taxonomic value of each sclerite. Also, certain sclerites whose structure or function is in dispute will be discussed. First, however, the homology and musculature of the skeleton will be briefly discussed.

5.2 Homology of the Sclerites

The homology of the Cyclorrhaphous larval head with the

primitive Dipteran head continues to be a matter of dispute. In the words of Traxler (1976), "Probably no other part of insect anatomy has been subjected to such a diverse amount of interpretation as that of the cephalopharyngeal apparatus of dipteran larvae." This fascinating topic has not been researched by the author, and the phylogenetic analysis presented in a later chapter is confined to relationships within the Cyclorrhapha. However, a very brief resume is given here.

Basically, there are two areas of dispute. Firstly, there are those who believe that the parts of the skeleton are not homologous with the head parts of other insects. The first to express this view was Weismann (1864) who postulated newly evolved structures to account for the mouth-hooks. Snodgrass (1924, 1935) suggested that the head of a Cyclorrhaphous larva was invaginated and that the skeleton was derived from the walls of the invagination; he did not believe that the skeleton was homologous with the primitive head capsule. Oldroyd (1954) also thought the skeleton was "a secondary development of jointed hooks", but he omitted this statement from the third edition of his book (1970).

The opposing school of thought considered that the skeleton was derived from the head capsule of the primitive insect and was not a new strucutre. The works of de Meijere (1916) and Cook (1949) indicated strongly that this was the case; later, Hartley (1963) presented further evidence to support this point of view. It is now generally accepted that this view is more likely to be true (Teskey, 1981). The difficulty with this theory, however, is the lack of any recognised transitional forms between the more primitive Diptera and the Cyclorrhapha, such as do exist between the Nematocera and Brachycera.

The second area of dispute is among those who accept that the parts of the skeleton are homologous with the primitive head, but disagree as to which particular sclerites were derived from which ancestral parts. For example Holmgren (1904), Hartley (1963) and Roberts (1971) believed that the mouth hooks were derived from the ancestral mandibles, whereas de Meifere (1916) and Menees (1961) believed that the mouth hooks were modified maxillae. There seems to be general agreement, however, that the skeleton arose through the fusion of parts of the external head structures (the mouthparts) and the tentorium.

Clearly further studies are needed to resolve this problem. It is suggested that detailed studies on the larvae of the Phoridae and the Platypezidae, in view of their intermediate position between the Brachycera and the Cyclorrhaph Aschiza, may be of value in clarifying these issues.

In view of the widespread disagreement regarding the homology of the sclerites, it must be pointed out that the terms used to designate the sclerites in this work are not intended to be statements of homology. The terms used are simply those that have the most widespread usage in the literature.

5.3 Musculature

Third instars of Calliphora vicina and Lucilia sericata were dissected and sectioned (see Materials and Methods) with the aim of studying the muscles associated with the skeleton. The purpose of this investigation was (a) to attempt to find interspecific differences in the musculature, and (b) to resolve some points of dispute arising from the work of previous authors.

No differences of systematic value were found between the two

species. However, it is felt that species having a very differently shaped skeleton from the above two species, e.g. Protocalliphora azurea may well reveal differences in the musculature.

The results of this investigation will not be presented in full here, since few new findings were made, and little has been added to the works of Miller, Ludwig and Roberts cited above. Exceptions, however, are the muscles controlling the mouth hooks and their associated structures, the attachment of which has been in dispute. These results are presented at the appropriate points below.

5.4 The First Instar Skeleton

In the first instar the skeleton consists of five element types (Figs. 213 & 214). At the anterior end lie the two mouth-hooks which are strongly angled structures, often of diagnostic value, being very robust and thickened anteriorly in certain species, and giving the impression of being more acutely angled in these species (compare Figs. 256 and 257). Anterior to the mouth hooks there are often present a number of very weakly sclerotised tooth-like structures which usually difficult to discern and are often invisible. They lie embedded in the cuticle. These structures are of no use in identification; I term these the anterior teeth, and they are omitted from the species illustrations. Immediately posterior and ventral to the mouth hooks on either side lie a group of three or four ill-defined sclerites termed the chitinised teeth. These rod- or club-shaped structures seem to be of little systematic use, apart from the fact that they are constantly very faint in some species.

Posterior and dorsal to the mouth hooks lies what may be termed the parastomal-pharyngeal sclerite. This is the largest single

sclerite in the first instar skeleton, but it is convenient to consider it in parts. The anterior half is composed of the two arms of the parastomal sclerite which extend anteriorly to join together and from the median tooth, and posteriorly to merge with the ventral cornua (Fig. 213). Dorsal to he ventral cornua lie the dorsal cornua which unite anteriorly to form the dorsal arch. The ventral and dorsal cornua are joined by the lateral plates. The most useful systematic feature shown by this sclerite is the narrowest width of the lateral plate in relation to the length of the median tooth. The shape of the median tooth is also a useful character, being narrower in relation to the basal part of the hypostomal sclerite (see below), when viewed laterally, in some species, but not so in others.

The hypostomal sclerite lies ventral to the parastomal sclerite; as noted above, the thickness of the basal part of this sclerite (in lateral view) is of diagnostic use. In addition, there exists in Calliphora vomitoria (and, in a much less developed form, in some other species, e.g. C. loewi) a more or less rounded sclerite lying posterior to the mouth-hook (Fig. 247); I have termed this the post-mandibular sclerite. As it exists only in some species it is, therefore, of diagnostic value.

The above account refers to the situation in most first instar larvae, but the first instar skeleton in Protocalliphora species is very different. In this genus the hypostomal sclerite is absent (Figs. 281 & 282). The mouth hooks are very robust for a first instar, and the parastomal bars do not meet and join anteriorly to form a median tooth, but each bar articulates separately with the mouth hook anterior to it. Between the two bars lie two plate-like sclerites. This situation was not observed in any other genus.

In the genus Amenia, the first instar skeleton is very much reduced, unsclerotised and extremely difficult to examine, being

effectively transparent; some details can be made out using phase contrast microscopy. All that can be seen is a very slender pharyngeal sclerite (Fig. 292). In addition, two sclerotised plates are present on the cuticle in the mouth region. First instar Amenia larva are uterine and do not leave the uterus until after the first moult. No larvae of the subfamily Phumosiinae were examined, but according to Ferrar (1978), the first instar of Euphumosia papua (Guerin) also has a very reduced skeleton. His illustration shows it to be very similar to those of Amenia species.

Lowne (1890) totally misinterprets the structure of the first instar skeleton. In his illustration on p.45, he shows the parastomal bars extending forwards to meet, and apparently fuse with, what is obviously the hypostomal sclerite. The arms of the hypostomal sclerite are illustrated as meeting and fusing anteriorly to form what is obviously the median tooth. As seen above, the median tooth is formed by the fusion of the parastomal bars, the hypostomal sclerite being a separate structure lying beneath them. Furthermore, Lowne states that he was "unable to find any trace of this sclerite [i.e. the hypostomal sclerite] before the second moult". As we have seen, this is not the case, this sclerite being present both in the first and second instars (see below).

5.5 The Second Instar Skeleton

The skeleton in this instar is a more complex structure than that of the first instar (Figs. 215 & 216). Each mouth-hook consists of an elongate basal part with a posterodorsal horn, and an anterior curved tooth. The length of the tooth in relation to the length of the base is important in distinguishing certain species of Lucilia

(Figs. 258 & 260). The thickness of the curved area of the tooth in relation to the posterior part of the tooth which merges into the base is of great diagnostic value, especially in the genera Calliphora (Figs. 236 and 237) and Lucilia. Ventrally there is present a dental sclerite which is attached to, and is part of, the mouth-hook, unlike the situation in the third instar (see below). The sclerotised connection between the dental sclerite and the mouth-hook may lie deeply in the tissues in some species and may thus give the misleading impression that the two elements are physically separate (compare Figs. 239 and 240).

Ventral to the posterior part of the mouth-hook base lies the liguloid arch, which is, when viewed ventrally or dorsally, a single, rather weakly sclerotised band lying between the two mouth-hooks; in the species studied it is too variable to be of taxonomic use. Posterior to the mouth-hooks lies the H-shaped hypostomal sclerite which is greatly variable between conspecific individuals. From the arms of the H anterior to the cross bar dorsally on either side there arises a thin dorsal process in most species; it is, however absent from certain species e.g. Elephantoloemus indicus, while in others, e.g. Protocalliphora spp., it is unusually robust (Fig.283).

In some species, e.g. Amenia sp. (Fig. 290) the hypostomal sclerite is very strongly linked with the pharyngeal sclerite, so much so that Ferrar (1976) states that in Amenia spp. there is only a single continuous sclerite posterior to the mouth-hooks. Detailed examination, however, will reveal the fact that the hypostomal and pharyngeal sclerites are separate. Ventral to the anterior part of the hypostomal sclerite lies a hypostomal plate on either side; they are of

no taxonomic value in this instar.

The pharyngeal sclerite consists of ventral and dorsal cornua and lateral plates, as in the first instar. Anteriorly the parastomal sclerites are reduced to two narrow bars; they are of no systematic use. On the other hand, the narrowest width of the lateral plate in relation to the length of the mouth-hook is a highly reliable character (compare Figs. 236 and 237). Areas of very weak or no sclerotisation (windows) are present on the dorsal and ventral cornua in some species, and this feature is of some supporting diagnostic use, but is subject to a great deal of variation (see below). Often windows are present only on the ventral cornua.

5.6 The Third Instar Skeleton

The structure of the third instar skeleton (Figs.217 and 218) is essentially similar to that of the second instar, with some important differences. the pharyngeal sclerite is (relative to the mouth-hooks) much larger and more elongate, and a good deal more heavily sclerotised. The general shape of the mouth-hooks is very different, lacking the 'angled' appearance of the second instar equivalent (compare Figs. 215 and 217).

The mouth-hook consists essentially of a broad basal part and a curved tooth (Fig. 219). The basal part consists of a dorsal horn, a dorsal ridge, a posterior condyle and a ventral angle (See Fig. 219). On the outer side of the basal part there is a large depression (Fig. 121), in the middle of which lies a pore which leads to the hollow lumen of the mouth-hook. A very useful diagnostic feature is

the length of the mouth-hook in relation to the length of the base (Fig. 219; compare e.g. Figs. 224 & 267). The general form and degree of curvature of the tooth are also useful (compare Figs. 225 and 262). The base also shows several features of systematic value, especially in the degree of prominence of the dorsal horn (compare Figs. 226 & 227) and the shape of the dorsal ridge (compare Figs. 224 & 289). Although these features are somewhat variable and difficult to quantify, they are nevertheless useful and are best represented by illustration rather than by actual measurements.

Ventral to the mouth-hook there lies a small dental sclerite, which, although frequently referred to in the literature as though it were a single sclerite, is, in fact, a complex of two structures set at right angles to one another (Fig. 220). Unit B of the complex is roughly triangular in outline and links to the more rounded unit A by means of an elongate process (p). Unit A was not found to be of much diagnostic use, but unit B, although variable, does exhibit some useful interspecific variation. This lies mainly in its size in relation to the mouth-hook; again it was not possible to quantify this feature precisely, it being best represented by illustration (compare e.g. Figs. 234 and 235). The dental sclerite as a whole is proportionately much smaller in certain species, e.g. Chrysomya bezziana, and totally absent in others, e.g. Protocalliphora azurea (Fig. 272 and 284).

It is important at this point to draw attention to some errors in the illustrations by Lowne (1890). His illustration on p.45 shows the mouth-hook possessing a posteriorly elongated and peg-like condyle. I have not seen such a structure in Calliphora vicina (the

species described by Lowne) or any other species. Another, rather remarkable feature illustrated by Lowne, is a thumb-like ventral angle possessing a brush of hairs at its ventral tip. Apart from the quite unusual shape of the angle, I have not seen any such hairs on any of the species studied; furthermore, it is difficult to see how Lowne could have made such an error, there being no structures in that area that could be mistaken for hairs. It is just possible that Lowne, seeing the mouth-hooks as mandible homologues, may have assumed that the ventral angle had a similar structure to the hairy prostheca of many insects.

The mode of functioning of the mouth-hooks has been a matter of some dispute among previous authors, and so an account of my studies on this aspect is given here. The abductor or elevator apodeme attaches to the dorsal horn in the manner shown in Fig. 219; in other words it reaches the horn from a posterior direction. This was shown by Ludwig (1949) and Roberts (1971), but Miller (1932) shows the apodeme as inserting from a posterodorsal direction. Dissections of Calliphora quadrimaculata (the species studied by Miller) during the present study have shown that the insertion is identical to the situation in C. vicina and L. sericata.

Regarding the point of insertion of the adductor or depressor apodeme, Miller stated that this was at the ventral angle of the mouth-hook itself. This was challenged by both Ludwig and Roberts, who stated that the apodeme inserted on the dental sclerite. Teskey (1981) quite rightly pointed out that if the apodeme inserted on the dental sclerite then the dental sclerite must be attached firmly to the mouth-hook base. However, he apparently accepted Ludwig's and Roberts'

views as he illustrates Phormia regina with the apodeme inserting on the dental sclerite.

My studies on this precise point have shown that the situation is rather more complex. By dissections of fresh larvae and moving of parts by pulling on the apodeme, and by close examination of flat slide preparations and of sections, the following was deduced (in Calliphora vicina). Two apodemes are involved. One proceeds forwards to attach to the ventral tip of unit B of the dental sclerite and then continues anteriorly to attach to the tip and anterior margin of the ventral angle (Fig. 120). The second apodeme inserts broadly onto unit B of the dental sclerite. The situation is shown diagramatically in Fig. 219).

The structure of the mouth-hook as seen with the S.E.M. shows two features of interest. Firstly, a ventro-lateral ridge may be seen running along the whole length of the tooth (Figs. 124 and 125), and the ventral surface of the tooth between the two ridges is relatively flat. The second feature of interest is the very smooth surface of the mouth-hook when compared with the rest of the skeleton.

Between the two mouth-hooks there lies a single unpaired structure, the oral sclerite (Fig. 218). This sclerite has often been stated to be either present or absent in certain species in the literature (e.g. Zumpt, 1965; Oldroyd and Smith, 1973) and has been used especially to distinguish between Calliphora and Lucilia. However, this study has shown that it is always present in the great majority of species, except in the species of Protocalliphora. The error originally arose because the sclerite is unpigmented in many species and is, therefore, difficult to see. Since it was thought to

be absent from many species it was termed the 'accessory' oral sclerite, but the first adjective should perhaps now be dropped from the terminology.

The oral sclerite is best examined from the ventral aspect (Fig. 218). It consists of a main, rod-like structure which tapers anteriorly, and a posterior pair of narrow, curved structures; I term these collectively the wish-bone structure. In addition, at a more ventral level, there arises from the central rod a pair of wing-like structures. It is important to note that the wish-bone structure lies on a more dorsal plane than the wing structure, since focus adjustment will be required to examine both these structures under the microscope. This may be seen clearly in Figs. 138 & 139 of Calliphora stygia; Fig. 138 shows the wish-bone structure from the ventral aspect, while Fig. 139 shows the wing structure in the same specimen in the same position. The wish-bone structure may be discerned through the wing structure in the second figure.

The oral sclerite is extremely useful in identification at the species level. Its most useful feature is the extent of pigmentation. In some species, e.g. Calliphora croceipalpis, practically the whole structure is pigmented (Fig. 132). In others, like Lucilia sericata, the structure is totally unpigmented (Fig. 145). In those species in which at least some pigmentation occurs, pigment is always present at the wider posterior end of the rod, at the junction with the wing and wish-bone sclerites. This 'minimum pigmentation' situation occurs e.g. in Calliphora hortona (Fig. 140). In other species almost the whole of the rod may be pigmented, as in e.g. Calliphora uralensis (Fig. 128), or at least an extensive part of it as in e.g. Calliphora

vicina (Fig. 126) and Calliphora vomitoria (Fig. 127). In many species, e.g. Chrysomya megacephala (Fig. 146) and Chrysomya marginalis (Fig. 147), the pigment is usually confined to the basal part of the rod. The wing and wishbone structures are also subject to pigmentation. A useful feature distinguishing Calliphora alpina (Fig. 129) from Calliphora subalpina (Fig. 130) is the fact that the wish-bone structure is pigmented in the former, but not in the latter. The wing structure is also pigmented in some species, but I have never seen a species where this structure is pigmented and the wish-bone structure is not, although the reverse is often the case.

Apart from pigmentation, the shape of the oral sclerite as a whole is a useful diagnostic feature, especially the form of the basal part of the rod. This may taper gently to form a cone shape as in Calliphora subalpina (Fig. 130) and Chrysomya marginalis (Fig. 147), or may expand to form a broad, rounded base as in Calliphora vicina (Fig. 126) and Calliphora alpina (Fig. 129). In Lucilia sericata (Fig. 145) the base is very narrow.

As might be expected, the above features exhibit a certain amount of variation, but they are, nevertheless, very reliable guides to identification. Finally, it must be pointed out that, in the literature, reference is frequently made to the spherical accessory oral sclerite of Lucilia ampullacea which is often depicted as shown in Fig. 264). This sclerite is not spherical, but it appears so since it is pigmented only at its posterior end, in the same way as the species discussed above.

Teskey (1981) stated that the function of the 'accessory' oral sclerite was unknown. However, Roberts (1971) had shown that, in

Calliphora vomitoria, the apodeme of an oral sclerite elevator muscle inserts on the basal part of the rod. Retraction of the muscle pulls in the oral sclerite and the upper lip to which it is attached, thus closing the mouth (Fig. 113). These findings were confirmed by the present study.

The mouth-hook condyle articulates posteriorly with the hypostomal sclerite (Fig. 218). This sclerite is H-shaped, with the cross-bar of the H sunk ventral to the level of the rest of the sclerite to form a ventral projection when viewed laterally. The hypostomal sclerite usually lacks a dorsal process in the third instar, but one is present in Protocalliphora spp. Generally, the hypostomal sclerite is of little use in identification, being rather variable. However, although its length in most species is less than the length of a mouth-hook, in Stomorhina cribrata (Fig. 294) it is longer. Also, in some species it is consistently much shorter (in relation to the mouth-hook) than usual and thicker in lateral view, e.g. Chrysomya rufifacies (Fig. 275). Another feature of some use in identification is the relative thickness of the cross-bar, being very robust in e.g. Calliphora vicina (Fig. 148), but much narrower in other species, e.g. Lucilia sericata (Fig. 162). It is very broad in Chrysomya albiceps (Fig. 164).

Hewitt (1914) stated that the duct of the salivary gland entered the pharynx anterior to the cross-bar of the hypostomal sclerite. Miller (1932) disputed this, stating that the duct entered the pharynx immediately behind the cross-bar. However, Hewitt was working on a Muscid (Musca domestica) not a Calliphorid. During the course of this study, many non-Calliphorid cyclorrhapha were examined, including

Musca domestica, and in all these species the salivary duct was found to join the pharynx posterior to the cross-bar.

Ventral to the anterior part of the hypostomal sclerite lie the two hypostomal plates (Fig. 218). The posterior parts of these comma-shaped structures articulate with the hypostomal sclerite at the angles made by the cross-bar and the side-branches of the sclerite anteriorly. Each hypostomal plate is more or less uniformly sclerotised, except at the postero-ventral part which is weakly sclerotised and perforated (Fig. 148). (N.B.: The plates are mounted on their sides and appear in this position in the photographs; in life the perforated parts lie ventrally).

The hypostomal plates are of diagnostic use in many ways. Firstly, the degree of pigmentation varies interspecifically, e.g. the plates are much darker (black) in Calliphora vicina and Calliphora quadrimaculata (Figs. 148 and 155), but are much lighter coloured in other species, appearing orange in Cynomyiopsis cadaverina (Fig. 160) or orange-brown in Lucilia sericata. Secondly, size is a very useful feature, but is best used when comparing two or more species, rather than for the identification of any one species. It is very useful, e.g. when separating Calliphora vicina (Fig. 148) which has large plates from Calliphora subalpina (Fig. 151) with its relatively small plates. Some species, e.g. Chrysomya bezziana, have particularly small plates (Fig. 165). The third feature of taxonomic use is the shape of the plate. The range of interspecific variation within one genus, e.g. Calliphora is not very great, but it is useful when comparing genera, e.g. Calliphora and Lucilia. In the latter genus the fenestrated area of the plate consistently takes up a larger proportion of the

structure (Fig. 162). In the genus Chrysomya however, the plates do vary greatly between species; compare, e.g. the distinctive plates of Ch. albiceps (Fig. 164) with those of Ch. bezziana (Fig. 165). In Protocalliphora spp. the plates are elongate and the fenestrated area is situated anteriorly (Fig. 166).

Lying ventral to the mouth-hooks between the hypostomal plates and the dental sclerites is the liguloid arch (Fig. 218). In many species it is a rather diffuse band of sclerotisation as, e.g. in Calliphora augur (Fig. 152). In other species, e.g. Calliphora vicina and Calliphora croceipalpis (Figs. 148 and 157) the band is broader and more heavily sclerotised. On the other hand, the band is weaker in other species, like Calliphora uralensis (Fig. 149) and Calliphora subalpina (Fig. 151). In Chrysomya bezziana (Fig. 165) the band is very narrow and weak, but shows areas of heavier sclerotisation along its length. The shape of the arch is also often of diagnostic value; e.g. in Calliphora quadrimaculata (Fig. 154) it is strongly V-shaped, whereas in Aldrichina grahami it is more U-shaped (Fig. 161). In some species the main body of the arch is weak, but the peripheries are very heavily sclerotised and assume very distinctive shapes. Examples are Calliphora hortona (Fig. 158) and Chrysomya albiceps (Fig. 164).

In addition to the above characteristics, the liguloid arch possesses a row of teeth on its anterior edge. These teeth are very difficult to see; they are of little taxonomic value apart from the fact that they are more prominent in those species where the arch as a whole is heavily sclerotised.

The largest single structure in the third instar skeleton is the pharyngeal sclerite (Fig. 218). The form of this sclerite is

essentially similar to the second instar equivalent, although it is relatively more elongate and narrower dorsoventrally. Although this sclerite is one indivisible whole, it is convenient to discuss the taxonomic value of particular areas of it separately.

The two anterior parastomal bars are of limited use taxonomically. They are usually thin, elongate structures (Fig. 218) with no distinguishing features. In some species, e.g. Calliphora vomitoria (Fig. 112), there is a tendency for some specimens to have the tip of the bars upturned, but this is a very variable feature and is no use in identification. However, in some species the tip is strongly curved upwards and backwards, e.g. in Lucilia bufonivora (Fig. 267); in these species the feature is a constant and reliable feature. In Protocalliphora spp. the bars are unusually thick (Fig. 284). In a very few species, e.g. Stomorhina cribrata (Fig. 294) and Chrysomya rufifacies (Fig. 275) the parastomal bars are totally lacking.

The parastomal bars are integral parts of the pharyngeal sclerite as a whole. In this connection Lowne's (1890) illustration (p.45) is misleading, since it shows the bars as, either separate structures, or as sclerites that are hinged to the main body of the pharyngeal sclerite.

Lying between the parastomal bars is a very faintly sclerotised structure, the epipharyngeal sclerite. It is usually very difficult to see, and is best examined from the dorsal aspect (Fig. 163). It bears a number of perforations through which, according to Roberts (1971), sensory processes pass. This sclerite was not found to be of any systematic use, other than being somewhat more heavily sclerotised in

certain species. It is not a very reliable feature, however.

Snodgrass (1924) reported the presence of a 'bridge plate' in roughly the same position as the epipharyngeal sclerite in Rhagoletis pomonella (Tephritidae). I have never seen any such plate in any Tephritid or other Cyclorrhaphous larva, although I have not seen Rh. pomonella. From his illustration (pl.3), this structure appears similar to the liguloid arch, although, of course, it is in the wrong position. However, the liguloid arch is visible dorsally and it is possible that Snodgrass misinterpreted its position.

Behind, and on either side of, the epipharyngeal sclerite there lie two elongate areas of sclerotisation, the epipharyngeal aciculae (Fig. 112). These are of no real taxonomic value, being highly variable in degree of sclerotisation; however, they do seem to be more developed in Calliphora spp. than in any other genus.

The dorsal arch exhibits a certain amount of interspecific variation. In some genera, e.g. Protocalliphora (Fig. 284), the arch is consistently weak, appearing pointed in lateral view . In other genera, especially Chrysomya, this feature differs between species, being robust in e.g. Ch. putoria (Fig. 271), but weak in Ch. albiceps (Fig. 274). In the genera Calliphora and Lucilia the arch is rather constant in appearance and is of no systematic use.

Between the dorsal arch and the parastomal bars ventrally lies an area of diffuse sclerotisation, the ocular depression. light-sensitive cells lie in this depression, which provides a dark background so that these cells can obtain a directional perception of illumination (Roberts, 1971). The depression varies widely in form and is thus of no systematic value; nonetheless, it is important to

recognise its physical limits when examining specimens. This is because, when viewed laterally, the depression may obscure the limits of the anterior margin of the lateral plate (Fig. 217). Strong light and careful focussing overcomes this problem. Some previous authors, e.g. Zumpt (1965), have failed to allow for this feature and consequently in many of their illustrations the anterior margin of the lateral plate apperas to extend forward more than it actually does. The irregular outline betrays the fact that it is the ocular depression and not the margin of the lateral plate that is illustrated. An example of this kind of illustration is given in Fig. 223 (compare with Fig. 217).

The narrowest width of the lateral plate in relation to the mouth-hook is a useful diagnostic feature in certain cases. In many species, as in most Calliphora spp., the lateral plate is more or less as wide as the mouth-hook is long, but in others, e.g. Chrysomya albiceps (Fig. 274) it greatly exceeds the length of the mouth-hook. In Cochliomyia hominivorax (Fig. 277) and certain Lucilia spp., among others, the width of the plate is appreciably less than the mouth-hook length.

The relative lengths of the dorsal and ventral cornua are also useful. The ventral cornu is always shorter than the dorsal; however, in many species, e.g. Calliphora vomitoria (Fig. 225) the ventral cornu is appreciably longer than half the length of the dorsal, while in others, e.g. Cynomya mortuorum (Fig. 262), the ventral cornu is equal to, or slightly longer than, half the length of the dorsal cornu.

The shape of the posterodorsal process of the ventral cornu is

of some limited diagnostic value. It is not a very reliable character, but is of some use as a general guide when distinguishing between certain species, e.g. compare Chrysomya albiceps (Fig. 274) and Chrysomya rufifacies (Fig. 275).

The dorsal cornu exhibits two features of diagnostic use. Firstly, its shape, i.e. the outline of its dorsal margin when viewed laterally, varies between species, but is not on its own a very reliable feature when dealing with closely related species. Thus, the outline shows a pronounced curve in Calliphora vomitoria (Fig. 225), but tends to be much straighter in Calliphora subalpina (Fig. 228). Secondly, the dorsoventral thickness of the cornu is of some use. This feature is closely linked with the previous feature, in other words, the greater the thickness the greater the curve. The two extreme conditions of this feature may be seen in the very narrow dorsal cornu of Pollenia rudis (Fig. 295) and the very broad cornu of Protocalliphora azurea (Fig. 284).

The presence or absence of 'windows' on the dorsal and ventral cornua, although much used in the literature, was found to be an unreliable feature. The feature is particularly unreliable in the dorsal cornu, being somewhat more constant in the ventral. However, occasionally certain species and not others will show particularly prominent windows, and in these cases reference to them is included in the species descriptions.

It is often repeated in the literature (e.g. Zumpt, 1965) that the Sarcophagidae may be distinguished from the Calliphoridae by virtue of the fact that the former always possess a deep cleft in the dorsal cornu (Fig. 317) while the latter never do. This is incorrect.

Certain Calliphoridae, e.g. Auchmeromyia lateola (Fig. 304) and Stomorhina cribrata (Fig. 294) do possess such a cleft. The cleft is simply a 'window' that reaches the margin of the cornu.

In an attempt to determine whether 'windows' are simply areas of weak sclerotisation or actual holes, the pharyngeal sclerite of a few specimens of Calliphora vicina were dissected out and examined under the S.E.M. The results showed that the 'window' is not a perforation, but an area of weak sclerotisation (Figs. 122 and 123).

The pharyngeal ridges (Figs. 118 and 218) were stated by Keilin (1912) to be present only in saprophagous larvae, while parasitic larvae lacked them. Dowding (1967) stated that these ridges were used to concentrate the ingested food of saprophagous larvae, but were absent from parasitic larvae whose food was more nutritious and did not require concentrating. During this study several parasitic species, e.g. Protocalliphora spp. and Chrysomya bezziana were found to possess such ridges, and it would seem that Keilin's generalisation does not hold in all cases. It is interesting to note that Ferrar (1979) in his study of the Muscidae, arrived at similar conclusions to mine.

The ridges are T-shaped and, in the third instar, seven are present (plus two one-lipped structures, one on either side, which are not visible ventrally). This number seems to be constant throughout the Calliphoridae and, therefore, these structures are of no diagnostic value. One interesting discovery made, however, was that only five ridges exist in the first instar (Fig. 119).

Finally, two other structures, although devoid of taxonomic value, deserve mention in order to avoid confusion, since they are

usually difficult to see, but in some preparations are very visible. This may give the impression that interspecific differences exist, which is not actually the case. The first structure is the prothoracic membrane which covers the atrium, or that area between the mouth-hooks and the pharyngeal sclerite (Fig. 223). The second group of structures are the unpigmented pharyngeal phragmata that extend backwards from the cornua (Fig. 223). The mouth-hook muscles originate from the posterior phragnea of the ventral cornu.

5.7 Ecdysis

Ecdysis, or the shedding of the larval cuticle, occurs twice during the life of the larva, between the first and second, and second and third instars. (The third instar larval cuticle is not shed, but hardens and darkens to form the puparium, as explained above. Apolysis, however, does occur, followed by a pharate state during which a pupal cuticle forms beneath the puparium. A pupa-adult apolysis occurs later, so that the emerging adult sheds both pupal and larval (puparial) cuticles).

During each moult, not only the cuticle is shed, but also the cephalopharyngeal skeleton. Before the skeleton is shed, the new skeleton begins to form. This means that, from time to time, it is possible to come across a larva whose skeleton includes elements of two instars. Such specimens must be recognised for what they are, i.e. 'interstages' between instars. In the past, such interstages have caused confusion; for example, an illustration by Hall (1948: pl. 45), labelled as the first instar skeleton of Cynomyiopsis cadaverina, is

without doubt such an interstage, containing both first and second instar elements. In his description, Hall refers to the first instar mouth-hooks as 'strongly arched'; this structure is, however, the developing second instar mouth-hook. Figs. 221 and 222 are examples of such interstages.

Interstages may also be recognised by the examination of the anterior and posterior spiracles, where the developing structures of the following instar may be seen.

5.8 The Variation of Sclerotisation

During the course of this work it was noticed that the degree of variation of the form and extent of pigmentation of the cephalopharyngeal skeleton was much greater in the third instar than in the first and second instars. Similar results were reported above (4.2.6) for the posterior spiracles.

Conventional taxonomic wisdom has always considered colour characters unreliable, more so in burrowing or subterranean animals in which colour is perhaps less subject to selective pressures, than in surface-dwelling ones. Calliphorid larvae, being strongly negatively phototactic, spend most of their lives burrowing deeply into the tissues of the carcase or under it. They may, therefore, be termed 'geophilous' for our purposes, and the extent of pigmentation must be expected to be particularly variable in this group.

Due to the fact that the larvae of Calliphoridae are relatively featureless and uniform in structure as a group, the traditional taxonomy of these larvae has relied heavily on the hard, pigmented

parts, especially the cephalopharyngeal skeleton and the posterior spiracles. This is reflected in the fact that illustrations of the cephalopharyngeal skeleton by previous authors are invariably shaded, showing areas of lighter pigmentation. In my opinion, this can be misleading, as it suggests rather constant differences between species which do not, in fact, exist. In this thesis, all illustrations are deliberately outlines only, and are not shaded. (Another reason for avoiding shading is that it obscures the limits of the various sclerites.)

In order to clarify the above remarks, an example of the sort of variation that occurs will now be given. If the illustration given in this thesis of the third instar skeleton of Calliphora vicina be compared with the illustrations given by Hall (1948) and Schumann (1954) of the same structure in the same species, a great degree of difference will be seen in the form of the dorsal and ventral cornua, although all three illustrations were faithfully drawn from actual specimens. It is obvious that C. vicina cannot be identified on the basis of the form of the pharyngeal sclerite alone. Also, the size of the windows, especially those on the dorsal cornua, is very variable, and the use of KOH for clearing has been found to cloud the issue further, as specimens lacking a window on the dorsal cornu may 'acquire' windows after KOH treatment.

It is obvious from these remarks that great caution must be exercised when the identification of third instar larvae is made on the basis of the shape and degree of pigmentation of the skeleton, especially the pharyngeal sclerite. This does not mean, however, that this sructure is without value, for it is, indeed, one of the most

useful and easily observed structures, but it is important to be aware of the extent and manner in which it varies. What caused confusion in the past was not so much the unreliability of the skeleton as a systematic character, but a lack of understanding of its morphological variability.

The question why the cephalopharyngeal skeleton varied much more in the third instar than in the earlier instars was considered. A possible answer is that, since the third instar is of much greater duration than either of the first two instars, it is likely that further sclerotisation occurs with age. Observation showed that larger third instar larvae tend to possess more robust skeletons than smaller ones.

An attempt was made to test this hypothesis. Ten larvae of Calliphora vicina were killed and preserved a few hours after moulting to the third instar, and a further ten from the same batch were similarly treated after three days. The following measurements of all these larvae were taken: Entire length of skeleton, length of mouth-hook, length of dorsal cornu, length of ventral cornu and greatest diameter of the posterior spiracle.

It would seem from Table VI that further sclerotisation does occur with age. This increase in size occurs without moulting; this is interesting in view of the statement, often made in the literature, that insect growth is discontinuous and moulting must occur before any growth can take place. E.g. Wigglesworth (1974) says that moulting "is the only means by which hard parts can increase in size". It seems to me that growth can, and does, occur to an appreciable extent between moults; this is evidenced, for example, by the very great increase in

TABLE VI

Means and Standard Deviations of C. vicina skeletal structures on 1st and 4th days of third instar growth.

	Whole skeleton		Mouth-hook		Dorsal cornu		Ventral cornu		Posterior spiracle	
	μ	STD	μ	STD	μ	STD	μ	STD	μ	STD
Day 1	1.04	0.05	0.25	0.01	0.71	0.02	0.51	0.01	0.20	0.01
Day 4	1.51	0.04	0.46	0.01	1.1	0.06	0.71	0.01	0.32	0.02

size of third instar larva as a whole, between the time of the second moult and the time it ceases feeding.

5.9 Biometrics

The use of relative measurements of the skeletal elements has long been a standard technique in Vertebrate Zoology, and is frequently used for diagnostic purposes. Therefore, during the early stages of this work, it was decided to attempt to diagnose species on this basis.

The method used was as follows: Thirty third instar specimens each of Calliphora vicina, Calliphora vomitoria and Calliphora uralensis were mounted on slides in the usual way (see above) taking particular care to align the skeletons correctly, so that they would present a strictly lateral view, and not a slightly dorso- or ventrolateral view. This was done in order to render the measurements strictly comparable. Eight measurements of the skeleton were taken (Fig. 217). These were as follows:

BH = Length of mouth-hook base from ventral angle to dorsal horn

LH = Total length of mouth-hook from condyle to tip of tooth

LB = Length of mouth-hook base from condyle to base of tooth

HB = Height of mouth-hook base from ventral angle to dorsal ridge

LP = Narrowest width of lateral plate

LDC = Length of dorsal cornu

LVC = Length of ventral cornu

LHS = Length of hypostomal sclerite

The data were fed into a computer for discriminant function analysis. Using this method the computer attempts to classify correctly each specimen (90 in total) according to each variable. The results are presented in Table VII.

It is obvious from these results that certain measurements, e.g. the lengths of the mouth-hook and the ventral cornu, are more useful than others in identification. It is also clear that, although a particular measurement may be of limited use in overall identification, it may be of great use in diagnosing or separating two of the species. An example is the length of the lateral plate. This measurement correctly classifies 93.3% of C. vicina and 90% of C. vomitoria, but only 50.0% of C. uralensis. As a result, the overall diagnosing power of this measurement is low (77.78%). A more extreme case is the height of the mouth-hook base which classified none of the C. uralensis specimens correctly. These results are not surprising, since C. uralensis is in many ways intermediate between the other two species morphologically.

C. vicina and C. vomitoria are by far the commonest blue-bottle species in the British Isles, C. uralensis being found only in northern and western Scotland. For most practical purposes, therefore, the problem will be a matter of deciding whether a particular specimen is C. vicina or C. vomitoria. Therefore, the analysis was repeated, this time omitting the C. uralensis data. The results are presented in Table VIII.

It is clear that the diagnosing power of several measurements has increased dramatically, e.g. LDC, LHC, LP and, in particular LVC, on the basis of which all the specimens were correctly classified.

TABLE VII

Results of Discriminant Function Analysis using Three Species

	% C. vicina correctly classified	% C. vomitoria correctly classified	% C. uralensis correctly classified	% Total correctly classified
BH	83.3	66.7	33	61.1
LH	96.7	76.7	66.7	80.0
LB	50.0	90.0	56.7	65.56
HB	80.0	76.7	0.0	52.22
LP	93.3	90.0	50.0	77.78
LDC	93.3	80.0	60.0	77.78
LVC	96.7	90.0	80.0	88.89
LHC	100	86.7	40.0	75.56

TABLE VIII

Results of Discriminant Function Analysis using Two Species

	% C. vicina correctly classified	% C. vomitoria correctly classified	% Total correctly classified
BH	83.3	93.3	88.33
LH	96.7	100	98.33
LB	100	90.0	95.0
HB	80.0	76.7	78.33
LP	100	93.3	96.67
LDC	100	96.7	98.33
LVC	100	100	100
LHC	100	96.7	98.33

As noted above this method of diagnosis was explored during the early stages of the work before more conventional taxonomic characters were discovered. It was decided, therefore, to discontinue this line of research since other characters were found, which would be of more practical assistance to the general worker wishing to identify specimens, and who would not have access to a computer.

However, this is not to say that this method should not be explored further. Preliminary studies on several Acalypterate families indicate that this method could be extremely useful for the specialist wishing to separate closely related species, and may, indeed, be the only method whereby such species can be identified reliably. Furthermore, additional measurements may be added. Also, meristic data, such as the number of anterior spiracular lobes or the number of spines per unit area, may usefully be tried.

In spite of its limited use to the field worker, it is felt that discriminant function analysis is potentially a very powerful tool for the specialist taxonomist. It would be particularly useful for the specialist asked to identify specimens from incomplete remains such as occur, e.g. in archaeological deposits. In such situations, the puparial operculum, with the third instar skeleton attached, is often found well preserved although the remainder of the puparium may be absent.

CHAPTER SIX

THE CEPHALOPHORYNGEAL SKELETON IN NON-CALLIPHORID CALYPTERATA

6.1 Introduction

Evidence is given in Chapter 11 for the view that the larvae of Calliphoridae are among the most primitive in the Calypterata. It is thus possible to interpret the structure of the skeletons of the other Calypterate Diptera in the light of the discussion of the Calliphorid skeleton in the previous chapter.

With the possible exception of the Sarcophagidae and Muscidae, little is known of the range of form and the detailed structure of the skeletons of non-Calliphorid Calypterates. The reasons for this are not hard to find. Regarding families like the Tachinidae and Cuterebridae, the adult taxonomy is in such an unsatisfactory state, that taxonomic studies on the larvae cannot yet progress meaningfully (but see later discussion on the value of immature stage taxonomy in Tachinidae (11.3)).

Paradoxically, the opposite reason is the cause of the paucity of knowledge of the skeleton in the families Oestridae and Gasterophilidae. The larvae (and adults) of these families are so well-known and relatively easily identifiable using external features, that the skeletal structures were ignored since there was no need to search for diagnostic characters by dissection.

During the present study, a large number of non-Calliphorid

Calypterate larvae were studied; a full list of species examined will be found in Chapter 11. The main aim of the present chapter, therefore, is to present new observations on the basic structure of the third instar skeletons of Calypterata and to draw attention to certain errors of interpretation made by previous authors. The possible diagnostic value of the various structures will also be discussed. Special attention is given to the families comprising the Calliphorid-line of evolution (i.e. the family "Tachinidae" sensu lato), but brief comments will also be made on the remaining families in the chapter on Evolution and Phylogeny.

6.2 Sarcophagidae

This family is very closely related to the Calliphoridae and it is generally agreed that the two families are sister groups. Certainly the larvae of Sarcophagidae are morphologically more similar to the Calliphoridae than to any other Calypterate group.

Much has been published on the skeletons of larval Sarcophagidae (e.g. Hafez, 1940; Cantrell, 1981); however, as in Calliphoridae, most authors were content to produce illustrations showing the general form (usually in lateral view) of the skeleton, and no attempt was made to evaluate the taxonomic importance and degree of variability of the various sclerites. Such an analysis now follows, dealing with the sclerites in the order adopted with the Calliphoridae in the previous chapter.

The mouth-hooks are of essentially the same form as in Calliphoridae, although there is a tendency in some species for the

base to be elongated dorsoventrally (i.e. the distance between the dorsal horn and the ventral angle is increased), e.g. as in Sarcophaga argyrostoma (Fig 317). In many species, the ventral angle is curved and pointed in a manner reminiscent of many acalypterate larvae, e.g. as in Helicophagella melanura (Fig. 318).

The oral sclerite is typically unpigmented and often much reduced, since the mouth-hooks are usually set closer together than is the case in Calliphorids. However, in Brachycoma devia the oral sclerite is not only well-developed but also pigmented, the pigmentation being mainly in the rod and wing structures, not in the wish-bone structure. This pigmentation is intriguing, for two reasons. Firstly, this is the first record of the presence of a pigmented oral sclerite outside the Calliphoridae (not including the paired oral bars of Muscidae). Secondly, in all Calliphoridae that possess a pigmented oral sclerite the larval habits are saprophagous or 'generalised'; no obligate parasitic, predatory or termitophilous species (i.e. no specialised' species) in Calliphoridae possesses a pigmented oral sclertie. Brachycoma devia is a highly specialised species, being a predator in the nests of bees (Bombus spp.).

The Sarcophagid dental sclerite is essentially similar to the Calliphorid structure, being composed of two units as described in the previous chapter. The range of form is similar to the range in Calliphoridae.

The liguloid arch does not exhibit the same range of interspecific variation as it does in the Calliphoridae, being typically broad, and either heavily or weakly pigmented (compare Figs. 167 and 168). Teeth are sometimes present in the more heavily

pigmented species, but are difficult to discern.

The hypostomal plates exhibit a great range of inter-specific variation. They are typically rather rounded, as in Sarcophaga argyrostoma (Fig. 170), but are often curved in a characteristic manner as in Brachycoma devia and Boettcherisca peregrina (Fig. 167); in species having this form of hypostomal plate, the anterior ends of the plates are almost touching. In other species, e.g. Tricharaea brevicornis, the plates have a characteristic parallelogram shape (Fig. 169).

The hypostomal sclerite is also a very useful diagnostic feature, exhibiting perhaps an even greater range of interspecific variation than the Calliphoridae; it may be short and robust, as in Boettcherisca peregrina (Fig. 167), or slender and elongate, as in Tricharaea brevicornis (Fig. 168).

The parastomal bars, as in Calliphoridae, are of little diagnostic value, although they do seem to be shorter and thicker in some species than in others; this feature reliably separates Tricharaea brevicornis (long and narrow) from most Sarcophaga, Parasarcophaga and Boettcherisca spp (short and thick). The bars seem to be very often placed more ventrally (i.e. closer to the hypostomal sclerite) than in Calliphoridae, making it difficult to distinguish them. It is also rather difficult to discern the posterior limits of the hypostomal sclerite, which is often so strongly applied to the pharyngeal sclerite that the two sclerites may appear as one structure. Arnaud (1954) illustrated the skeleton of Hilarella hilarella (Zetterstedt); his figure shows the hypostomal and pharyngeal sclerites as one structure, and no parastomal bars are

present. I have not seen this species, but I consider it highly unlikely that the two sclerites are fused, as in all Sarcophagid and Calliphorid species that I have examined, including those previously illustrated as having fused hypostomal and pharyngeal sclerites, these two sclerites were found, by dissection, to be discrete. The absence of parastomal bars from Hilarella is, of course, possible, but all Sarcophagidae examined by me possessed parastomal bars.

The epipharyngeal sclerite is often considerably more developed than in Calliphoridae, e.g. as in Tricharaea brevicornis (Fig.168), but it is also often only weakly developed in other species.

The dorsal and ventral cornua are of essentially the same form as in Calliphoridae, although the dorsal cornu is typically 'cleft' (Fig. 317). This so-called cleft is nothing more than a window that reaches the margin. As was pointed out in the previous chapter, some Calliphoridae also possess such a cleft, and the character can no longer be regarded as diagnostic for Sarcophagidae, although it is true that it is only rarely found in Calliphoridae, whereas it is the rule in Sarcophagidae. The Sarcophagid dorsal cornu was not examined by S.E.M. during the present study, but it is probable that the cleft is only an area of weak sclerotisation, rather than an actual gap or perforation. In some species, the window of the dorsal cornu (which is always large, compared with the situation in Calliphoridae) does not reach the margin, e.g. as in Parasarcophaga crassipalpis.

The ventral cornu shows the same range of form as in Calliphoridae; it invariably possesses a window which in some species, e.g. Tricharaea brevicornis, reaches the margin. Ventral ridges were present in all species examined, although Cantrell (1981) states that

they are absent from Blaesoxipha spp.

6.3 Tachinidae

The known larvae of the species of this vast family exhibit a remarkable range of interspecific variation, a fact which seems to support the former division of this family into a number of separate families (e.g. Dexiidae, Rutiliidae etc.). At any rate, when sufficient species are critically described, the subfamilial limits of the Tachinidae may turn out to be more clearly defined in the larval, rather than the adult, stage.

Due to the great structural modification shown by some species, it will not be possible to discuss each individual sclerite in turn, as was done for the Sarcophagidae. Rather, the skeleton of one of the more 'normal' species will be described, followed by a discussion of how the skeletons of other species deviate from this plan. This is done purely for the sake of convenience, and is not intended to imply that the 'normal' condition about to be described is necessarily the ancentral condition.

The mouth-hooks of Zygobothria ciliata (Fig. 309) are similar to those of Calliphoridae, but the ventral angle is greatly produced ventrally. No trace of an oral sclerite is present. The dental sclerite is absent, as well as the liguloid arch. The hypostomal plates are present and fused (Fig. 310), the whole structure having only two perforations. The hypostomal sclerite is robust and generally similar to the Calliphorid sclerite.

The pharyngeal sclerite consists of a very broad dorsal cornu;

it lacks a window and is rather reminiscent of Protocalliphora spp. The ventral cornu possesses a large, round window, but otherwise is very similar to the Calliphorid structure. Ventral ridges, parastomal bars and epipharyngeal sclerite are all absent.

In many species, e.g. Argyrophylax aureiventris (Fig. 308) and Plesiocyptera sp. indet (Fig. 314), the dorsal horn is extremely long, and may be as long as, or longer than, the mouth-book tooth. In other species, the mouth-hook is strongly applied to the hypostomal sclerite, as in Phryxe vulgaris (Fig. 316), and it is very difficult to separate the two sclerites during dissection. Complete fusion of both these sclerites occurs in Schistocercophaga dampfi (Fig. 311). I infer that the resulting structure is a product of fusion rather than loss of the hypostomal sclerite, because of the presence of the ventrally produced cross-bar typical of the hypostomal sclerite, a well as the presence of the hypostomal plates immediately in front of it.

The oral and dental sclerites were absent from all species studied. The liguloid arch was absent from most species, but was present in a very weak form in Argyrophylax aureiventris. The hypostomal plates are typically present (fused or separate) and the fenestrations seem always to be fused to a single perforation per plate.

The range of form of the hypostomal sclerite is very great, being very short and thick, as in Phryxe vulgaris (Fig. 316), or long and narrow as in Medina egregia (Fig. 312). In some species, e.g. Actia painei (Fig. 315) the hypostomal and pharyngeal sclerites are strongly fused. An additional, and rather puzzling, feature of this

species, is the presence of an elongate, rather weakly sclerotised, structure ventral to the hypostomal sclerite; I have not been able to ascertain the origin of this structure. The hypostomal sclerite in Plesiocyptera seems to be displaced ventrally and the pharyngeal sclerite produced anteriorly above it (Fig. 314).

The dorsal cornu is typically very broad (Figs. 308, 309 and 314), while the ventral cornu is usually unremarkable. In Phryxe vulgaris (Fig. 316) the dorsal and ventral cornua meet and fuse to form a single broad, posterior sclerite. In most Tachinids, the dorsal arch slopes backwards, as e.g. in Zygobothria ciliata, but in a few species, e.g. Medina egregia it curves forwards as in most Calliphorids. The lateral plate may be very broad, as in Plesiocyptera (Fig. 314), or very narrow and elongate (dorsoventrally), as in Schistocercophaga dampfi (Fig. 311). The whole pharyngeal sclerite in Tachinids is typically much shorter than its Calliphorid and Sarcophagid counterparts. Both sets of cornua are typically devoid of windows.

The remarkable species Therobia abdominalis deserves special mention, as it possesses several most unusual features. Firstly, it possesses well developed parastomal bars (Fig. 313). This is the first such record from a Tachinid species; the absence of these structures is usually considered to be diagnostic of the Tachinidae. Secondly, the presence of a well-defined window on the dorsal cornu is also unknown amongst other Tachinidae. Thirdly, the presence of an ocular depression is certainly atypical, although a similar structure exists in Schistocercophaga dampfi (Fig. 311). Its most typically Tachinid feature is the absence of the dental sclerite.

(The identity of this larva is not in doubt. Adults reared from the same batch of larvae were identified by Dr R.W. Crosskey of the BM (NH)).

In some ways it is not unexpected that Therobia should have such an unusual skeleton. The tribe to which it belongs, the Ormiini, contains some of the most aberrant adult forms in the Tachinidae; the first instar larvae have been described as "the most perfectly formed planidium occurring in the Diptera" (Crosskey, 1973).

It is clear from the limited studies undertaken during the present work that an immense range of form exists in Tachinid larvae. Hennig's (1952) account gives little indication of this range, although he highlights the great range of structure of the posterior spiracles. A wide and important field awaits the attention of a future worker.

6.4 Oestridae

The structure of the Oestrid skeleton, although highly specialised, exhibits a greater uniformity of structure in the family, than does that of the Tachinidae.

The mouth-hooks are characteristically robust and very strongly curved. In Oestrus ovis, the sheep nostril fly, the mouth-hook tooth is not, relative to most other Oestrids, excessively curved (Fig.326), whereas in Pharyngobolus africanus, a parasite of the African elephant (Loxodonta africana), the curvature is very pronounced indeed (Fig. 325). The region of the dorsal horn in these two species is interesting, as a much more weakly pigmented area of the mouth-hook is

apparent in this region, especially in O. ovis. At first sight, the impression is that of a deep cleft anterior to the dorsal horn and posterior to the tooth. This led to Cameron (1932) giving an erroneous illustration of this species, omitting the weakly sclerotised part. This error led to another, as Cameron did not consider the base of the mouth-hook to be part of the mouth-hook at all; he termed the dorsal part of the base "the hypopharyngeal sclerite" and the ventral part "the anterior transverse sclerite" by which I understand him to mean the liguloid arch. This interpretation cannot be correct. Firstly, it is obvious that the anterior ridge of the weakly sclerotised part is equivalent to the dorsal ridge in Calliphoridae, and the posterior ridge to the dorsal horn. Secondly, the perforation in the centre of the structure shows clearly that this is the base of the mouth-hook, such a perforation existing in the mouth-hook base in Calliphoridae, Sarcophagidae and Tachinidae (see 5.6). Thirdly, the elevator apodeme inserts at the top of this structure (Cameron's hypopharyngeal sclerite), while the depressor apodeme is attached to the ventral part (Cameron's anterior transverse sclerite). Clearly, this structure is the mouth-hook base.

In both Oestrus and Pharyngobolus a small dental sclerite is present, although this is absent from all the other species examined. No oral sclerite was discernible in any species. A liguloid arch is present in Oestrus ovis; it is a weakly pigmented V-shaped structure, bearing strong teeth on its anterior edge. The liguloid arch is absent from the remaining species, except Tracheomyia macropi, where it is a robust, rod-like sclerite.

The hypostomal plates exhibit an interesting range of form, being slender and rod-like in Oestrus ovis (Fig. 326), but very large in Tracheomyia macropi, a parasite of kangaroos (Macropus spp.) (Fig. 324). In Cephenomyia auribarbis, a red deer (Cervus elaphus) parasite, the plates are fused and only two fenestrations are present (Fig. 328). Rhinoestrus vanzyli, a parasite of the springbok (Antidorcas marsupialis), is unusual in that it lacks all the minor sclerites (oral and dental sclerites and liguloid arch), it does, however, possess very small hypostomal plates (Fig. 327).

The hypostomal sclerite may be either free or fused to the pharyngeal sclerite. When it is free (as in Oestrus, Rhinoestrus and Pharyngobolus) it is a unremarkable, H-shaped, rather robust sclerite. When it is fused to the pharyngeal sclerite, as in Tracheomyia and Cephenomyia, it is V-shaped, with a weakly pigmented cross-bar connecting the two arms of the V, which join and are continuous with the fused ventral cornua of the pharyngeal sclerite (Fig. 328).

The two sets of cornua are typically almost touching, or touching, as in Oestrus ovis (Fig. 326). In Pharyngobolus africanus (Fig. 325), the dorsal and ventral cornua fuse. No parastomal bars were found in any of the species, and windows were present only in Tracheomyia (Fig. 324).

6.5 Cuterebridae

The skeleton of Cuterebrids appears to be a simplified version of the Oestrid structure. In Cuterebra spp., the mouth-hooks are large in relation to the remainder of the skelton, but are otherwise

unremarkable (Fig. 329). Posterior to the mouth-hooks lies a robust, H-shaped, hypostomal sclerite, behind which lies a short pharyngeal sclerite with a broad dorsal cornu. Parastomal bars are absent. The shape of the pharyngeal sclerite is amazingly variable interspecifically and of no diagnostic use whatsoever. In addition, there is present in Cuterebra a very fine liguloid arch which possesses many teeth on its anterior margin. The liguloid arch is absent from the other Cuterebrid species examined. Dental and oral sclerites and hypostomal plates are absent from all species.

Only two structures may be said to have any real diagnostic value. The first is the liguloid arch, by virtue of its presence in Cuterebra and absence from other genera. The second is the mouth-hook, which may be very large, as in Dermatobia hominis, a parasite of Man and many other mammals (Fig. 330), or very much smaller, as in Alouattamyia baeri, a parasite of howler monkeys (Fig. 331). The form of the mouth-hook is also very different between the two species.

The hypostomal sclerite is very variable intraspecifically, but does seem to be consistently relatively longer in Alouattamyia.

6.6 Gasterophilidae

Zumpt (1965) says that the genus Gasterophilus is "today the most intensively studied group of oestroid flies", and that their eggs, larvae and adults are extremely well known. While this is certainly true, it is also true to say that the skeletons of these larvae are effectively totally unknown. I have not been able to find a single illustration or description in the literature, except for

figures of the protruding mouth-hooks in general illustrations of the whole larva.

The family is divided into four subfamilies: Gasterophilinae, Cobboldiinae, Rutteniinae and Neocuterebrinae. The first of these consists of species that are parasitic in horses and rhinoceroses, while the species of the three remaining subfamilies are all parasitic in elephants. Material of only the first two subfamilies was available for study.

The skeleton structure is very unusual, and the two subfamilies studied differed markedly in their basic plans.

In the Gasterophilinae the entire skeleton is fused into one whole structure; Fig. 320 is a lateral view of the skeleton of Gyrostigma pavesii, a parasite of the two African species of rhinoceros. The mouth-hooks are very large and strongly curved, with the ventral angle pointing anteriorly. Posteriorly, the mouth-hooks fuse with the hypostomal sclerite (Fig. 321) which is a shallow V-shaped structure. The hypostomal sclerite fuses posteriorly to the pharyngeal sclerite (Fig. 321) although a connection between the two sclerites can be clearly seen. The pharyngeal sclerite is very long, but rather ill-defined as far as its posterior limits are concerned. The dorsal arch is produced anteriorly and projects between the mouth-hooks. The whole structure, including the mouth-hooks, although very robust, is very weakly pigmented, the mouth-hooks appearing orange and the pharyngeal sclerite pale yellow under the microscope. The dorsal arch is rather more heavily pigmented than the rest of the pharyngeal sclerite, appearing orange like the mouth-hooks; the link between the two halves of the arch is absent. No

trace of oral or dental sclerites, or of the liguloid arch, hypostomal plates or parastomal bars was present.

In the genus Gasterophilus, e.g. in G. pecorum, a parasite of Burchell's Zebra (Fig. 323), the connection or groove lying between the hypostomal sclerite and the pharyngeal sclerite is absent, and fusion is complete. Apart from this difference, the basic plan of the Gasterophilus skeleton is essentially similar to that of Gyrostigma, although the dorsal horn is more pronounced in Gasterophilus.

The mouth-hooks of Gasterophilinae deserve special mention. Under low-power, they appear to have a reticulated pattern on their surfaces, but under high this is revealed as a covering of overlapping plates, rather like tiles on a roof, giving the mouth-hook an all round serrated edge (Fig. 177). Presumably this aids in enabling the larva to obtain a grip on the mucous membranes of the host's stomach. This structure is in marked contrast to the smooth mouth-hooks of all other Cyclorrhapha studied.

The skeleton of Cobboldiinae, as exemplified by Platycobboldia loxodontis, a parasite of the African elephant (Fig. 322), is very different. The mouth-hooks are free (not fused to the hypostomal sclerite) and, while strongly curved, not as strongly curved as in Gasterophilinae. They possess well-developed dorsal horns and are also covered with a reticulate pattern, but the overlapping plates are only weakly developed.

Posterior to the mouth-hooks lies a single, median sclerite (Fig. 323); this may be the fused hypostomal plates, but I am not certain of this. The hypostomal sclerite is fused posteriorly to the pharyngeal sclerite; the two lateral halves of the resulting structure

are joined together by a connection which is strongly reminiscent of the sutures between the various bones of the mammalian skull. Anteriorly, the arms of the hypostomal sclerite are hollowed out to accomodate the mouth-hook condyles. The dorsal cornua are very narrow and extremely weakly pigmented, and the dorsal arch does not project anteriorly.

While a discussion of phylogeny is dealt with in a later chapter, it is, perhaps, worthwhile making a few comments here on the systematic position of Gasterophilidae. Previous authors have differed as to where the family's affinities lie; some included the group as a subfamily of Oestridae, others as a subfamily of Muscidae, and yet others have placed it as a separate family of Acalypteratae. It is not intended here to discuss the various points of view, but merely to suggest that a detailed study of the skeletons of Gasterophilids of all instars may contribute to a solution of the problem. The present study is too limited to enable any deep analysis to be made, but it is interesting to note that the Cobboldiine skeleton (Fig. 322) is very similar to, and derivable from, an Oestrid skeleton of the Cephenomyia type (Fig. 328). All that is required to arrive at the Cobboldiine skeleton from the Cephenormyia one, is the loss of the hypostomal sclerite cross-bar and the fusion of the two arms of the sclerite. If the single, median sclerite in Cobboldiinae is indeed the product of the fusion of the hypostomal plates, then this structure is very obviously derivable from the fused plates of Cephenomyia. Further studies on this group would be of great interest.

6.7 Hypodermatidae

Zumpt (1965) says of the third instar larva of Hypoderma: "The cephaloskeleton is strongly reduced and external mouth-hooks are not visible."

During the course of this work dissections of the three British species of Hypoderma (H. bovis, H. diana and H. lineatum) were carried out. In none of these species could any trace of the skeleton be found; in fact, it appears to have been totally lost during the course of evolution. The first instar is stated by Zumpt to possess a skeleton, but he does not comment on this structure in the second instar. No material of the earlier instars were available for study.

The only sclerotised parts noted in the third instar were pigmented plates placed around the mouth.

CHAPTER SEVEN

SYSTEMATIC ACCOUNT: 1. CALLIPHORINAE

7.1 Introduction

In this and the following two chapters the full descriptions of the species studied are presented. If a given stage is absent from a particular species description, this is because no material was available for study.

No synonymies are given, but full synonymies of the species dealt with may be found in the works of Kloet and Hincks (1976), Zumpt (1956a), Delfinado and Hardy (1977), Crosskey et. al (1980), Kurahashi (1971), Stone et al (1965), Hall (1948) and Guimaraes (1977).

All descriptions in this and the following two chapters are of the larval stages only. The eggs have been dealt with in Chapter 3, and the information on the puparia is given in Tables II, III and IV . The spinal features of the puparia are, of course, the same as those of the third instar. In order to save space, all measurements and meristic data are omitted from the descriptions and are included in Tables II, III and IV.

Two characters have been omitted from the descriptions of species of Calliphorinae; these are the parastomal bars and the posterior spiracles. Although these characters are useful in the family as a whole, they are very uniform in the present subfamily. In all species of Calliphorinae examined, the parastomal bars are present

and unremarkable except in L. bufonivora. The posterior spiracles have a peritreme of medium thickness (Fig. 204), the button is always pigmented (although, as seen above, some specimens are only faintly pigmented) and the sun-ray structure is well-developed and without distinguishing features.

7.2 Genus Calliphora Robineau-Desvoidy

Calliphora vicina Robineau-Desvoidy

First Instar. Skeleton (Fig. 246) with lateral plate slender, breadth at narrowest point about half length of median tooth; ventral and dorsal cornua slightly divergent; basal section of hypostomal sclerite in lateral view much thicker than greatest thickness of median tooth in lateral view; median tooth longer than length of mouth-hook; dorsal horn of median tooth not prominent. Anterior spinal bands (segs. 2-12) complete on 2-9, very faint dorsally on 10, absent dorsally on 11 and 12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11), incomplete dorsally on 6, complete dorsally on 7-11; semi-circle of spines ventrally around anal area on seg. 12.

Second Instar. Skeleton (Fig. 236) with breadth of lateral plate at narrowest point much less than length of mouth-hook; mouth-hook horns usually angled; tooth of mouth-hook much thickened at region of curvature, such that the tooth is considerably thicker there than it is at its basal part. Anterior spinal bands (segs. 2-12) complete

on 2-9, incomplete dorsally on 10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11), complete on 7-11, incomplete dorsally on 6; sometimes very few spines present ventrally on 5. Patch of spines dorsally and ventrally on anal region of seg. 12.

Third Instar. Skeleton (Fig. 224) with mouth-hook tooth usually only slightly longer than depth of mouth-hook base; oral sclerite heavily pigmented in rod and wishbone structure areas, wing structure weakly pigmented, base of rod considerably (Fig. 126) thickened; dental sclerite usually slender with comma-shaped tail; liguloid arch broad (Fig. 126); hypostomal plates large and heavily pigmented (Fig. 148); hypostomal sclerite cross-bar broad (Fig. 148); window clear on ventral cornu, usually absent on dorsal cornu; posterodorsal process of ventral cornu weakly developed; dorsal cornu only slightly arched dorsally; angle between dorsal and ventral cornua sharp, not roundly arched. Anterior spinal bands (segs. 2-12), incomplete dorsally on 10-12, although that on 10 often present in very faint form; bands on 6-11 cleft ventrally. Posterior spinal bands (segs. 6-11), that on 6 ventral and weak, those on 7-9 incomplete dorsally and those on 10 and 11 complete. Semi-circle of spines present dorsal and ventral to anus (Fig. 205). Very few spines present between anus and anal lobes, and these weakly pigmented. All spines of bands pointed and moderately pigmented (Fig. 40). Width of base of each of P_1, P_2 and P_3 much less than distance between them. P_2 closer to P_3 than to P_1.

Taxonomic Remarks

The above descriptions refer wholly to British specimens and differ slightly from those of Hall (1948), who studied North American specimens. In particular, the distribution of the bands seems to be different in Nearctic specimens; for example, Hall states that the anterior bands of segments 2-7 in the first instar are complete (the others being incomplete), but in British specimens these bands are also complete on segments 8 and 9. Also, Hall states that the number of lobes of the anterior spiracles has the same range in both second and third instars; this is not so in British specimens, although there is a degree of overlap. He also states that the number of lobes is 7-9 (most often 8) in the third instar, while Schumann (1954), working on Middle European specimens, states that the number is 7-10; in the specimens of Durham material examined not a single specimen had only 7 lobes, and only rarely was one with 8 lobes seen (although very few specimens examined from the south of England had only 7 lobes). The usual range in British specimens is 9-11.

Specimens examined: U.K. (Durham, London, Norwich); U.S.A. (Washington State); Japan.

Biology and Distribution

This species is a widespread and common synanthropic carrion-breeder in the Holarctic, Afrotropical, Oriental and Australasian regions. It is a known myiasis agent in Man and a number of wild and domestic mammal species (Zumpt, 1965).

Calliphora vomitoria (Linnaeus)

First Instar. Skeleton (Fig. 247) with lateral plate robust, breadth at narrowest point equal to (or greater than) length of median tooth; dorsal and ventral cornua distinctly divergent; basal section of hypostomal sclerite in lateral view narrower than median tooth in lateral view; median tooth about same length as mouth-hook, or very slightly longer; dorsal horn of median tooth prominent. Anterior spinal bands (segs. 2-12), complete dorsally on 2-7, faint dorsally on 8, incomplete dorsally on 9-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 7-11) ventrally and ventrolaterally on 7-10, ventrally and dorsally (but not mid-laterally) on 11. Patch of strong spines present dorsally on anal region, weaker spines ventrally.

Second Instar. Skeleton (Fig. 237) with breadth of lateral plate at narrowest point appreciably greater than length of mouth-hook; mouth-hook horns usually short and not angled; tooth of mouth-hook tapering at region of curvature, such that the tooth is considerably narrower at this area than it is at basal area of tooth. Anterior spinal bands (segs. 2-12), complete on 2-9, faint dorsally on 10-11, absent dorsally on 12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 7-11), incomplete dorsally on 7-10; ventral and dorsal (but absent laterally) on 11. Anus with spines dorsally and ventrally, but very few laterally.

Third Instar. Skeleton (Fig. 225) with mouth-hook tooth usually longer than depth of mouth-hook base; rod of oral sclerite heavily pigmented, wing and wish-bone structures unpigmented, base of rod thickened (Fig. 127); dental sclerite usually robust, rarely with comma-shaped tail; liguloid arch broad with well-defined anterior teeth; hypostomal plates large and heavily pigmented; hypostomal sclerite cross-bar broad; windows clear on ventral cornua, usually absent on dorsal cornua; posterodorsal process of ventral cornu prominent; dorsal cornu strongly arched dorsally; angle between dorsal and ventral cornua sharp (not roundly arched). Anterior spinal bands (segs. 2-12), complete on 2-10, very faint (single row) or absent dorsally on 11, incomplete dorsally on 12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11), incomplete dorsally on 6-9, present ventrally and dorsally (but not laterally) on 10-11, although often faint or absent dorsally as well. Spines large, with rounded teeth, never with more than one tooth each (Fig. 41). Anal region covered with spines, including area between anus and anal lobes; patch of dark spines present dorsal to anus (Fig. 206). P_1, P_2 and P_3 more or less equidistant from one another, or P_2 slightly closer to P_3. Width of base of each of P_1, P_2 and P_3 not less than distances between them.

Taxonomic Remarks

The third instar was described (by illustration) by Hall (1948). The features shown by Hall, however, are not sufficient to distinguish this species from C. vicina. C. vomitoria is very distinctive in all

its larval stages. It is, generally, much more heavily sclerotised than any other species of British Calliphora, having, in particular, large posterior spiracles and strong spines in the third instar. These spines are a very reliable diagnostic character; specimens from Japan and the U.S.A. that were examined could easily be distinguished from specimens of C. vicina from those countries on the basis of the form of the spines.

Specimens examined: U.K. (Durham); U.S.A. (Washington State); Japan.

Biology and Distribution

This species is a common carrion-breeder throughout the Holarctic region and, to a lesser extent, the Oriental and Australasian regions; it is absent from the Afrotropical region (Zumpt, 1965). It is a known myiasis agent.

Calliphora uralensis Villeneuve

First Instar. Skeleton (Fig. 248) with length of mouth-hook tooth usually only slightly less than length of base; lateral plate slightly narrower at narrowest point than length of median tooth; ventral and dorsal cornua slightly divergent; basal section of hypostomal sclerite in lateral view not thicker than greatest thickness of median tooth in lateral view; median tooth longer than mouth-hook; dorsal arch with distinct ventral curve. Anterior spinal bands (segs. 2-12), complete on 2-9; band on 8 with unpigmented spines dorsally; incomplete on

10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 7-11), incomplete on 7-9, but with faint patchy areas of spines dorso-laterally; complete on 10-11, but weak dorsally. Patch of spines present dorsal to anus.

Second Instar. Skeleton (Fig. 238) with breadth of lateral plate at narrowest point less than length of mouth-hook; mouth-hook horns rather long; mouth-hook uniform in thickness from base to area of curvature, such that the dorsal and ventral margins of this area appear parallel in lateral view. Anterior spinal bands (segs. 2-12), complete on 2-8; band on 9 very faint and with weakly pigmented spines dorsally; incomplete or faint dorsally on 10-11 (although band on 10 usually faint dorsally). Patch of strong spines present dorsal to anus and semi-circle of spines ventral to anus.

Third Instar. Skeleton (Fig. 226) with tooth of mouth-hook typically much longer than depth of base; oral sclerite rod largely pigmented, except at tip; wing and wish-bone structures unpigmented; base of rod only slightly thickened (Fig. 128); dental sclerite variable, but rarely with comma-shaped tail; liguloid arch weak (Fig. 149); hypostomal plates well pigmented, but posterior section tapering (Fig.149); hypostomal sclerite cross-bar broad; windows present on ventral cornua, but usually absent on dorsal cornua; posterodorsal process on ventral cornu prominent; dorsal cornua well-arched dorsally; angle between dorsal and ventral cornua usually wide. Anterior spinal bands (segs. 2-12), complete on 2-8; faint dorsally on 9; incomplete on 10-12; bands on 8-12 cleft ventrally. Posterior

spinal bands (segs. 7-11), incomplete on 7-8, faint dorsally on 9; complete on 10-11. Spines well-pigmented, frequently with two or three teeth (Fig. 42). Patch of strong spines present dorsal to anus and many strong spines in a wide semi-circle ventrally; some spines between anus and anal lobes. P_2 slightly closer to P_3 or P_1, P_2 and P_3 equidistant; P_4 prominent. Width of base of each of P_1, P_2 and P_3 less than distances between them.

Taxonomic Remarks

This species is, to my knowledge, previously undescribed in the immature stages. It shows several features that are intermediate between C. vicina and C. vomitoria, in particular, the structure of the mouth-hook in the second instar, and the SDF and spine structure in the third. As a whole, however, this species appears (in the larval stages) to be rather more closely related to C. vomitoria, although in the adult stage it is very similar to C. vicina.

Specimens examined: Scotland (Ailsa Craig).

Biology and Distribution

This species is a carrion-breeder of northern Europe, but it is also found in the mountainous regions of central Europe (Zumpt, 1956a). In the British Isles it is confined to northern and western Scotland (van Emden, 1954). It is not known to cause myiasis.

Calliphora alpina (Zetterstedt)

First Instar. Skeleton (Fig. 249) with lateral plate very slender and much narrower at narrowest point than length of median tooth (as narrow at narrowest point as length of mouth-hook tooth); ventral and dorsal cornua effectively parallel at extreme ends; basal section of hypostomal sclerite in lateral view much thicker than greatest thickness of median tooth in lateral view; median tooth longer than mouth-hook. Anterior spinal bands (segs. 2-12), complete on 2-9; incomplete on 10-11; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11), incomplete on 6; complete on 7-11; in addition, there are often a few ventral spines on 5. Patch of spines present dorsal to anus.

Second Instar. Skeleton (Fig. 239) with narrowest width of lateral plate much narrower than length of mouth-hook; mouth-hook horns long, almost as long as mouth-hook base; tooth of mouth-hook very considerably thickened at area of curvature and constricted at base of tooth. Anterior spinal bands (segs. 2-12), complete on 2-9; incomplete on 10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 5-11), incomplete on 5-6; complete on 7-11. Patch of spines present dorsally to anus.

Third Instar. Skeleton (Fig. 227) with tooth of mouth-hook not longer than depth of base; oral sclerite rod well-pigmented, wish-bone structure well-pigmented, but wing structure unpigmented, base of rod greatly thickened (Fig. 129); dental sclerite usually with

comma-shaped tail; liguloid arch weak; hypostomal plates moderately pigmented; hypostomal sclerite cross-bar narrow; clear windows usually present on ventral and dorsal cornua; dorsal cornu slender and not strongly arched; posterodorsal process of ventral cornu not prominent, angle between dorsal and ventral cornua sharp; mouth-hook with a very prominent horn; area between horn and base of tooth usually arched. Anterior spinal bands (segs. 2-12), complete on 2-6; faint dorsally on 7; incomplete on 8-12. Posterior spinal bands (segs. 5-11), bands on 5-10 ventral only; band on 11 ventral and dorsal, with a bare area laterally. All bands are difficult to discern. Spines pointed and weakly pigmented (Fig. 43). Spines in anal region distributed in a manner similar to C. vicina. P_1, P_2 and P_3 equidistant from one another or P_2 slightly closer to P_3. Distances between papillae greater than width of bases.

Taxonomic Remarks

This species is readily distinguishable from C. vicina by the characters in the key (see Chapter 10). C. alpina is previously undescribed in the immature stages.

Specimens examined: England (Durham)

Biology and Distribution

This European carrion-breeder is confined to northern Britain, Scandinavia and the Alps (Zumpt, 1956a). It is not known as an agent of myiasis.

Calliphora subalpina Ringdahl

First Instar. Skeleton (Fig. 250) with lateral plate much narrower at narrowest point than length of median tooth; ventral and dorsal cornua slightly divergent; basal section of hypostomal sclerite less thick in lateral view than greatest thickness of median tooth; median tooth a little longer than mouth-hook. Anterior spinal bands (segs. 2-12), complete on 2-9; faint dorsally on 10; incomplete on 11-12. Posterior spinal bands (segs. 5-11), band on 5 ventral only; complete on 6-11. Patch of spines present dorsal to anus.

Second Instar. Skeleton (Fig. 240) with narrowest width of lateral plate less than length of mouth-hook; mouth-hook horns rather long, almost as long as mouth-hook tooth from base to area of curvature; tooth of mouth-hook much thickened at area of curvature. Anterior spinal bands (segs. 2-12), complete on 2-9; incomplete on 10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 5-11), incomplete on 5-6; complete on 7-11. Patch of spines present dorsal and ventral to anus.

Third Instar. Skeleton (Fig. 228) with mouth-hook tooth not longer than depth of base; oral sclerite rod partly pigmented (Fig. 130), pigmented area tapering anteriorly to form cone-shape; wing and wish-bone structures unpigmented; dental sclerite very slender and with comma-shaped tail; hypostomal plates (Fig. 151) moderately pigmented, weakly pigmented ventrally; liguloid arch very weak; hypostomal sclerite cross-bar narrow (Fig. 151); windows usually very

large and clear on ventral cornua; dorsal cornua very slender and with only a very slight dorsal curve; ventral cornua short, slightly more than half the length of the dorsal cornu; angle between dorsal and ventral cornua sharp. Anterior spinal bands (segs. 2-12) complete on 2-8; incomplete on 9-12; bands on 7-12 cleft ventrally. Posterior spinal bands (segs. 5-11); incomplete on 6 and 7; complete on 8-11; band on 5 ventral only. Anal spinal arrangement similar to C. vicina. P_2 slightly closer to P_3. Width of papillar bases less then distance between them.

Taxonomic Remarks

This species is previously undescribed in the immature stages.

Specimens examined: England (Durham); Japan.

Biology and Distribution

This carrion-breeding species is restricted to the mountainous or upland regions of northern and central Europe (Zumpt, 1956a), and the northern parts of the Palaearctic region as far east as Japan (Kano and Shinonaga, 1968). It is not known to cause myiasis.

Calliphora loewi Enderlein

First Instar. Skeleton (Fig. 251) with mouth-hook tooth almost as long as base; lateral plate narrower at narrowest point than length of median tooth; ventral and dorsal cornua parallel or slightly divergent

at posterior tips; basal section of hypostomal sclerite in lateral view more or less as thick as greatest thickness of median tooth; median tooth with prominent horn and longer than mouth-hook; a very weak patch of sclerotisation is present dorsal to the chitinised teeth. Anterior spinal bands (segs. 2-12), complete on 2-8; faint dorsally on 9; incomplete on 10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11), incomplete on 6-7; complete on 8-11. Very few, weakly sclerotised spines present dorsally and ventrally in anal region.

Second Instar. Skeleton (Fig. 241) with lateral plate narrower at narrowest point than length of mouth-hook; mouth-hook tooth much thicker at area of curvature than at basal area of tooth. Anterior spinal bands (segs. 2-12), complete on 2-8, faint dorsally on 9; incomplete on 10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11), incomplete on 6-7; complete dorsally on 8-11. Patch of spines present dorsal to anus.

Third Instar. Skeleton (Fig. 229) with mouth-hook tooth usually longer than depth of base; oral sclerite rod well-pigmented; wing and wish-bone structures pigmented; base of rod moderately thickened (Fig. 131); dental sclerite slender, with comma-shaped tail; liguloid arch diffuse; hypostomal plates moderately pigmented; hypostomal sclerite cross-bar narrow; window clear on ventral cornu; angle between dorsal and ventral cornua sharp. Anterior spinal bands (segs. 2-12), complete on 2-8; faint dorsally on 9; incomplete on 10-12; bands on 7-12 cleft ventrally. Posterior

spinal bands (segs. 5-11), ventral only on 5-6; faint dorsally on 7-8; complete on 9-11. Anal spinal arrangement similar to C. vicina. P_2 closer to P_3 than to P_1. Distances between papillae greater than width of bases.

Taxonomic Remarks

The third instar of this species has been described by Ishijima (1967) working on Japanese specimens. The present description differs from his in that the ventral cornu is not abnormally short in relation to the dorsal cornu, unlike C. subalpina. I have examined Japanese specimens and find that this is a very variable character in those specimens.

Dr L. Davies (pers. comm.) tells me that he is informed by Dr G. Shewell that the Nearctic C. mortica Shannon is synonymous with C. loewi, on the basis of an examination of adult British and Norwegian specimens sent to him by Dr Davies.

Specimens examined: England (Durham); Japan.

Biology and Distribution

This carrion-breeding species is an inhabitant of the northern and mountainous areas of the Palaearctic region (Zumpt, 1956a); the above-mentioned new synonymy means that the range of this species includes the northern Nearctic. C. loewi is not known to cause myiasis.

Calliphora lata Coquillett

Third Instar. Skeleton (Fig. 231) with mouth-hooks robust; rod of oral sclerite pigmented along most of its length; wing and wish-bone structures unpigmented; rod thickened at base (Fig. 133); dental sclerite proportionately large; liguloid arch well-pigmented, but narrow (Fig. 156); hypostomal plates moderately pigmented and relatively (to other Calliphora spp.) small (Fig. 156); hypostomal sclerite cross-bar narrow; windows large on both dorsal and ventral cornua; angle between dorsal and ventral cornua not very wide. Anterior spinal bands (segs. 2-12), complete on 2-9, faint dorsally on 10, incomplete on 11 and 12. Posterior spinal bands (segs. 6-11), incomplete on 6-9, present dorsally and ventrally (but not laterally) on 10 and 11. Spines pointed, moderately pigmented, often with two teeth. Anal region covered with spines; distribution of spines between anus and anal papillae intermediate between C. vicina and C. vomitoria (Figs. 205 and 206). P_2 closer to P_3 than to P_1; P_4 well developed; distances between first three papillae greater than broadest base of each papilla.

Taxonomic Remarks

Kano and Okazaki (1955) described the third instar of this species and compared it with C. vomitoria. Their key to separate these two species does not work, since it states that the distance between the posterior spiracles is less than the diameter of one spiracle in C. lata, but greater in C. vomitoria - this is definitely not the

case, the SDF being well below one in both species. Kano and Okazaki worked with Japanese material, and the description above is also based on Japanese material. In addition, Japanese C. vomitoria were examined (see remarks under C. vomitoria).

Kano and Okazaki used the spinal band patterns (especially on segment 10) to distinguish between these species. This is a difficult character, and the most useful feature distinguishing the two species is the shape of the spines (compare Figs. 41 and 51).

Specimens examined: Japan.

Biology and Distribution

This species is known only from Siberia and Japan (Zumpt, 1956a). Ishijima (1967) states that it breeds in "dead mammals, fish, birds, privies, garbage and human faeces". Unknown to cause myiasis.

Calliphora livida Hall

Third Instar. Skeleton with mouth-hook tooth longer than depth of base; rod of oral sclerite well-pigmented along more than half its length; wing and wish-bone structures unpigmented; rod somewhat thickened at base; dental sclerite robust; liguloid arch narrow; hypostomal plates moderately pigmented; hypostomal sclerite cross-bar narrow; windows clear on ventral cornua; rarely on dorsal cornua; angle between dorsal and ventral cornua sharp. Anterior spinal bands (segs. 2-12), complete on 2-9, incomplete on 10-12; bands on 6-12 cleft ventrally. Posterior

spinal bands (segs. 6-11), complete on 9-11 (although sometimes very faint on 9), incomplete on 6-8. Anal spines rather similar in distribution to C. vicina; very few spines ventrally between anus and anal lobes. Spines pointed, moderately pigmented; each spine with one tooth only, tooth often very short with broad base. P_2 closer to P_3 than to P_1; distance between papillae greater than width of their bases.

Taxonomic Remarks

The third instar was described by Hall (1948) who stated that the anterior spiracles had 8 lobes; in the specimens seen by me the number was 10-11. Furthermore, Hall states that the anterior spinal bands are complete only on segments 2-8, that on segment 9 being incomplete. In fact, it is complete on this segment, but is difficult to see, as it consists of only two or three rows of spines dorsally. This type of error is very common in previous descriptions and emphasises the need for good lighting when examining the spinal bands.

Specimens examined: U.S.A. (Georgia).

Biology and Distribution

This carrion-breeding species is widespread in North America (Hall, 1948).

Calliphora terraenovae Macquart

First Instar. Skeleton with lateral plate robust, more or less as wide at narrowest point as length of median tooth; ventral and dorsal cornua divergent; basal section of hypostomal sclerite in lateral view less thick than greatest thickness of median tooth in lateral view; median tooth longer than length of mouth-hook; dorsal horn of median tooth prominent. Anterior spinal bands (segs. 2-12), complete on 2-9, incomplete on 9-12, bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11), complete on 10-11, incomplete on 6-9.

Second Instar. Skeleton (Fig. 243) with lateral plate narrower at narrowest point than length of mouth-hook; mouth-hook horns short; tooth of mouth-hook narrower at area of curvature than at base of tooth. Anterior spinal bands (segs. 2-12), complete on 2-9, incomplete on 9-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11), incomplete on 6-9, complete on 10-11; patches of spines present dorsal and ventral to anus.

Third Instar. Skeleton with mouth-hook tooth greater than length of base; rod of oral sclerite well-pigmented (except at tip) and slightly thickened at base; wing and wish-bone structures unpigmented; dental sclerite moderately robust; liguloid arch broad, darkly pigmented and with anterior teeth; hypostomal plates well-pigmented and large; hypostomal sclerite cross-bar broad; windows large on ventral cornua, not obvious on dorsal

cornua; angle between dorsal and ventral cornua sharp; dorsal cornua relatively slender. Anterior spinal bands (segs. 2-12), complete on 2-10 (although faint dorsally on 10), incomplete on 11-12; bands on 6-12 only partially cleft. Posterior spinal bands (segs. 6-12), incomplete on 6, complete on 7-12 (faint dorsally on 7); many spines in area between anal lobes and anus, with a patch of spines dorsal to anus. Spines pointed, well-pigmented and often with two or three teeth (Fig. 52). P_1, P_2 and P_3 equidistant; bases of P_1-P_3 equal to distances between them; papillae all well-developed, P_5 somewhat upward pointing.

Taxonomic Remarks

Due to the faintness of anterior spinal band 10 dorsally in the third instar, Hall (1948) stated that this band was incomplete, a similar error to the one he made with the previous species. Hall described only the third instar of this species.

Specimens examined: U.S.A. (Colorado).

Biology and Distribution

This is a common carrion-breeder in North America, especially in the Rocky Mountain districts (Hall, 1948).

Calliphora croceipalpis Jaennicke

First Instar. Skeleton (Fig. 252) with width of lateral plate at

narrowest point appreciably greater than half the length of median tooth; ventral and dorsal cornua slightly divergent; basal section of hypostomal sclerite in lateral view less thick than greatest thickness of median tooth in lateral view; median tooth equal to, or very slightly longer than, length of mouth-hook; dorsal horn of median tooth moderately prominent. Anterior spinal bands (segs. 2-12), complete on 2-9, incomplete on 10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11), incomplete on 6-9, complete on 10-11. Patch of spines present ventral to anus.

Second Instar. Skeleton (Fig. 242) with breadth of lateral plate at narrowest point much less than length of mouth-hook; mouth-hook horns robust; tooth of mouth-hook thicker at area of curvature than at base of tooth. Anterior spinal bands (segs. 2-12), complete on 2-9, incomplete on 10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11), incomplete on 6-9, complete on 10-11. Patch of spines present ventral to anus.

Third Instar. Skeleton (Fig. 234) with mouth-hook tooth only slightly longer than depth of mouth-hook base; rod, wing and wish-bone structures of oral sclerite heavily pigmented (Fig. 132); base of rod slightly thickened; dental sclerite very slender; liguloid arch moderately pigmented, with anterior teeth; hypostomal plates well-pigmented (Fig. 157); hypostomal sclerite cross-bar broad (Fig. 157); windows often clear on ventral cornua, usually absent on dorsal cornua; posterodorsal process of ventral cornu prominent; dorsal cornu only slightly arched dorsally. Anterior spinal bands (segs. 2-12),

complete on 2-10, incomplete on 11-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11), incomplete on 6-7, complete (but faint) on 8-11. Anal spine distribution similar to C. vicina. Papillae moderately developed; P_2 closer to P_3 than to P_1. Distances between papillae greater than width of papillae bases. All spines pointed, often with two teeth; spines usually not arranged in definite rows (Fig. 50).

Taxonomic Remarks

The immature stages of this species are previously undescribed. They are very similar to those of C. vicina, but are, nonetheless, separable from the latter species (see key in Chapter 10).

Specimens examined: South Africa (Cape Province).

Biology and Distribution

This is a common carrion-breeder of the southern, eastern and upland regions of the Afrotropical region (Zumpt, 1956b). It is recorded as a myiasis agent.

Calliphora augur (Fabricius)

First Instar. Skeleton with lateral plate robust, more or less equal to length of median tooth, but a little less than length of mouth-hook; ventral and dorsal cornua divergent; basal section of hypostomal sclerite in lateral view less thick than greatest thickness of median tooth in lateral view; mouth-hook slightly longer than

median tooth; median tooth robust and arched dorsally; chitinised teeth absent; a weak post-mandibular sclerite present. Anterior spinal bands (segs. 2-12), complete on 2-8 (faint dorsally on 9), incomplete on 10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11), incomplete on 6-7 (sometimes faintly complete on 7), complete on 8-11. Patch of spines present dorsal to anus.

Second Instar. Skeleton with width of lateral plate at narrowest point less than length of mouth-hook; tooth of mouth-hook thickened at area of curvature, but less so than in C. vicina; ventral and dorsal cornua more or less parallel or slightly converging. Anterior spinal bands (segs. 2-12), complete on 2-8, incomplete on 8-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11), incomplete on 6-7, complete on 8-11. Patch of spines present dorsal to anus.

Third Instar. Skeleton (Fig. 232) with mouth-hook tooth usually less than depth of base; oral sclerite with heavily pigmented rod, and unpigmented wing and wish-bone structures; base of rod thickened; dental sclerite slender; liguloid arch rather narrow, but well-defined (Fig. 152); hypostomal plates relatively small, and weakly pigmented at the edges; hypostomal sclerite cross-bar rather narrow (Fig. 152); windows clear on ventral cornua, usually absent from dorsal cornua; posterodorsal process of ventral cornu prominent; angle between ventral and dorsal cornua roundly arched. Anterior spinal bands (segs. 2-12), complete on 2-10 (although often faint dorsally on 10), incomplete on 11-12; bands on 6-12 cleft ventrally. Posterior spinal

bands (segs. 6-11), incomplete on 6-9, complete on 10-11. Anal spines distributed in a manner similar to C. vicina. Papillae small; P_1, P_2 and P_3 equidistant; distances between papillae greater than width of bases. Spines small, pointed and rather weakly pigmented (Fig. 46); hardly ever with more than one tooth.

Taxonomic Remarks

The third instar was described by Fuller (1932), but her description is inadequate to distinguish this species from other Australian Calliphora. For example, she states that the details of the spinulation is identical in this species and in C. stygia. This is definitely not so, as there are very distinctive differences between these two species, both in the structure of the spines themselves and the pattern of the bands. O'Flynn and Moorhouse (1980) published photographs of the skeletons of the early instars, but, as Cantrell (1982) points out, such photographs "lack clarity" and are of little use in identification (see Materials and Methods).

Specimens examined: Australia (Queensland, New South Wales).

Biology and Distribution

This is a carrion-breeder specialising in small carcasses like small birds, snails and insects (Zumpt, 1965). It is a myiasis agent, and an important sheep-strike fly in Australia. It is limited to Australia and Tasmania.

Calliphora stygia (Fabricius)

Second Instar. Skeleton (Fig. 244) with width of lateral plate at narrowest point less than length of mouth-hook; area of curvature of mouth-hook tooth more or less equal in thickness to base of tooth. Anterior spinal bands (segs. 2-12), complete on 2-8 (although faint dorsally on 6, 7 and 8); incomplete on 9-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11), incomplete on 6-10, complete on 11. Patch of spines present dorsally and ventrally around anus.

Third Instar. Skeleton (Fig. 230) with mouth-hook tooth long-curved and appreciably longer than depth of base; rod of oral sclerite well-pigmented (except at tip) and thickened basally; wing and wish-bone structures unpigmented; dental sclerite moderately robust (Fig. 230); liguloid arch rather broad, but diffuse; hypostomal plates large and well-pigmented; hypostomal sclerite cross-bar narrow; windows usually clear on ventral cornua, absent on dorsal cornua; posterodorsal process on ventral cornu prominent; dorsal cornu only slightly arched dorsally; angle between dorsal and ventral cornua roundly arched. Anterior spinal bands (segs. 2-12), complete on 2-9 (although faint dorsally on 9), incomplete on 10-12; bands on 5-12 cleft ventrally. Posterior spinal bands (segs. 6-11), incomplete on all segments. Anal region heavily spined, rather similar to C. vomitoria, with patch of heavy spines present dorsal to anus. Spines strong and rounded, but lightly pigmented (Fig. 47).

Taxonomic Remarks

Zumpt (1965) described the third instar of this species, but his description is inadequate to distinguish it from C. augur or any other Australian species of the genus.

Specimens examined: Australia (Queensland); new Zealand.

Biology and Distribution

This is a common carrion-breeder of Australia, Tasmania and New Zealand. It is an agent of myiasis, being an important cause of sheep-strike, especially in New Zealand.

Calliphora ochracea Schiner

Third Instar. Skeleton with mouth-hook tooth long-curved and longer than depth of base; dorsal horn prominent; rod of oral sclerite pigmented along about half its length; wing and wish-bone structures unpigmented; rod cone-shaped (Fig. 137); dental sclerite robust; liguloid arch rather narrow, but well-pigmented; hypostomal plates small and only moderately pigmented; hypostomal sclerite cross-bar narrow (Fig. 159); windows usually clear on ventral cornua; dorsal cornu not arched; ventral cornu slightly longer than half the length of dorsal cornu; posterodorsal process of ventral cornu prominent; angle between dorsal and ventral cornua roundly arched. Anterior spinal bands (segs. 2-12), complete on 2-6, incomplete on 7-12; none of the bands appreciably cleft, but segs. 5-12 with small

bare ventral area. Posterior spinal bands (segs. 5-11); incomplete on 5-10, complete on 11. Spines in anal region similar to C. stygia. Spines moderately pigmented, small, with one or two teeth per spine. Posterior papillae well-developed and larger than in any other Calliphora sp.

Taxonomic Remarks

This species was described by Fuller (1931), but again her description is not detailed enough to enable reliable identification.

Specimens examined: Australia (Queensland).

Biology and Distribution

This is a common carrion-breeder of Australia (Fuller, 1931). It is not known to cause myiasis.

Calliphora quadrimaculata (Swederus)

Third instar. Skeleton (Fig. 233) with length of mouth-hook tooth longer than depth of base; oral sclerite totally unpigmented; dental sclerite moderately robust; liguloid arch well-pigmented and V-shaped, with row of anterior teeth; hypostomal plates rather small but well-pigmented; hypostomal sclerite cross-bar narrow (Fig. 155); small windows present on ventral cornua, absent on dorsal cornua; dorsal cornu not strongly arched dorsally; angle between dorsal and ventral cornua roundly arched. Anterior spinal bands (segs. 2-12), complete on

2-11 (although often faint dorsally on 11), incomplete on 12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 8-11); incomplete on 8-9, complete on 10-11. Anal region with many strong spines. Spines large and rounded, with well-pigmented bases (Fig. 48). Anal papillae very well-developed.

Taxonomic Remarks

Miller (1932) described this species in the third instar, but his concern was mainly with the functional morphology of the skeleton, not with identification. However, his description of the skeleton is very detailed and accurate.

Specimens examined: New Zealand.

Biology and Distribution

This species is endemic in New Zealand. It breeds in carrion, and has also been recorded as a myiasis agent.

Calliphora hortona (Walker)

First Instar. Skeleton (Fig. 253) with lateral plate robust, width at narrowest point equal to, or greater than, length of median tooth; ventral and dorsal cornua slightly divergent; basal section of hypostomal sclerite more or less as thick in lateral view as thickness of median tooth in lateral view; mouth-hook considerably longer than median tooth; dorsal horn of median tooth not prominent. Anterior

spinal bands (segs. 2-12), complete on 2-9, incomplete on 10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 7-11), incomplete on 7-19, complete on 11.

Second Instar. Skeleton (Fig. 245) with lateral plate relatively robust, but narrower at narrowest point than length of mouth-hook; mouth-hook horns short; tooth of mouth-hook only slightly thickened; dorsal cornu much narrower in this species than any other member of the genus. Anterior spinal bands (segs. 2-12), complete on 2-9, incomplete on 10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 7-11), incomplete on 7-10, complete on 11.

Third Instar. Skeleton (Fig. 235) with mouth-hook tooth longer than depth of base; rod of oral sclerite pigmented only at its base, never along more than a quarter of its length; wing and wish-bone structures unpigmented (Fig. 140); dental sclerite robust; liguloid arch very characteristically shaped (Fig. 158), with middle part weakly pigmented and lateral ends heavily pigmented; hypostomal plates rather small and moderately pigmented; hypostomal sclerite cross-bar narrow; ventral cornua with small windows, dorsal cornua usually without; dorsal cornu only slightly arched dorsally; angle between dorsal and ventral cornua sharp, not roundly arched. Anterior spinal bands (segs. 2-12), complete on 2-9, incomplete on 10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs 7-11), incomplete on 7-10, complete on 11. Spines small, pointed and weakly pigmented (Fig. 49), very rarely with two teeth. Posterior papillae moderately developed; P_1, P_2 and P_3 equidistant.

Taxonomic Remarks

Only the third instar of this species was described by Miller (1939). The description is one of the most detailed of the early descriptions. However, it contained a number of errors; e.g. there is no mention of the oral sclerite and it does not appear in the illustration of the skeleton.

Specimens examined: New Zealand.

Biology and Distribution

This species is endemic in New Zealand and has a rather unusual life-history for a Calliphorid. Zumpt (1965) states that it breeds mainly in decaying seaweed on the sea-shore. He also states that it has been recorded from a few cases of sheep-strike. The specimens examined by me all came from a laboratory culture in New Zealand where the larvae were reared on cow-dung. As far as I am aware, this species has never been found in carrion.

7.3 Genus Cynomya Robineau-Desvoidy

Cynomya mortuorum (Linnaeus)

First Instar. Skeleton (Fig. 257) with lateral plate very narrow at narrowest point, about equal in thickness to depth of basal section of hypostomal sclerite in lateral view; ventral and dorsal cornua

convergent; basal section of hypostomal sclerite almost as thick as greatest thickness of median tooth in lateral view; median tooth longer than mouth-hook. Anterior spinal bands (segs. 2-12), complete on 2-8 (often faint, or completely absent, dorsally on 8), incomplete on 9-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11), faint dorsally on 6, complete on 7-11, sometimes very few spines ventrally on 5. Patch of spines present dorsal to anus.

Second Instar. Skeleton (Fig. 259) with lateral plate narrower at narrowest point than length of mouth-hook; mouth-hook tooth thickened at area of curvature in a manner reminiscent of C. vicina, but the tip of the tooth is more clearly defined and pointed than in C. vicina. Anterior spinal bands (segs. 2-12), complete on 2-9, incomplete on 10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 7-11), complete on 8-11, faint dorsally on 7. Patch of spines present dorsally to anus, and semi-circle of spines present ventrally.

Third Instar. Skeleton (Fig. 262) with mouth-hook tooth longer than depth of base; dorsal margin of tooth (in lateral view) straight, and curving rather abruptly at the tip; oral sclerite rod pigmented along a little more than half its length (Fig. 141); rod not much thickened basally; wing and wish-bone structures unpigmented; dental sclerite robust; liguloid arch somewhat diffuse; hypostomal plates weakly pigmented and small; hypostomal sclerite cross-bar narrow; ventral cornu very thick posteriorly and with prominent posterodorsal process; ventral cornu slightly more than half the length of dorsal cornu; windows on both cornua very small or absent; angle between dorsal and

ventral cornua sharp. Anterior spinal bands (segs. 2-12), complete on 2-8, incomplete on 9-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 7-11), incomplete on 7-9, complete on 10-11. Anal spinal arrangement similar to C. vicina. P_1 larger than P_2 and P_3; P_2 closer to P_3 than to P_1. Distances between papillae greater than width of bases. Spines small, pointed and darkly pigmented. (Fig. 53)

Taxonomic Remarks

Schumann's (1954) description of this species agrees closely with the present one, showing that this species shows much less geographical variation than other species in the subfamily for which other descriptions are available. However, in Schumann's description of German specimens the first instar skeleton seems to be rather more robust than they are in British specimens.

Specimens examined: U.K. (Durham).

Biology and Distribution

This species is widely distributed in the northern parts of the Holarctic region, and has been recorded as far east as Turkestan (Zumpt, 1956a). It is a carrion-breeder and is not known to cause myiasis.

7.4 Genus Cynomyopsis Townsend

Cynomyopsis cadaverina (Robineau-Desvoidy)

Third Instar. Skeleton with mouth-hook tooth much longer than depth of base; dorsal margin of tooth straight in lateral view and abruptly curved at tip; oral sclerite rod pigmented along about two-thirds of its length and thickened basally (Fig. 142); wing and wish-bone structures unpigmented; dental sclerite robust; liguloid arch weak; hypostomal plates small and weakly pigmented (Fig. 160); hypostomal sclerite cross-bar narrow; windows unclear on either cornu; ventral cornu slightly more than half length of dorsal cornu; posterodorsal process of ventral cornu prominent; angle between ventral and dorsal cornua wider than in Cy. mortuorum. Anterior spinal bands (segs. 2-12), complete on 2-9 (although faint dorsally on 9), incomplete on 10-12; bands on 5-12 cleft ventrally. Posterior spinal bands (segs. 5-12) complete on 9-11, incomplete on 5-8. Spines present dorsal and ventral to anus, but no spines between anus and anal lobes. Spines slender and weakly pigmented; each spine with one tooth, very rarely indeed with two teeth. P_1 much larger than P_2 or P_3; P_2 closer to, and smaller than, P_3.

Taxonomic Remarks

This species is very similar to Cynomya mortuorum, a fact which supports the view that the genus Cynomyopsis is synonymous with Cynomya. The species was described by Hall (1948) and his description

is similar to the above, although he used unreliable characters, e.g. button pigmentation, to distinguish it from other species. The description of the skeleton is inadequate.

Specimens examined: U.S.A. (Ohio, Washington State).

Biology and Distribution

This Nearctic species favours particularly putrid carrion in which to breed (Hall, 1948). It is also known as a secondary invader in a number of cases of myiasis.

7.5. Genus Triceratopyga Rohdendorf

Triceratopyga calliphoroides Rohdendorf

First Instar. Skeleton (Fig. 256) with lateral plate narrower at narrowest point than length of median tooth; basal section of hypostomal sclerite thicker than greatest thickness of median tooth in lateral view; median tooth longer than mouth-hook; ventral and dorsal cornua divergent; many chitinised teeth present. Anterior spinal bands (segs. 2-12), complete on 2-10, incomplete on 11-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11), incomplete on 6-7, faint dorsally on 8, complete on 9-11.

Third Instar. Skeleton (Fig. 261) with very robust mouth-hooks; mouth-hook tooth not longer than depth of base; oral sclerite with well-pigmented rod and wish-bone sclerite; wing structure unpigmented;

rod club-shaped (Fig. 143); dental sclerite moderately robust; liguloid arch narrow; hypostomal plates moderately pigmented; hypostomal sclerite very thick in lateral view; dorsal cornu narrow, with a more or less straight dorsal margin; ventral cornu slightly more than half length of dorsal cornu and with prominent posterodorsal process; windows present on ventral cornua, absent from dorsal cornua; angle between dorsal and ventral cornua wide. Anterior spinal bands (segs. 2-12), complete on 2-10, incomplete on 11-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11), incomplete on 6-7, faint dorsally on 8, complete on 9-11. Spines present dorsal and ventral to anus. Spines rather broad with pointed tips and moderately pigmented; only one tooth per spine. P_2 closer to P_3 than to P_1.

Taxonomic Remarks

Ishijima (1967) described the third instar, but his description relies heavily on unreliable characters, such as the posterior spiracular peritreme, and is of little use in separating it from other species. He uses the spiracular character to distinguish Triceratopyga from Calliphora on the basis of the presence or absence of an inner peritremal projection. As seen above (4.2.6) this character is particularly unreliable.

Specimens examined: Japan.

Biology and Distribution

This carrion-breeding species is found in Siberia, China and Japan. It is not known to cause myiasis.

7.6 Genus Aldrichina Townsend

Aldrichina grahami (Aldrich)

Third Instar. Skeleton with mouth-hook tooth longer than depth of base; oral sclerite rod pigmented basally, and rather weakly more anteriorly (Fig. 144); rod much thickened basally; wing structure unpigmented; wish-bone structure weakly pigmented; dental sclerite rather small; liguloid arch well-pigmented and U-shaped (Fig. 161) pigment concentrated mainly at edges of arch; hypostomal sclerites moderately pigmented; hypostomal sclerite cross-bar narrow (Fig. 161); windows usually present on ventral and dorsal cornua; dorsal cornu strongly arched dorsally; angle between ventral and dorsal cornua very wide. Anterior spinal bands (segs. 2-12), complete on 2-9, (although usually faint dorsally on 9), incomplete on 11-12; bands on 7-12 with a very small spineless median area ventrally. Posterior spinal bands (segs. 6-11), incomplete on 6-9; complete on 10-11. Spines with one pointed tooth each (Fig. 54) and weakly pigmented. P_1, P_2 and P_3 equidistant.

Specimens examined: Japan; Canada.

Taxonomic Remarks

This species was described by Ishijima (1967); again, the characters he uses are not sufficient to distinguish it from other Calliphorinae.

Biology and Distribution

This carrion-breeding species occurs in Siberia, China, Japan and North America (Zumpt, 1956a). It is not known to cause myiasis.

7.7 Genus Eucalliphora Townsend

Eucalliphora latifrons (Hough)

First Instar. Skeleton with lateral plate narrower at narrowest point than length of median tooth; basal section of hypostomal sclerite in lateral view less thick than thickness of median tooth in lateral view; median tooth and mouth-hook approximately equal in length; chitinised teeth absent, but two diffuse areas of weak sclerotisation present. Anterior spinal bands (segs. 2-12), complete on 2-8, incomplete on 9-12; bands on 6-12 slightly cleft ventrally. Posterior spinal bands (segs. 7-11) incomplete on 7-9, complete on 10-11.

Third Instar. Skeleton with mouth-hook tooth shorter than depth of base; oral sclerite rod pigmented along most of its length, and somewhat thickened basally; wing and wish-bone structures unpigmented; dental sclerite slender; liguloid arch narrow and weakly pigmented; hypostomal plates moderately pigmented; hypostomal sclerite rather broad in lateral view; windows large on ventral cornua, absent from dorsal cornua; ventral cornu slightly longer than dorsal cornu; angle between dorsal and ventral cornua wide. Anterior spinal bands

(segs. 2-12), complete on 2-8, incomplete on 9-12, bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 7-11), incomplete on 7-9, complete on 10-11. Spines with one pointed tooth each and moderately pigmented.

Taxonomic Remarks

This species is previously undescribed. Hall (1948) described the second and third instars of "Eucalliphora lilaea", but it is not certain to which species he was referring. His description is not detailed enough for comparison with the above, although his illustration of the third instar skeleton is similar to mine.

Specimens examined: Canada (Ontario).

Biology and Distribution

This is a carrion-breeding species of the Nearctic region.

7.8 Genus Lucilia Robineau-Desvoidy

The genus Lucilia is here interpreted in the wide sense to include Phaenicia Robineau-Desvoidy, and not in the restricted sense of American authors. The genus Hemipyrellia Townsend, formerly a subgenus of Lucilia, is treated separately below.

Lucilia sericata (Meigen)

First Instar. Skeleton (Fig. 254) with lateral plate at narrowest point more or less equal to length of median tooth; basal section of hypostomal sclerite more or less equal in thickness to thickness of median tooth in lateral view; mouth-hook obtuse-angled. Anterior spinal bands (segs. 2-12), complete on 2-6, incomplete on 7-12; bands on 6-12 with small spineless patch ventrally. Posterior spinal bands (segs. 6-11), all incomplete. Few colourless spines dorsal to anus.

Second Instar. Skeleton (Fig. 258) with mouth-hook as long as, or slightly longer than, length of base; area of curvature of tooth only very slightly thickened. Anterior spinal bands (segs. 2-12), complete on 2-6, incomplete on 7-12; bands on 6-12 with small spineless patch ventrally. Posterior spinal bands (segs. 5-11) all incomplete. Few colourless spines dorsal to anus.

Third Instar. Skeleton (Fig.265) with mouth-hook tooth appreciably longer than depth of base; oral sclerite narrow and totally unpigmented; dental sclerite rather slender; liguloid arch narrow and weakly pigmented; hypostomal plates small and weakly pigmented; hypostomal sclerite narrow in lateral view and cross-bar narrow (Fig. 162); windows usually only on ventral cornua; ventral cornu with prominent posterodorsal process; angle between dorsal and ventral cornua wide. Anterior spinal bands (segs. 2-12), complete on 2-8, incomplete on 9-12; bands on 6-12 cleft ventrally. Posterior spinal

bands (segs. 6-11), incomplete on 6-9, faint dorsally on 10, complete on 11. Very few spines present dorsal to anus. P_1, P_2 and P_3 small and equidistant. All spines small, pointed and weakly pigmented; hardly ever with more than one tooth. (Fig. 56)

Taxonomic Remarks

This species has been described by Hall (1948) and Kano and Sato (1952) in all larval stages. Hall's description is by far the more detailed, but his emphasis on unreliable characters has meant that this species could not be reliably separated from other members of the genus. Unfortunately, Zumpt (1965) used Kano and Sato's much less detailed description in his book on myiasis.

Specimens examined: U.K. (lab. culture originating from Weybridge); U.S.A.; Japan; South Africa; Australia.

Biology and Distribution

A very common carrion-breeder and facultative parasite of the Holarctic region; it has also been introduced into certain parts of the southern hemisphere, notably Australia, New Zealand and South Africa. It is an important agent of sheep-strike in many parts of the world and its biology has been intensively studied (see Norris, 1965; Zumpt, 1965).

Lucilia caesar (Linnaeus)

First Instar. Skeleton with lateral plate more or less at narrowest point equal to length of median tooth; basal section of hypostomal sclerite more or less equal in thickness to median tooth in lateral view; mouth-hook obtuse-angled. Anterior spinal bands (segs. 2-12), complete on 2-7, incomplete on 8-12; bands on 6-12 with small spineless area ventrally. Posterior spinal bands (segs. 6-11) all incomplete. Few colourless spines dorsal to anus.

Second Instar. Skeleton with mouth-hook tooth as long as, or longer than, length of base; area of curvature of tooth only very slightly thickened. Anterior spinal bands (segs. 2-12), complete on 2-7, incomplete on 8-12; bands on 6-12 with small spineless area ventrally. Posterior spinal bands (segs. 6-11) all incomplete. Few colourless spines dorsal to anus.

Third Instar. Skeleton with mouth-hook tooth appreciably longer than depth of base; oral sclerite narrow and totally unpigmented; dental sclerite slender; liguloid arch narrow and moderately pigmented; hypostomol plates small and weakly pigmented; hypostomal sclerite narrow in lateral view and cross-bar narrow; windows usually only on ventral cornua; angle between dorsal and ventral cornua wide. Anterior spinal bands (segs. 2-12) complete on 2-9, incomplete or faint on 10, incomplete on 11-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11) complete on 6-7, faint dorsally on 8-9, incomplete on 10-11. Spines present in several

rows dorsal to anus, with a concentration of spines centrally; only one row of spines ventral to anus. All spines small, one-pointed and weakly pigmented. P_1, P_2 and P_3 small and equidistant.

Taxonomic Remarks

There is no previous description of this species in any detail. Zumpt (1965) says that he could not distinguish it from L. illustris (Meigen).

Specimens examined: U.K. (Durham).

Biology and Distribution

This is a common carrion-breeder of the Western Palaearctic. It is known to cause myiasis in sheep and Man (Zumpt, 1965).

Lucilia cuprina (Wiedemann)

First Instar. Skeleton (Fig. 255) with lateral plate at narrowest point more or less equal to length of median tooth; basal section of hypostomal sclerite more or less equal in thickness to thickness of median tooth in lateral view; mouth-hook acute-angled; dorsal arch robust. Anterior spinal bands (segs. 2-12) complete on 2-7, incomplete on 8-12; bands on 7-12 with small spineless area ventrally. Posterior spinal bands (segs. 7-11) incomplete on all segments. Few faint spines dorsal to anus.

Second Instar. Skeleton (Fig. 260) with mouth-hook tooth as long as, or shorter than, length of base; area of curvature of tooth narrower than basal area. Anterior spinal bands (segs. 2-12) complete on 2-8, incomplete on 9-12; bands on 7-12 with small spineless area ventrally. Posterior spinal bands (segs. 7-11) incomplete on all segments. Few spines present dorsal to anus.

Third Instar. Skeleton (Fig. 266) with mouth-hook tooth appreciably longer than depth of base; oral sclerite totally unpigmented and narrow; dental sclerite moderately developed; liguloid arch narrow and weakly pigmented; hypostomal plates weakly pigmented, but of moderate size, hypostomal sclerite broader in lateral view than most species of Lucilia, but cross-bar narrow; windows large on ventral cornua, absent from dorsal cornua; dorsal cornu short relative to ventral cornu; angle between dorsal and ventral cornua very wide. Anterior spinal bands (segs. 2-12) complete on 2-9, faint dorsally on 10, incomplete on 11-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 7-11) incomplete on 7-10, complete on 11. Single patch of strong heavily pigmented spines present dorsal to anus. Spines small one-pointed and moderately pigmented. P_2 closer to P_1 than P_3; all papillae very small.

Taxonomic Remarks

This species was described by Waterhouse and Paramonov (1950), Kano and Sato (1952) and Zumpt (1965). All three descriptions are detailed, but do not permit reliable separation from L. sericata (see

Chapter 10).

Specimens examined: South Africa; Australia.

Biology and Distribution

This is a common carrion-breeder of Africa and Tropical Asia, and has also been introduced into Australia (Zumpt, 1965). It is a very important agent of sheep-strike in the southern hemisphere.

Lucilia ampullacea Villeneuve

First Instar. Skeleton with lateral plate at narrowest point more or less equal to length of median tooth; basal section of hypostomal sclerite more or less equal in thickness to median tooth in lateral view; mouth-hook acute-angled. Anterior spinal bands (segs. 2-12) complete on 2-7, incomplete on 8-12; bands on 7-12 with clear spineless area ventrally. Posterior spinal bands (segs. 7-11) incomplete on all segments. Few spines dorsal to anus.

Second Instar. Skeleton with mouth-hook tooth as long as, or longer than, length of base; area of curvature of tooth only very slightly thickened. Anterior spinal bands (segs. 2-12) complete on 2-7, incomplete on 8-12; bands on 7-12 with small spineless area ventrally. Posterior spinal bands (segs. 7-11) all incomplete. Few spines present dorsal to anus.

Third Instar. Skeleton (Fig. 264) with mouth-hook tooth only slightly longer than depth of base; oral sclerite rod pigmented basally; wing and wish-bone structures unpigmented; dental sclerite robust; liguloid arch narrow and moderately pigmented; hypostomal plates moderately pigmented and of moderate size; hypostomal sclerite narrow in lateral view, but cross-bar slightly broader than most Lucilia spp.; very small windows sometimes present on dorsal and ventral cornua; dorsal cornu distinctly narrower than in other Lucilia spp. Anterior spinal bands (segs. 2-12) complete on 2-9, incomplete on 10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11) incomplete on 6-9, complete on 10-11. A few rows of weak spines present dorsal to anus; a single row ventrally. All spines weakly pigmented, small and one-pointed. Papillae small and equidistant.

Taxonomic Remarks

This is the species that was originally described by Kano and Sato (1952) as possessing a "reduced accessory oral sclerite" (see 5.6); as seen above, however, the sclerite is not reduced and is present in most species, the lack of pigmentation in many species giving the impression of absence.

Specimens examined: Japan.

Biology and Distribution

This is a carrion-breeder of the Palaearctic and Oriental regions. It is recorded as a myiasis agent.

Lucilia porphyrina (Walker)

Third Instar. Skeleton with mouth-hook tooth appreciably longer than depth of base; oral sclerite rod and wish-bone structure pigmented; wing structure unpigmented; dental sclerite slender; liguloid arch narrow and weakly pigmented; hypostomal plates small and weakly pigmented; hypostomal sclerite narrow in lateral view, cross-bar narrow but broader than L. sericata; windows usually absent from dorsal and ventral cornua; angle between dorsal and ventral cornua sharp. Anterior spinal bands (segs. 2-12) complete on 2-8, incomplete or faint on 9, incomplete on 10-12; bands on 7-12 cleft ventrally. Posterior spinal bands (segs. 7-11) incomplete on 7-9, complete on 10-11. Anal spines present dorsally and laterally, but not ventrally to anus. Spines small, one-pointed and weakly pigmented. Papillae small and equidistant.

Taxonomic Remarks

Ishijima (1967) published a photograph of a lateral view of the skeleton; this is misleading since the specimen was boiled in KOH prior to mounting. The result is that the oral sclerite pigmentation is not visible and the pharyngeal sclerite appears reduced, due to loss of pigmentation from the dorsal region of the dorsal cornu.

Specimens examined: Japan.

Biology and Distribution

This Oriental species is normally a carrion-breeder, but has been recorded by Dasgupta (1962) as parasitising toads (Bufo melanostictus).

Lucilia bufonivora Moniez

Second Instar. Skeleton with mouth-hook tooth parallel sided from base to area of curvature, such that the area of curvature is neither thicker nor narrower than basal area; dorsal horn very well developed. Anterior spinal bands (segs. 2-12) complete on 2-10, incomplete on 11-12; bands on 6-12 cleft ventrally. Posterior spinal bands (6-11) all complete.

Third Instar. Skeleton (Fig. 267) with mouth-hook tooth considerably longer than base of depth, much more so than any other Calliphorine; dorsal horn well developed; oral sclerite narrow and totally unpigmented; dental sclerite very slender; liguloid arch very weakly pigmented and diffuse; hypostomal plates small and weakly pigmented; parastomal bars characteristically curved; ventral cornu very broad in lateral view; small windows present on dorsal and ventral cornua; angle between dorsal and ventral cornua sharp. Anterior spinal bands (segs. 2-12) complete on 2-11, incomplete on 12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 7-11) all complete. Spines rather long, pointed and weakly pigmented (Fig. 57). P_1, P_2 and P_3 small and equidistant.

Taxonomic Remarks

Schumann (1954) described the third instar of this species, but his description and his illustration of the skeleton are so fundamentally different to the above that I must assume that the adults were misidentified. L. bufonivora has a very distinctive skeleton, but that figured by Schumann is indistinguishable from any other Lucilia spp.

Specimens examined: U.K. (Norfolk, Manchester).

Biology and Distribution

This Holarctic species is an obligate parasite of various species of frogs and toads (Brumpt, 1934).

Lucilia caeruleiviridis Macquart

Third Instar. Skeleton with mouth-hook tooth slightly longer than depth of base; oral sclerite narrow and totally unpigmented; dental sclerite slender; liguloid arch narrow and weakly pigmented; hypostomal plates small and weakly pigmented; hypostomal sclerite very narrow in lateral view; cross-bar narrow; small windows often present on ventral cornua, absent from dorsal cornua; ventral cornu with prominent postero-dorsal process; angle between dorsal and ventral cornua sharp. Anterior spinal bands (segs. 2-12) complete on 2-9, faint dorsally on 10, incomplete on 11-12; bands on 7-12 cleft

ventrally. Posterior spinal bands (segs. 7-11) incomplete on 7-10, complete on 11. Anal spines in two or three rows dorsally and one row ventrally. Spines small, pointed and weakly pigmented.

Taxonomic Remarks

Hall's (1948) description does not permit reliable separation of this species from other Nearctic Lucilia (see Chapter 10).

Specimens examined: U.S.A.

Biology and Distribution

This is a common nearctic carrion-breeder. It is recorded as causing myiasis in an unwounded kitten (Davis, 1928).

Lucilia pallescens Shannon

Third Instar. Skeleton with mouth-hook tooth slightly longer than depth of base; oral sclerite narrow and totally unpigmented; dental sclerite slender; liguloid arch robust and heavily pigmented; hypostomal plates small and weakly pigmented; hypostomal sclerite narrow in lateral view and cross-bar narrow; small windows often present on ventral cornua; ventral cornu with prominent postero-dorsal process; dorsal cornu strongly arched; angle between dorsal and ventral cornua wide. Anterior spinal bands (segs. 2-12) complete on 2-9, incomplete on 10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11) incomplete on 6-10, complete on

11. Anal spines present in profusion dorsally, one or two rows ventrally. Spines large and well-pigmented for a Lucilia sp.; spines one-pointed.

Taxonomic Remarks

The remarks under the previous species apply.

Specimens examined: U.S.A. (Washington, D.C.).

Biology and Distribution

This carrion-breeding species is said to be mainly restricted to the southern United States (Hall, 1948). It is not known to cause myiasis.

7.9 Genus Hemipyrellia Townsend

Hemipyrellia ligurriens (Wiedemann)

First Instar. Skeleton with lateral plate at narrowest point equal to length of median tooth; basal section of hypostomal sclerite more or less equal in thickness to median tooth in lateral view; mouth-hook acute-angled. Anterior spinal bands (segs. 2-12) complete on 2-5, incomplete on 6-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11) all incomplete. Very few unpigmented spines dorsal to anus.

Second Instar. Skeleton with mouth-hook tooth longer than length of base, and abruptly curved at tip; area of curvature of tooth either not thickened or only very slightly thicker than basal area of tooth. Anterior spinal bands (segs. 2-12) complete on 2-5, incomplete on 6-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11) all incomplete. Few unpigmented spines dorsal to anus.

Third Instar. Skeleton with mouth-hook tooth longer than depth of base; oral sclerite rod pigmented along posterior half, wing and wish-bone structures totally unpigmented; dental sclerite moderately robust; liguloid arch narrow and weakly pigmented; hypostomal plates small and weakly pigmented; hypostomal sclerite narrow in lateral view and cross-bar narrow; small windows often present on ventral cornua, absent from dorsal cornua; dorsal cornu strongly arched; ventral cornu with prominent posterodorsal process; angle between dorsal and ventral cornua wide. Anterior spinal bands (segs. 2-12) complete on 2-8, faint dorsally on 9, incomplete on 10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 7-11) incomplete on 7-10, complete on 11. Three or four rows of weak spines dorsal to anus, one row ventrally. All spines small, one-pointed and weakly pigmented.

Taxonomic Remarks

This species was well described by Kano and Sato (1952) and their description agrees well with the above. Nevertheless, their illustrations show that they have totally misinterpreted many of the

smaller sclerites.

Specimens examined: Japan.

Biology and Distribution

This is a carrion-breeder of the Oriental and Eastern Palaearctic regions. It is not known to cause myiasis.

Hemipyrellia fernandica (Macquart)

Third Instar. Skeleton (Fig. 263) with mouth-hook tooth not longer, and may be shorter, than depth of base; oral sclerite narrow with basal part of rod pigmented; dental sclerite moderately robust; liguloid arch narrow and weakly pigmented; hypostomal plates small and weakly pigmented; hypostomal sclerite narrow in lateral view and cross-bar narrow; dorsal cornu strongly arched; ventral cornu with prominent posterodorsal process; angle between dorsal and ventral cornua wide. Anterior spinal bands (segs. 2-12) complete on 2-9, incomplete on 10-12; bands on 7-12 cleft ventrally. Posterior spinal bands (segs. 7-11) incomplete on 7-9, complete on 10-11. Anal spines present dorsal to anus only. Spines small, one-pointed and weakly pigmented.

Taxonomic Remarks

This species is previously undescribed in the larval stage.

Specimens examined. Congo [Zaire] (Uele).

Biology and Distribution

This is a very common carrion-breeder of Africa. It is not known to cause myiasis, according to the literature (but see 7.11).

7.10 Biology of Calliphorinae

The larval structure of the Calliphorinae is generally rather uniform when compared with the Chrysomyiinae. Their habits too are rather uniform, being essentially carrion-breeders with some species acting as facultative parasites occasionally.

Only two exceptions to this rule are known to me: Lucilia bufonivora, the only obligate parasitic Calliphorine known, and Calliphora hortona, the only species known to me to breed mainly in decaying vegetable matter (seaweed). As pointed out above, C. hortona is also known as a myiasis agent and dung-breeder, but not as a carrion-breeder. This seems to me most unusual and further studies on this species seem to be indicated.

The extent to which Calliphorines breed in dung is not really known. Kano and Shinonaga (1963) state that C. vomitoria breeds in human faeces and Ishijima (1967) refers to C. lata as a breeder in garbage and human faeces, but none of these authors cite any specific data. Haddow and Thomson (1937) state that Bogdanov reared 11 generations of C. vicina on human faeces, and this is the only record I know of concerning this habit in C. vicina. The extent to which dung-breeding may take place in Nature has not been studied, and is well worth investigating; I have never reared any Calliphorine from dung.

7.11 New Host Records for Calliphorinae

The following new host records came to light during the present study:

1. Civettictis civetta (Mammalia: Viverridae) parasitised by Hemipyrellia fernandica. Specimens in a tube labelled "Congo, 1937" from the Musee Royale de L'Afrique Centrale, Tervuren, Belgium.

2. Testudo hermanni (Reptilia: Testudinidae) parasitised by C. vicina and L. ampullacea. Specimens from captive tortoises at the Institut fur Parasitologie, Vienna, Austria, 1983. Two tortoises were involved, one of which was attacked by both species and one by C. vicina alone.

CHAPTER EIGHT

SYSTEMATIC ACCOUNT: 2. CHRYSOMYIINAE

8.1 Introduction

Unlike the Calliphorinae, the Chrysomyiinae show a great diversity in the structure of the posterior spiracles. The parastomal bars are usually present, but are absent from a few species; in the descriptions the parastomal bars are to be taken as present, unless otherwise stated. A full description of the posterior spiracles is included in each species description.

8.2 Genus Chrysomya Robineau-Desvoidy

Chrysomya putoria (Wiedemann)

First Instar. Skeleton (Fig. 280) with lateral plate at narrowest point appreciably wider than length of median tooth; basal section of hypostomal sclerite in lateral view more or less the same thickness as median tooth; mouth-hooks well-developed and of peculiar structure, being composed of the hook itself plus a very deeply pigmented and large post-mandibular sclerite which is closely apposed to the posterior part of the hook, the whole structure being appreciably longer than median tooth; chitinised teeth very long; dorsal and ventral cornua not divergent; dorsal part of ventral cornu with broad,

diffuse area of sclerotisation. Anterior spinal bands (segs. 2-12), complete on 2-9, faint dorsally on 10, incomplete on 11-12; bands on 7-12 cleft ventrally. Posterior spinal bands (segs. 7-11), incomplete on 7-9, complete, but very faint laterally, on 10-11. Very few spines present dorsal to anus.

Second Instar. Skeleton (Fig. 279) with lateral plate at narrowest point equal to length of mouth-hook; mouth-hook tooth describes a smooth, tapering curve, but with a distinct bulge about midway along region of curvature. Anterior spinal bands (segs. 2-12), complete on 2-8, faint dorsally on 9, incomplete on 10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 8-11), incomplete on 8-10, complete on 11; very few spines present ventrally on 7. Spines present ventrally and dorsally to anus.

Third Instar. Skeleton (Fig. 271) with mouth-hook tooth longer than depth of base; mouth-hook with prominent dorsal ridge; oral sclerite totally unpigmented; dental sclerite robust; liguloid arch shallow V-shaped and well-pigmented; hypostomal plates weakly pigmented but large; hypostomal sclerite cross-bar narrow; windows small on both dorsal and ventral cornua; posterodorsal process of ventral cornu prominent. Posterior spiracles with thick peritreme and unpigmented button; sun-ray structure well-developed. Anterior spinal bands (segs. 2-12) complete on 2-7, faint dorsally on 8, incomplete on 9-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 8-11) all incomplete. Spines present dorsally and ventrally to anus, but no spines between anus and anal papillae. Spines pointed, most

with two or three teeth. P_2 smaller than P_1 and P_3, closer to P_3 than to P_1 and set slightly closer to larval midline than P_1 and P_3.

Taxonomic Remarks

This species is previously undescribed in the immature stages. Due to the very close similarity of the adults of this species to Ch. chloropyga, the two forms have often been thought to be the same species (Zumpt, 1965). As a result, Zumpt has suggested that the larval structure of Ch. putoria would "probably coincide with those of Ch. chloropyga". It does not, although the two forms are rather similar (see comments under Ch. chloropyga).

Specimens examined: Lab. culture from Tanzanian stock (Dar-es-Salaam).

Biology and Distribution

This is a common species of West, Central and East Africa, especially the warmer parts of these regions. It is known as a carrion- and dung-breeder, and also as a myiasis agent (Oldroyd and Smith, 1973).

Chrysomya chloropyga (Wiedemann)

Third Instar. Skeleton (Fig. 270) with mouth-hook tooth longer than depth of base; mouth-hook with prominent dorsal ridge; oral sclerite totally unpigmented; dental sclerite robust; liguloid arch shallow

V-shaped and moderately pigmented; hypostomal plates weakly pigmented, but large; hypostomal sclerite cross-bar narrow; windows small on both dorsal and ventral cornua; posterodorsal process of ventral cornu prominent. Posterior spiracles with thick peritreme and unpigmented button; sun-ray structure well-developed. Anterior spinal bands (segs. 2-12) complete on 2-7, faint dorsally on 8, incomplete on 9-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 7-11) incomplete on 7-10, complete on 11. Spines present all round anus including area between anus and anal lobes. Spines pointed, most with two or three teeth; whole spine usually broader than in Ch. putoria. P_2 smaller than P_1 and P_3.

Taxonomic Remarks

The third instar was illustrated by Patton and Evans (1929); the illustration is unclear and the brief accompanying description inadequate.

Zumpt (1965) believes that this species and Ch. putoria are synonyms, since intermediate forms (of the adult) are to be found. However, he states that crossing experiments have shown that the two forms are at least partly genetically isolated and, therefore, for practical purposes he favoured the retention of both names for the two forms. Pont (in Crosskey, 1980) considered Ch. putoria a synonym of Ch. chloropyga; Pont (pers. comm.) tells me that this move was made after consultation with Zumpt. Finally, Mr P.E. Hulley (pers. comm.) of Grahamstown, South Africa, tells me that both forms occur around his home and differ so much in appearance and

seasonality, that he is in no doubt that they are separate species (see Biology and Distribution).

The most useful features in distinguishing third instar Ch. chloropyga from Ch. putoria are the spinal patterns in the anal region, and, to a lesser extent, the form of the spines themselves.

Specimens examined: South Africa (Cape Province).

Biology and Distribution

This is a carrion- and dung-breeder of the cooler parts of southern Africa and the upland areas farther north (but see comments by Hulley above). It is also a myiasis agent (Zumpt, 1965).

Chrysomya marginalis (Wiedemann)

Third Instar. Skeleton (Fig. 269) with mouth-hooks proportionately large; mouth-hook tooth longer than depth of base; mouth-hook with prominent dorsal ridge; oral sclerite heavily pigmented at base of rod and wing and wish-bone structures; unpigmented along most of rod, rod tapering from base to tip and, as a whole, rather robust; dental sclerite robust; liguloid arch narrow and moderately pigmented; hypostomal plates small and moderately pigmented; hypostomal sclerite medium-sized; dorsal cornu rather narrow and lacking windows; ventral cornua with small windows. Posterior spiracle with thick peritreme and unpigmented button, sun-ray structure well-developed. Anterior spinal bands (segs. 2-12) complete on 2-11, incomplete on 12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 5-11) all incomplete.

Anal spines present all round anus, but fewer between anus and anal papillae. Spines with rounded tips, never forked (Fig. 58). P_2 closer to P_1 than to P_3.

Taxonomic Remarks

This species has not previously been described in the larval stage.

Specimens examined: South Africa (Natal); Namibia.

Biology and Distribution

This is a very common carrion breeder of Africa south of the Sahara, southern Arabia and India west of the Indus Valley (Zumpt, 1965). It is also known as a myiasis agent.

Chrysomya megacephala (Fabricius)

Second Instar. Skeleton with lateral plate at narrowest point equal to length of mouth-hooks; mouth-hook horns small and rounded; mouth-hook tooth smoothly curving and, while thick at base of tooth, not thicker at that area than at area of curvature. Anterior spinal bands (segs. 2-12) complete on 2-9, faint dorsally on 10, incomplete on 11-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 7-11) incomplete on 7-10, complete on 11. Spines present all round anal region.

Third Instar. Skeleton (Fig. 268) with mouth-hook tooth much longer than depth of base; oral sclerite small and pigmented at base of rod and at wing and wish-bone structures (Fig. 146); rod unpigmented anteriorly and tapering; dental sclerite weak; liguloid arch narrow but well-pigmented; hypostomal plates well-pigmented; windows usually present on ventral and dorsal cornua; angle between dorsal and ventral cornua wide. Posterior spiracles with peritremes only moderately thick and button unpigmented. Anterior spinal bands (segs. 2-12) complete on 2-8, absent laterally but present dorsally and ventrally on 9, incomplete on 10-12; bands on 6-12 cleft ventrally; bands on 2-8 with anterior pleural band. Posterior spinal bands (segs. 6-11) incomplete on 6-10, complete on 11 but faint ventrally. Spines present all round anal region, but fewer between anus and anal papillae. Spines often with two or three teeth, each with rounded tip. P_2 closer to P_1 than to P_3.

Taxonomic Remarks

The third instar was described by Patton (1922) and Patton and Evans (1929), but the descriptions are inadequate. The specimens examined by these authors were boiled in KOH and this is, no doubt, why no trace of the pigmentation of the oral sclerite remained in their preparations, since they make no mention of this structure in their description, nor does it figure in their illustration.

The form of the spines is the most reliable feature that may be used to separate third instar Ch. magacephala from Ch. marginalis.

Specimens examined: Australia (Queensland); Japan; Java.

Biology and Distribution

This is a very common carrion-breeder of the Oriental and Australasian regions, and also the neighbouring parts of the Palaearctic region, such as China and Japan. It is known to cause myiasis.

Chrysomya pinguis (Walker)

Second Instar. Skeleton with lateral plate at narrowest width less than length of mouth-hook; mouth-hook horns short and rounded; tooth of mouth-hook short and rounded; mouth-hook tooth smoothly curved, but thicker at area of curvature than at its base. Anterior spinal bands (segs. 2-12) complete on 2-9, incomplete on 10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11) incomplete on 6-10, ventral and dorsal (but not lateral) on 11. Spines present all round anal region.

Third Instar. Skeleton (Fig. 273) with mouth-hook tooth longer than depth of base; oral sclerite small and pigmented only at base of rod and wing and wish-bone structures; dental sclerite weak; liguloid arch narrow and weakly pigmented; hypostomal plates small and weakly pigmented; windows usually present on dorsal and ventral cornua; posterodorsal process of ventral cornu prominent; angle between ventral and dorsal cornua sharp. Posterior spiracle with peritreme thick, especially towards button area; button unpigmented. Anterior spinal bands (segs. 2-12) complete on 2-8, complete (but very faint

dorsally) on 9-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11) all incomplete. Spines present surrounding anus, but not very numerous ventrally. Spines usually with two or three rounded teeth each, P_2 closer to P_3 than to P_1.

Taxonomic Remarks

Ishijima (1967) described the third instar, but his description differs considerably from the above, especially with regards the details of spinulation. For example, he states that the anterior spinal bands are complete on segments 2-10, but incomplete on 11-12; the situation described in the above is very different.

Specimens examined: Japan.

Biology and Distribution

This is a carrion- and dung-breeding species of the Oriental and eastern Palaearctic regions (Zumpt, 1956a). It is not known to cause myiasis.

Chrysomya bezziana Villeneuve

Second Instar. Skeleton with mouth-hook tooth much longer than length of base; dorsal horns prominent; large windows present on ventral cornua, absent from dorsal cornua. Anterior spinal bands (segs. 2-12) all complete, 6-12 with well-developed pleural bands; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11)

very variable, usually all incomplete, but sometimes faintly complete on 10-11.

Third Instar. Skeleton (Fig. 272) with mouth-hook tooth considerably longer than depth of base; oral sclerite totally unpigmented; dental sclerite very weak; liguloid arch narrow and very weakly pigmented, with areas of heavier pigmentation along its length (Fig. 165); hypostomal plates small and moderately pigmented; hypostomal sclerite cross-bar medium-sized (Fig. 165); ventral and dorsal cornua with very small windows or windows absent; angle between dorsal and ventral cornua sharp. Posterior spiracles very heavily sclerotised; peritreme incomplete; sun-ray structure weak. Anterior spinal bands (segs. 2-12) all complete and broad; 6-12 with pleural bands; bands on 6-12 cleft ventrally. Posterior spinal bands very variable, usually present ventrally (very few spines) on 6-9, but faintly complete dorsally on 10-11; often no bands at all on one or all of segs. 6-9. Anus entirely surrounded by spines; spines somewhat weaker between anus and anal papillae. Spines large with rounded tips, never forked (Fig. 63). P_2 closer to P_3 than to P_1.

Taxonomic Remarks

The immature stages were described by Zumpt (1965) and Kitching (1976b). The former author gave very brief descriptions, and the latter gave very detailed descriptions based on S.E.M. examination, but ignored the structure of the skeleton. This is the most variable species, with regard to the pattern of spinulation, that I have

examined.

Specimens examined: Uganda; Oman (Khabura); Papua New Guinea.

Biology and Distribution

This is the Old World screw-worm fly, an obligate parasite of Man and domestic animals in Africa and the tropical parts of Asia. It also occurs in New Guinea, but, apparently, not in Australia.

Chrysomya semimetallica (Malloch)

Third Instar. Skeleton with mouth-hook tooth longer than depth of base; oral sclerite narrow and totally unpigmented; dental sclerite weak; liguloid arch broad but very weakly pigmented; hypostomal plates small and weakly pigmented; windows large on ventral cornua; angle between ventral and dorsal cornua wide. Posterior spiracle with thick peritreme; button unpigmented. Anterior spinal bands (segs. 2-12) complete on 2-8, incomplete on 9-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11) all incomplete. Spines present densely all round anal region. Spines with 2-4 teeth each. P_2 closer to P_1 than to P_3.

Taxonomic Remarks

Kitching and Voeten (1977) published a S.E.M. description of this species, but did not examine the skeleton. (See Chapter 10 for a discussion of Kitching's Chrysomya characters).

Specimens examined: Australia.

Biology and Distribution

This is a carrion-breeder of Northern Australia. It is also recorded from dung and as a myiasis agent.

Chrysomya saffranea (Bigot)

Third Instar. Skeleton with mouth-hook tooth longer than depth of base; oral sclerite totally unpigmented; dental sclerite moderately developed; liguloid arch narrow and very weakly pigmented; hypostomal plates small and weakly pigmented; large windows present on ventral cornua; angle between dorsal and ventral cornua wide; posterodorsal process of ventral cornu prominent. Posterior spiracle with thick peritreme; button unpigmented. Anterior spinal bands (segs. 2-12) complete on 2-8, incomplete on 9-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11) all incomplete. Spines present all round anal area, but somewhat less densely than in Ch. semimetallica. P_2 closer to P_1 than P_3.

Taxonomic Remarks

Kitching (1976b) published a S.E.M. description of this species, but, as with the preceding species, he did not examine the skeleton.

Specimens examined: Australia.

Biology and Distribution

This carrion-breeding species is found in northern Australia and Papua New Guinea. It is known to cause myiasis.

Chrysomya albiceps (Wiedemann)

Second Instar. Skeleton (Fig. 278) with very well-developed mouth-hooks; mouth-hook with very deep base, somewhat reminiscent of Sarcophaga spp.; mouth-hooks as long as, or slightly longer than narrowest width of lateral plate; tooth of mouth-hook parallel-sided from base to area of curvature, tapering from that point to tip; base of mouth-hook triangular and very different in shape from all previous Chrysomya spp.; dental sclerite not fused to mouth-hook base; windows present on dorsal and ventral cornua. Body processes as in third instar, but shorter. Spines as in third instar.

Third Instar. Skeleton (Fig. 274) with lateral plate at narrowest point much greater than length of mouth-hook; mouth-hook tooth much longer than depth of base; base rather elongate; oral sclerite narrow and totally unpigmented; liguloid arch very weakly pigmented centrally, but very broad and heavily pigmented peripherally, and hypostomal plates pointed anteriorly and heavily pigmented (Fig. 164); dental sclerite weak; hypostomal sclerite very broad in lateral view and cross-bar very broad (Fig. 164); windows usually present on dorsal and ventral cornua; posterodorsal process of ventral cornu well-developed. Posterior spiracle with peritreme of medium thickness;

button unpigmented. Body processes present and as described above (4.2.4.3); process 1 lacks spines on its stalk (Fig.114), but spines are present on the stalks of all other processes. Spines round and knob-like (Fig. 71) distributed all over cuticle, but spines long at tips of processes. Many of the knob-like spines possessing 3-4 points. parastomal bars absent.

Taxonomic Remarks

This is one of the 'hairy' maggots. It has been described by Patton and Evans (1929), Zumpt (1965) and Kitching (1976b). None of these descriptions enable separation of this species from the closely related Ch. rufifacies, however.

Specimens examined: Congo [Zaire] ; Oman (Khabura); South Africa (Natal).

Biology and Distribution

This carrion- and dung-breeder is found throughout Africa and southern Europe, and also in the extreme western parts of the Oriental region. It is known to cause myiasis and is often predatory upon other larvae.

Chrysomya rufifacies (Macquart)

Second Instar. Skeleton with mouth-hook length equal to, or a little shorter than, narrowest width of lateral plate; base of

mouth-hook with very large weakly sclerotised area centrally; dental sclerite robust and not fused to mouth-hook; shape of mouth-hook base similar to Ch. albiceps; dorsal and ventral cornua with clear windows; hypostomal sclerite long and ventral projection unusually long. Spines and body processes as in third instar.

Third Instar. Skeleton (Fig. 275) with lateral plate at narrowest point much greater than length of mouth-hook; mouth-hook tooth much greater than depth of base; base rather elongate; oral sclerite narrow and totally unpigmented; liguloid arch as in Ch. albiceps; hypostomal plates as in Ch. albiceps; dental sclerite weak; hypostomal sclerite very broad in lateral view and cross-bar very broad; windows present on dorsal and ventral cornua; posterodorsal process of ventral cornu very well-developed. Posterior spiracle with peritreme very thick and almost complete (the two arms of the peritreme surrounding the button almost meeting); sun-ray structure rather weak. Body processes as described above (4.2.4.3). Spines round and knob-like with 2-4 teeth each. Anus completely surrounded with spines. Many spines present on stalk of process 1. Parastomal bars absent.

Taxonomic Remarks

This species has often been thought of as a synonym of Ch. albiceps on the basis of their great similarity, both as adults and as larvae. However, several well-defined and constant characters enable separation of these two forms.

The most reliable feature separating this species from

Ch. albiceps is the presence of many spines on the stalk of process 1.

Specimens examined: Japan; Australia.

Biology and Distribution

This carrion-breeding and myiasis-causing species is widespread in the Oriental and Australasian regions.

Chrysomya incisuralis (Macquart)

Third Instar. Skeleton with length of mouth-hook much greater than depth of base; dental sclerite robust; liguloid arch not examined; hypostomal plates narrow in lateral view, but not minutely examined; lateral plate at narrowest point much greater than length of mouth-hook; oral sclerite totally unpigmented; ventral cornu with prominent posterodorsal process; clear windows present on ventral cornua; windows absent from dorsal cornua; parostomal bars absent; angle between dorsal and ventral cornua sharp. Posterior spiracle with peritreme complete and thick. Body processes as described above (4.2.4.3); process 1 covered with spines; process 4a present. Spines at tips of processes relatively shorter than their equivalents in Ch. albiceps and Ch. rufifacies; all other spines end conically (or with rounded points); spines are distributed all over body surface, including anal region.

Taxonomic Remarks

The above description is based on the examination of only a single specimen, as no other material was forthcoming. Kitching and Voeten (1977) published a S.E.M. description of this species, but ignored the skeletal structures. Their description is of limited use (see remarks in Chapter 10).

Specimen examined: Australia (Queensland).

Biology and Distribution

This is an endemic species of eastern Australia. According to Kitching and Voeten (1977) "virtually nothing is known of its biology".

Chrysomya varipes (Macquart)

Third Instar. Skeleton with mouth-hook much longer than width of lateral plate at narrowest point; mouth-hook tooth much longer than depth of base; oral sclerite narrow and totally unpigmented; dental sclerite robust; liguloid arch rather broad, but very weakly pigmented; hypostomal plates small and weakly pigmented, rather similar to Lucilia spp.; hypostomal sclerite narrow in lateral view; cross-bar narrow; dorsal cornua relatively narrow and lacking windows; ventral cornua with clear windows; posterodorsal process of ventral cornu not prominent; angle between dorsal and ventral cornua

wide; parastomal bars present. Posterior spiracle with peritreme thick and incomplete; sun-ray structure very weak. Anterior spinal bands (segs. 2-12) complete on 2-5, incomplete on 6-12. No posterior spinal bands present. Four body processes present on each of segs. 5-11. Spines with 2-4 teeth each. Spines densely present dorsal and ventral to anus, but less densely between the anus and anal papillae.

Taxonomic Remarks

Fuller (1932) described the third instar, and her description agrees closely with the present one.

Specimens examined: Australia.

Biology and Distribution

This carrion-breeding species is restricted to Australia. It is known to cause myiasis (Norris, 1959).

8.3 Genus Cochliomyia Townsend

Cochliomyia hominivorax Coquerel

Third Instar. Skeleton (Fig. 277) with mouth-hook very long, more or less length of ventral cornu; mouth-hook tooth much longer than depth of base; oral sclerite narrow and totally unpigmented; liguloid arch weakly pigmented; hypostomal plates moderately pigmented; hypostomal sclerite broad in lateral view; cross-bar broad; dental sclerite very

small; dorsal cornu very narrow; windows present on ventral cornua, absent from dorsal cornua; lateral plate at narrowest point considerably less than length of mouth-hook; angle between dorsal and ventral cornua wide. Posterior spiracle with peritreme incomplete; sun-ray structure well-developed; spiracles sunk in shallow pit. Anterior spinal bands (segs. 2-12) complete on 2-10; often not quite complete dorsally on 11, incomplete on 12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 5-11) all incomplete; spines on all posterior bands (except 11) pointing backwards. Spines present dorsal and ventral to anus, with very few between anus and anal papillae. Spines strong and well-pigmented with 1 or 2 teeth each. All posterior papillae weakly developed.

Taxonomic Remarks

This species was excellently described by Laake, Cushing and Parish (1936) and the present description agrees closely with theirs. However, the above description includes mention of the spinal morphology, which is lacking in their description.

Specimens examined: U.S.A. (Texas); Mexico.

Biology and Distribution

This is the New World screw-worm fly of the southern United States and South America. It is an obligate parasite on a wide variety of wild and domestic animals, and also on Man.

Cochliomyia macellaria (Fabricius)

First Instar. Skeleton with lateral plate at narrowest point more or less equal to length of median tooth; basal section of hypostomal sclerite in lateral view slightly less thick than depth of median tooth; weakly pigmented post-mandibular sclerite present; one large chitinised tooth present; mouth-hook acute-angled; dorsal cornu very robust and arched; ventral cornu relatively broad and with large, clear window; dorsal and ventral cornua divergent. Anterior spinal bands (segs. 2-12) complete on 2-8, incomplete on 9-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11) all incomplete. Very few spines present dorsal to anus.

Second Instar. Skeleton with lateral plate at narrowest point less than length of mouth-hook; mouth-hook tooth slightly narrower at area of curvature than at its base. Anterior spinal bands (segs. 2-12) complete on 2-9, incomplete on 10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11) all incomplete. Spines present dorsally and ventrally to anus.

Third Instar. Skeleton (Fig. 276) with mouth-hook tooth longer than depth of base; whole mouth-hook much less than length of ventral cornu; oral sclerite narrow and totally unpigmented; dental sclerite robust; windows seemingly absent from both dorsal and ventral cornua; lateral plate at narrowest point less than length of mouth-hook; dorsal cornu more robust than in Co. hominivorax; liguloid arch narrow and weakly pigmented; hypostomal plates moderately pigmented;

hypostomal sclerite narrow in ventral view and cross-bar narrow; angle between dorsal and ventral cornua wide. Posterior spiracle with peritreme narrow and incomplete; sun-ray structure, especially intermediate structure, rather weak. Anterior spinal bands (segs. 2-12) complete on 2-10 (10 often with 'bald' patch at mid-dorsal region) incomplete on 11-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 5-10) all incomplete. Anal spines arranged in characteristic pattern. Spines strong and well-pigmented, with 2 or 3 teeth each. All papillae weakly developed, except P_3 which is moderately developed.

Taxonomic Remarks

The present description agrees very well with that of Laake, Cushing and Parish (1936), but, as with the previous species, these authors omitted any mention of spinal morphology.

Specimens examined: U.S.A.

Biology and Distribution

This carrion-breeding and facultative myiasis agent is widespread in the Nearctic and Neotropical regions as far north as southern Canada and southwards to Argentina.

8.4 Biology of Chrysomyiinae

The diversity of larval structure in this subfamily is coupled with a diversity of habits. Thus carrion- and dung-breeding species are known, as well as obligate parasites and predators upon other larvae. Some species, e.g. Chrysomya albiceps, are capable of breeding on carrion, dung and living hosts, and also of preying upon other Diptera larvae in the breeding medium.

Although much is known of the biological importance of many species as sheep-strike agents (Norris, 1959), little is known of the favoured pabula of the various species in the wild. For example, is dung or carrion the main reservoir of the many facultative parasitic species involved in sheep-strike? The answer to this question should go a long way towards lessening the problem.

8.5 New Host Record for Chrysomyiinae

During the present study the following new host record came to light:

Civettictis civetta (Mammalia: Viverridae) parasitised by Chrysomya albiceps. Data from tube labelled "Congo, 1937" from Musee Royale de L'Afrique Centrale, Tervuren, Belgium.

CHAPTER NINE

SYSTEMATIC ACCOUNT: 3. PHORMIINAE AND OTHER GROUPS

9.1 Introduction

The group of species dealt with in this chapter show a great diversity in the structure of the parastomal bars and posterior spiracles and full descriptions of these structures are included for each species.

9.2 Phormiinae

9.2.1 Genus Phormia Robineau-Desvoidy

Phormia terraenovae Robineau-Desvoidy

First Instar. Skeleton with lateral plate at narrowest point at least as broad as (usually broader than) length of median tooth; basal section of hypostomal sclerite in lateral view as thick as, or thicker than, thickness of median tooth; mouth-hooks acute-angled; ventral and dorsal cornua divergent; median tooth rather uniform in thickness and lacking a pronounced horn. Anterior spinal bands (segs. 2-12) complete on 2-7, faint dorsally on 8 and 9, incomplete on 10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 8-11) all incomplete. Spines present dorsally in anal region.

Second Instar. Skeleton with lateral plate at narrowest point more or less equal to length of mouth-hook; mouth-hook tooth tapering beyond area of curvature; mouth-horn angled; sub-mandibular bars slender; dental sclerite slender; dorsal and ventral cornua with clear windows. Anterior spinal bands (segs. 2-12) complete on 2-7, faint dorsally on 8 and 9, incomplete on 10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 8-11) all incomplete. Spines present dorsally and ventrally in anal region. Posterior papillae well-developed.

Third Instar. Skeleton (Fig. 289) with mouth-hooks of characteristic shape, the horn being followed by a depression anteriorly which is in turn followed by a small elevated node, followed by the tooth tapering to a point; oral sclerite rather broad, but totally unpigmented; mouth-hook tooth longer than depth of base; dental sclerite somewhat elongate; liguloid arch well-pigmented; hypostomal plates small and weakly pigmented; hypostomal sclerite narrow in lateral view and cross-bar narrow; parastomal bars short; windows usually present on ventral cornua, absent from dorsal cornua; angle between dorsal and ventral cornua sharp. Posterior spiracle with peritreme incomplete, or very weakly pigmented in button area; spiracles set in deep pit. Anterior spinal bands (segs. 2-12) complete on 2-7, faint dorsally on 8 and 9, incomplete on 10-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 8-11) all incomplete. Posterior papillae very well-developed; P_2 closer to P_3 than to P_1; P_5 very large and pointing dorsally;P_2 much smaller than P_1 or P_3. Spines pointed and moderately well-pigmented, many with 2 or 3 teeth per spine. Rows of spines present dorsally and ventrally to anus.

Taxonomic Remarks

The present description does not agree with that of Hall (1948), especially as regards the spinulation; Hall's description does not enable separation from closely related species.

Specimens examined: U.K.; Finland.

Biology and Distribution

This species has a wide distribution in the northern Holarctic. It is a carrion-breeder, but it is also known as an agent of myiasis and a parasite of nestling birds.

Phormia regina (Meigen)

First Instar. Skeleton with lateral plate at narrowest point greater than length of median tooth; basal section of hypostomal sclerite in lateral view thicker than greatest depth of median tooth; mouth-hooks acute-angled; ventral and dorsal cornua parallel at tips; median tooth rather uniform in thickness and lacking a prominent dorsal horn. Anterior spinal bands (segs. 2-12) complete on 2-10, incomplete on 11-12; bands on 9-12 cleft ventrally. Posterior spinal bands (segs. 8-11) incomplete on 8-10, complete on 11. Double row of spines present dorsal to anus.

Second Instar. Skeleton (Fig. 287) with lateral plate at narrowest

point narrower than length of mouth-hook; mouth-hook with pronounced curved dorsal horn; sub-mandibular bars slender; windows present on ventral cornua, usually absent from dorsal cornua; dental sclerite slender. Posterior spiracle with peritreme very weakly pigmented opposite inner aperture. Anterior spinal bands (segs. 2-12) complete on 2-10, incomplete on 11-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-11) incomplete on 6-9, complete on 10-11. A few spines present dorsally and ventrally to anus.

Third Instar. Skeleton (Fig. 288) with mouth-book tooth robust and sharply curved; mouth-hook base with prominent dorsal horn; mouth-hook tooth slightly longer than depth of base; oral sclerite narrow and totally unpigmented; dental sclerite slender; liguloid arch moderately pigmented; hypostomal plates weakly pigmented; hypostomal sclerite narrow in lateral view and cross-bar narrow; windows present on ventral cornua, absent from dorsal cornua; angle between ventral and dorsal cornua wide. Posterior spiracle with peritreme incomplete. Anterior spinal bands (segs. 2-12) complete on 2-9, faint dorsally on 10, incomplete on 11-12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 6-12) incomplete on 6-9, complete on 10-11. Rows of spines present ventral to anus, with patch of spines dorsally. Spines strong and moderately pigmented, each often with 2 or 3 teeth. All papillae very well-developed.

Taxonomic Remarks

This species was described by Hall (1948), but the above

description differs from his as regards the details of the spinulation (see remarks under Phormia terraenovae).

Specimens examined: U.S.A. (Washington State).

Biology and Distribution

This species belongs to the northern Holarctic and any records from more southern parts, e.g. southern England, are probably of escapees from laboratory cultures. Ph. regina is a carrion-breeder and a myiasis agent.

9.2.2 Genus Boreellus Aldrich and Shannon

Boreellus atriceps (Zetterstedt)

Third Instar. Skeleton (Fig. 286) with mouth-hook tooth greater than depth of base; oral sclerite narrow and totally unpigmented; dental sclerite slender; liguloid arch moderately pigmented; hypostomal plates weakly pigmented; hypostomal sclerite narrow in lateral view and cross-bar narrow; windows present on ventral cornua, usually absent from dorsal cornua; angle between dorsal and ventral cornua variable. Posterior spiracle with peritreme incomplete. Anterior spinal bands (segs. 2-12) complete on 2-11 (often weak dorsally on 11) incomplete on 12; bands on 6-12 cleft ventrally. Posterior spinal bands (segs. 5-11) incomplete on 5-10, complete on 11. Spines with two or three teeth each.

Taxonomic Remarks

This species is previously undescribed in the larval stage. The above description is based on an examination of only 5 specimens, which, however, showed features that enable their separation from the two Phormia species.

Specimens examined: Canada (Baffin Island).

Biology and Distribution

This is a Holarctic carrion-breeding species, restricted to the areas north of the Arctic circle. It is thus the most northerly blowfly species known, and the vernacular name "Arctic Blowfly" is hereby proposed for it.

9.2.3 Genus Protocalliphora Hough

Protocalliphora azurea (Fallen)

First Instar. Skeleton (Figs. 281 & 282) of peculiar structure; median tooth lacking and parastomal bars not meeting and fusing; mouth-hooks smoothly curved and with prominent dorsal horns; hypostomal sclerite absent, but two small sclerites present between the parastomal bars anteriorly; chitinised teeth absent; lateral plate at narrowest width almost twice length of mouth-hook; dorsal cornu broad; ventral and dorsal cornua widely divergent. Spines covering whole body surface.

Second Instar. Skeleton (Fig. 283) with lateral plate at narrowest point greater than length of mouth-hook; mouth-hook strongly curved; hypostomal sclerite robust and with very thick dorsal process; angle between dorsal and ventral cornua sharp; windows present on ventral cornua; at most only a narrow ventral line of weak sclerotisation on dorsal cornu; dorsal cornu broad. Spines covering whole body surface.

Third Instar. Skeleton (Fig. 284) with lateral plate at narrowest point more than twice the length of mouth-hook; oral sclerite absent; dental sclerite fused to mouth-hook; liguloid arch absent; hypostomal plates elongate and with fenestrated area situated anteriorly (Fig. 166); mouth-hook tooth more or less equal to depth of base; mouth-hook small, with short pointed tooth and prominent dorsal horn; hypostomal sclerite broad in lateral view, but cross-bar narrow (Fig. 166); posterodorsal process of ventral cornu prominent; dorsal cornu very broad, at least as wide as (often wider than) ventral cornu; angle between ventral and dorsal cornua sharp; windows present on ventral cornua, at most only a narrow ventral line of weak sclerotisation on dorsal cornua; parastomal bars short and thick. Posterior spiracle with apertures almost parallel, anastomosing bands few in number; sun-ray structure weak; peritreme thin and weakly pigmented, especially in button region. Spines very long and pointed (Fig. 67) covering whole of body surface, but very weak at posterior margins of segments. Spines generally point posteriorly, but on dorsal half of segments they point dorsally or posterodorsally; on the ventral half of segments they point ventrally or posteroventrally; on 12th segment they point anteriorly and posteriorly; 2nd segment with

only very small spines; 1st segment flattened antero-posteriorly to form a sucker, with fringe of very long, hair-like spines (Fig. 68); flattened anterior part of 1st segment with very small spines. All papillae weakly developed.

Taxonomic Remarks

Rohdendorf (1957) described the third instar, but did not examine the skeleton. In other ways his description agrees closely with the present one. The early instars are previously undescribed.

Specimens examined: U.K. (Durham).

Biology and Distribution

This species is an obligate blood-sucking parasite of nestling birds, usually Passerines. Zumpt (1965) gives a list of recorded hosts. P. azurea is widely distributed in Europe from Britain to the Urals; it is also found in North Africa and western Asia. According to Zumpt (1965) it may be found even further east.

Protocalliphora avium Shannon and Dobroscky

Third Instar. Skeleton with lateral plate at narrowest point more than length of mouth-hook; oral sclerite absent; dental sclerite fused to mouth-hook base; liguloid arch absent; mouth-hook tooth rather curved and slightly longer than depth of base; hypostomal sclerite broad in lateral view; hypostomal plates elongate; parastomal

bars short and very thick; posterodorsal process of ventral cornu prominent; dorsal cornu very broad, but not quite twice as broad as ventral cornu; windows present and large on ventral cornua, at most only a narrow line of weak sclerotisation on dorsal cornua; angle between ventral and dorsal cornua rather wide. Posterior spiracle with apertures almost parallel; anastomosing bands few in number; sun-ray structure weak; peritreme thin and weakly pigmented, especially in button area, although sometimes pigmented on ventral side of button. Spinulation similar to P. azurea, but sucker hairs much weaker.

Taxonomic Remarks

Hall (1948) described this species and his description agrees generally with the above, although it is not detailed enough for critical comparison. He erected the genus Apaulina to include all the American Protocalliphora species, but this move was not generally accepted. There are no larval features that could justify separation of these species into two genera.

Specimens examined: Canada.

Biology and Distribution

P. avium is an obligate blood-sucker of nestling birds. Hall (1948) gives an extensive list of hosts of this species. It includes a number of crow species (Corvidae) and birds of prey (Accipitridae). It is a widespread Nearctic species.

Protocalliphora sialia Shannon & Dobroscky

Third Instar. Skeleton (Fig. 285) with lateral plate at narrowest point more than length of mouth-hook; mouth-hook tooth not greater than depth of base; oral sclerite absent; dental sclerite fused to mouth-hook; liguloid arch absent; hypostomal plates elongate; hypostomal sclerite broad in lateral view; posterodorsal process of ventral cornu prominent; dorsal cornu broader than ventral cornu; windows present on ventral cornua, at most thin ventral lines of weak sclerotisation on dorsal cornua; angle between dorsal and ventral cornua wide; parastomal bars short and thick. Posterior spiracle with peritreme thin and weakly pigmented; button unpigmented, except weakly ventrally. Spinulation as in P. azurea; sucker hairs strong.

Taxonomic Remarks

This species is previously undescribed in the larval stage. It is easily separable from P. avium on the basis of the strong sucker hairs.

Specimens examined: U.S.A.

Biology and Distribution

This is an obligate blood-sucker of nestling birds. It is restricted to the Nearctic region.

9.3 Other Genera

9.3.1 Genus Amenia Robineau-Desvoidy

Amenia imperialis Robineau-Desvoidy

Second Instar. Skeleton (Fig. 291) highly specialised; mouth-hook tooth extremely long, much longer than depth of base, strongly curved and abruptly bent so that it points posteriorly; ventral margin of mouth-hook base rounded; an elongate, paired sclerotised structure present between the mouth-hooks anteriorly; mouth-hook dorsal horn prominent and rounded; dental sclerite small and very weak; hypostomal plates robust and posteriorly situated; liguloid arch broad; hypostomal sclerite long and slightly curved; hypostomal processes absent; pharyngeal sclerite elongate and slender; dorsal arch robust and produced anteriorly to curve over hypostomal sclerite; dorsal cornu very narrow; parastomal bars absent; lateral plate extremely narrow; windows absent from all cornua. Anterior spiracles with narrow trunks and very many lobes clustered in tree-like fashion. Posterior spiracle with peritreme incomplete, but thick; two apertures present, outer one larger and strongly curved so that a large area separates the two apertures at the centre. Anterior spinal bands (segs. 2-10) complete on 2-8, incomplete on 9 and 10; bands on 5-10 cleft ventrally; anterior part of each cleft band connected with main band by only very few spines; on 9 and 10 bands broken above cleft part resulting in lateral patches of spines. Posterior spinal bands (segs. 5-11) incomplete on 5-8, faint dorsally on 9, complete on 10 and 11.

V-shaped patch of spines present ventrally and laterally around anus. All spines pointed, with rounded bases (Fig. 70) and densely packed. Posterior papillae very weak; P_2 closer to P_3 than to P_1. A fine covering of hairs present on all segments, especially seg. 12.

Taxonomic Remarks

The above description is based upon the examination of only a single specimen derived from the uterus of an adult. The second instar was described by Ferrar (1976), but his description differs considerably from mine in the details of the skeleton. The main difference is that Ferrar believes that there is only "a single large pharyngeal (or basal) sclerite" lying behind the mouth-hooks. His figure shows the hypostomal sclerite and the pharyngeal sclerite as one continuous structure, and the dorsal arch not produced anteriorly. It is easy to see how such an interpretation was arrived at, since if the slide preparation was made without attempting to separate the sclerites slightly, the hypostomal sclerite would lie very closely to the pharyngeal, giving the appearance in Ferrar's figure. Ferrar also omitted mention of the dental sclerite.

The genus Amenia and related genera (subfamily Ameniinae) used to be regarded as Tachinidae, but Crosskey (1965) transferred them to Calliphoridae, while recognising that they are in many ways intermediate between Calliphoridae and Sarcophagidae. Crosskey's conclusions were based on a study of adult characters; the larval features contribute little to a resolution of the problem due to their highly specialised nature. The specimen examined belonged to the

subspecies dubitalis Malloch.

Specimens examined: Australia (Northern Territory).

Biology and Distribution

Little is known of the biology of this species, but the evidence suggests that it is an obligate parasite of snails. The female is macrolarviparous and gives birth to a second instar larva, which is the stage that is though to enter the snail (see remarks under the following species). A. imperialis is a native of Australia.

Amenia leonina (Fabricius)

First Instar. Skeleton (Fig. 292) very slender and very weakly pigmented; seemingly composed of one elongate sclerite; two small, moderately well sclerotised plates present at anteroventral region of first segment, appearing as compound granular or posticulate structures when viewed from the ventral aspect, rather than as two discrete sclerites. Anterior sensory papillae totally lacking. Posterior spiracles of the normal bilobed kind but very small. Spinal bands absent, except for the following: rather weakly pigmented, pointed spines present at buccal region; patch of heavily sclerotised rod-like spines present ventrally at anterior parts of segments 5 and 6; patch of well sclerotised, pointed spines present on either side of anus. Mouth well developed. Minute hairs present at posterior part of segment 12.

Second Instar. Skeleton (Fig. 290) highly specialised; with mouth-hook tooth extremely long and abruptly curved beyond base so that the tip points posteriorly; dorsal horn of mouth-hook very prominent and rounded; ventral margin of mouth-hook base rounded in lateral view; dental sclerite absent; liguloid arch weak; hypostomal plates narrow; hypostomal sclerite curved and larger anteriorly than posteriorly; pharyngeal sclerite slender but elongate; dorsal arch produced anteriorly so as to curve over hypostomal sclerite; lateral plate very narrow; parastomal bars absnet; dorsal cornua with distinct windows; ventral cornua with indistinct windows. Anterior spiracles with narrow trunks and numerous lobes arranged in tree-like fashion (Fig. 293). Posterior spiracle with two apertures, outer one greatly curved; peritreme incomplete. Anterior spinal bands (segs. 2-12) complete on 2-8 (although band on 8 broken laterally at two points) incomplete on 9-12; bands on 5-12 cleft ventrally, and both anterior and posterior parts of cleft band separated from main band by a clear spineless area; band on 12 faint. Posterior spinal bands (segs. 6-11) incomplete on 6-9 (although some weak spines present dorsally on 8 and 9) complete on 10 and 11. Row of spines present dorsal to anus and semi-circle of spines present ventral to anus. Fine hairs present on body surface, especially segment 12.

Taxonomic Remarks

Ferrar (1976) described all three instars of this species, but illustrated only the third instar skeleton. His description of the second instar skeleton contains the same errors as his description of

A. imperialis. Only one specimen each of the first and second instars were available for study. The specimens belonged to the subspecies albomaculata Macquart.

Specimens examined: Australia (Northern Territory).

Biology and Distribution

Ferrar (1976) cites definite evidence that this species is parasitic on snails. It is known only from Australia.

9.3.2 Genus Stomorhina Rondani

Stomorhina cribrata Bigot

Third Instar Skeleton. This description is based on the skeletal remains in the puparial operculum of a single specimen (Fig. 294). Mouth-hook of rather irregular shape; oral sclerite not discernible; dental sclerite rounded; liguloid arch not discernible; hypostomal plates rather well-pigmented; hypostomal sclerite rather long, longer than mouth-hook; cross-bar posteriorly situated; two hypostomal processes present; parastomal bars absent; lateral plate much wider than length of mouth-hook; slit-like windows present on ventral cornua; dorsal cornua deeply cleft; posterodorsal processes present; parastomal bars absent; lateral plate much wider than length of mouth-hook; slit-like windows present on ventral cornua; dorsal cornua deeply cleft; posterodorsal process of ventral cornu not prominent; angle between dorsal and ventral cornua wide. Additional larval

features gleaned from the puparium: only two apertures present in posterior spiracle; no spines whatsoever apparent on the cuticle.

Taxonomic Remarks

As far as I am aware, this species is previously undescribed in any of its immature stages.

Specimen examined: South Africa (Natal).

Biology and Distribution

This species is found all over Africa and as far north as the Middle East (Zumpt, 1956b). Nothing is known of its biology, but the related S. lunata (Fabricus) is known as a predator upon locust egg-pods (Cuthbertson, 1935).

9.3.3 Genus Tricyclea Wulp

Tricyclea deemingi Zumpt

Third Instar. Skeleton (Fig. 296) with mouth-hook tooth longer than depth of base; oral sclerite very much reduced and not pigmented; dental sclerite elongate; hypostomal plates diffuse; hypostomal sclerite narrow in lateral view; liguloid arch very weakly pigmented; parastomal bars present; whole skeleton rather weakly pigmented. Antenno-maxillary (Fig. 298) complex protruding and well-developed;

antennae and maxillary palps long; supramaxillary papillae very well-developed; oral ridges on upper lip produced to form elongate feathery structures; many hair-like spines anteriorly on the body; spines weakly pigmented and divided into many long branches. Twelfth segment with highly sclerotised anal pad (Fig. 297).

Taxonomic Remarks

This species is previously undescribed, but, as far as the presence of a well-sclerotised pad on the twelfth segment is concerned, T. deemingi resembles T. pallens Curran as described by Cuthbertson (1937).

Specimens examined: Nigeria.

Biology and Distribution

This species is an obligate termitophile (Zumpt, 1973) as many other Tricyclea species seem to be. T. deemingi is known only from West Africa.

9.3.4 Genus Auchmeromyia Brauer and Bergenstamm

Auchmeromyia luteola (Fabricius)

Third Instar. Skeleton (Fig. 304) with mouth-hook tooth much longer than depth of base; mouth-hook dorsal horn prominent; oral sclerite not discernible; dental sclerite boomerang-shaped; liguloid arch

absent; hypostomal plates robust and long; hypostomal sclerite rather broad in lateral view; parastomal bars present, thick and long, longer than hypostomal sclerite; lateral plate narrower than length of mouth-hook; angle between dorsal and ventral cornua very wide; dorsal cornu broad, but with deep cleft; ventral cornu without prominent posterodorsal horn, but with clear window. Anterior spiracles with broad trunks and with lobes situated in a row at same level, not arranged in a fan-shape. Posterior spiracle with three parallel apertures; peritreme very thin and very weakly sclerotised; sun-ray structure not discernible. Body surface uniformly covered with weak spines. Cuticle much folded. Strong spines present in three semi-circles on either side of the mouth-hooks. Other spines very weakly pigmented and small; spines pointed, with one point which is often slightly cleft at the tip. Posterior parts of segments with shorter, broader spines. Five long, thin posterior papillae present.

Taxonomic Remarks

Although this well-known species has been described many times (e.g. Rouband, 1913; Zumpt, 1965) the descriptions are lacking in detail, perhaps because the larva is so distinctive that it cannot be mistaken for any other species. The skeleton is previously undescribed.

Specimens examined: Congo [Zaire] .

Biology and Distribution

This is the notorious Congo Floor Maggot which sucks the blood of Man at night. Much has been published about its biology (e.g. Garrett-Jones, 1951). It is restricted to the Afrotropical region, and is absent from Madagascar.

9.3.5 Genus Elephantoloemus Austen

Elephantoloemus indicus Austen

Second Instar. Skeleton (Fig. 306) with lateral plate at narrowest point narrower than length of mouth-hook; mouth-hook tooth longer than depth of base; hypostomal sclerite lacking hypostomal processes; dorsal and ventral cornua diverging; dorsal cornu broad and with deep cleft; ventral cornu with slit-like window and tapering posteriorly, lacking a prominent postero-dorsal process. Whole body surface covered with small spines.

Third Instar. Skeleton (Fig. 307) with mouth-hook tooth much longer than depth of base; oral sclerite seemingly absent; liguloid arch absent; dental sclerite fused to mouth-hook base; parastomal bars absent; windows small on ventral cornua, absent from dorsal cornua; dorsal cornu much wider than ventral cornu; postero-dorsal process of ventral cornu prominent and backward pointing; lateral plate narrower than length of mouth-hook; angle between dorsal and ventral cornua wide. Anterior spiracles with lobes in tree-like cluster. Posterior

spiracles situated more or less dorsally; spiracles very weakly clerotised and apertures radiate from dorsal point (i.e. spiracles upside down with reference to usual condition); peritreme very weak, but complete; no normal sun-ray structure (blister structures absent, but intermediate structure present) but fine filaments radiate from button and tips of apertures (opposite ends to button). Whole body surface covered with very small, weakly pigmented spines on anterior parts of segments, and unpigmented spines on posterior parts of segments. Strong spines present either side of mouth-hook. No posterior papillae evident.

Taxonomic Remarks

Austen (1930) first described this fly and its larva, although he did not include a description of the skeleton. His larval description, though not detailed, is adequate for the recognition of this distinctive species. The second instar is previously undescribed.

Specimens examined: Burma.

Biology and Distribution

This species is an obligate cutaneous parasite of the Indian Elephant (Elephas maximus). Although of great veterinary importance, especially in view of the fact that the Indian Elephant is a domestic animal in large parts of Asia, very little is known of the biology of this fly. As Zumpt (1965) points out very little seems to be known of the arthropod parasites of the Indian Elephant. E. indicus is known only from Burma.

9.3.6 Genus Booponus Aldrich

Booponus intonsus Aldrich

Third Instar. Skeleton (Fig. 305) with mouth-hook tooth much longer than depth of base; oral sclerite absent; dental sclerite fused to mouth-hook base; liguloid arch absent; hypostomal plates well-pigmented; parastomal bars absent; hypostomal sclerite broad in lateral view; windows large on both dorsal and ventral cornua; dorsal arch weak, sloping backwards. Posterior spiracles very weakly sclerotised; three apertures almost parallel; peritreme weak and hardly discernible; sun-ray structure absent. Spines distributed irregularly over body surface; spines weakly pigmented and conical, with rounded bases.

Taxonomic Remarks

Patton (1936) described the third instar, and his description is quite adequate for specific identification as was the description of Woodworth and Ashcroft (1923), the discoverers of this fly.

Specimens examined: The Philippines.

Biology and Distribution

This species is an obligate parasite of water-buffaloes, cattle and goats. The larvae burrow under the skin around the hoofs and lower legs of these animals. B. intonsus is known only from the Philippines and the Celebes.

9.3.7 Genus Cordylobia Grunberg

Cordylobia anthropophaga (Blanchard)

Second Instar. Skeleton with lateral plate at narrowest point narrower than length of mouth-hook; mouth-hook with rather short tooth, but with very prominent dorsal horn; dorsal and ventral cornua diverging; dorsal cornu deeply cleft. Spines covering most of segments 1-9, with very few spines on the last three segments. Anterior half of body broader than posterior half.

Third Instar. Skeleton (Fig. 299) with mouth-hook tooth longer than depth of base; oral sclerite not discernible; dental sclerite fused to mouth-hook base; liguloid arch absent; hypostomal plates small; hypostomal sclerite broad in lateral view; parastomal bars present and rather thick; dorsal cornu somewhat broader than ventral cornu; windows faint on all cornua; lateral plate narrower than length of mouth-hook; posterodorsal process of ventral cornu prominent. Posterior spiracles with apertures slightly bent; peritreme very weak and incomplete dorsally and ventrally; button dorsal; sun-ray structure absent; spiracles inverted. Spines scattered unevenly over body surface; very few spines on last 3 segments, and these mainly at anterior and posterior margins. All spines short, thick and with rounded tips. No posterior papillae evident.

Taxonomic Remarks

Blacklock and Thompson (1923) described this species in great detail and their description agrees well with the present one. However, Zumpt (1965) states that in some specimens of the third instar, the last 3 segments are also covered with spines and that this character is a variable one. All specimens seen by me had very few spines on these segments. Finally, it is interesting to note that the inversion of the posterior spiracle has never been referred to in the literature.

Specimens examined: Nigeria; Congo [Zaire] ; Uganda.

Biology and Distribution

This, the larva of the Tumbu Fly, is an important obligate cutaneous parasite of Man and wild and domestic animals in Africa; it is also known from Arabia.

Cordylobia ruandae Fain

Third Instar. Skeleton (Fig. 301) with mouth-hooks short, shorter than depth of base; oral sclerite absent; dental sclerite fused to mouth-hook base; hypostomal sclerite robust; parastomal bars extremely broad, but weakly pigmented; dorsal cornu very broad; ventral cornu very long and narrow; lateral plate equal to, or less than, length of mouth-hook; liguloid arch absent. Posterior spiracles similar to C. anthropophaga (Fig. 303). Body surface covered with spines,

including last 3 segments. Spines arranged in rosettes (Fig. 76).

Taxonomic Remarks

The third instar was described by Zumpt (1965). His description agrees closely with the above.

Specimens examined: Ruanda (Astrida).

Biology and Distribution

This species seems to be an obligate parasite of the African forest mouse, Grammomys dolichurus. It is known only from Ruanda.

Cordylobia rodhaini Gedoelst

Third Instar. Skeleton (Fig. 302) with mouth-hook tooth longer than depth of base; oral sclerite absent; dental sclerite fused to mouth-hook base; parastomal bars very short; lateral plate narrower than length of mouth-hook; windows often present, but weak, on ventral cornua, absent from dorsal cornua; posterodorsal process of ventral cornu prominent; dorsal cornu rather narrow; ventral cornu long posterior to posterodorsal process; dorsal and ventral cornua rather close together. Posterior spiracles with very tortuous apertures, the outer aperture of each spiracle often broken into two apertures; peritreme weak; sun-ray structure absent. Spines scattered all over body surface; last 3 segments with very few spines; spines rather longer than in C. anthropophoaga and pointed.

Taxonomic Remarks

Zumpt (1965) described and figured this species, and his illustration of the third instar shows the last three segments as densely covered with spines as the other segments. It is probable, therefore, that, as in C. anthropophaga, that this is a variable character.

Specimens examined: Congo (Uele).

Biology and Distribution

This is an obligate parasite of Man and wild animals; domestic animals do not seem to be parasitised. C. rodhaini is restricted to the forested regions of Africa.

9.3.8 Genus Pollenia Robineau-Desvoidy

Pollenia rudis (Fabricius)

Third Instar. Skeleton (Fig. 295) with mouth-hooks relatively enormous; mouth-hook tooth much longer than depth of base; oral sclerite absent; liguloid arch absent; hypostomal plates robust; dental sclerite fused to mouth-hook base; hypostomal sclerite moderately robust and with cross-bar anteriorly situated; parastomal bars very short; dorsal cornu very narrow; lateral plate very narrow; dorsal and ventral cornua more or less equal in length. Posterior spiracles set in a somewhat sunken pit; apertures rather strongly

diverging (Fig. 101). Spines distributed unevenly over body surface; spines very small and weakly pigmented or totally unpigmented.

Taxonomic Remarks

This species has been described by Keilin (1915), De Coursey (1927) and Hall (1948). All these descriptions are useful for reliable identification and the present description adds little to what is already known. Tawfik and El-Husseini (1972) described the larva of Pollenia dasypoda portchinski and their description shows this species to be very similar to P. rudis.

Specimens examined: Canada (Ontario).

Biology and Distribution

This widespread Holarctic species is known to be an obligate parasite of earthworms (Keilin, 1915). However, Dr J. Satchell (pers. comm.) tells me that, in over thirty years study of earthworms in Britain, he has never come across a single specimen parasitised by this fly.

9.3.9 Biology of Phormiinae and other Groups

The species dealt with in this chapter exhibit a great diversity of structure and biology and their habits have been briefly discussed under the relevant headings, and only some comments on the biology of Protocalliphora azurea will be made here.

During the fieldwork carried out for the present study, it was noted that very many P. azurea specimens could be reared from one nest. In one case, over 300 flies were reared from a swallow's nest after all five nestlings had flown, apparently none the worse for the presence of such large numbers of parasites. The larvae examined from nests in which the nestlings were still being reared, were often found to be full of blood, but never did I witness a larva actually sucking the blood of a nestling. In all nests examined by me, the larvae were always found deep in the nest debris, not on the nestlings (except in one case when a single first instar was seen crawling along the abdomen of a nestling swallow). Careful examination of nestling birds revealed no marks suggesting attack by the parasite, and the nestlings always appeared to be healthy, although it is often stated in the literature (e.g. Zumpt, 1965) that heavy infestations will result in the death of the birds.

Mr N. Aebischer (pers. comm.) has suggested that the maggots may actually suck the blood, not of the nestlings, but of the adults when they stay in the nest at night. The highly vascularised brood pouch may attract the larvae. This idea is supported by the fact that the parasites always seem to lie deep in the nest material during the day. This would indicate that they probably feed at night, when the parent bird would be present. Further studies on this interesting fly are needed, especially with regard to its effect on bird populations.

9.3.10 New Host Records

New host records that came to light during the present study are as follows:

1. Herpestes galerella sanguineus (Mammalia: Viverridae) parasitised by Cordylobia anthropophaga. Data from tube labelled "Congo, 1950" from Musee Royale de L'Afrique Centrale, Tervuren, Belgium.

2. Certhia familiaris (Aves: Certhiidae) (Tree-creeper), parasitised by Protocalliphora azurea. Collected by J. Richardson in May 1983 at the field station of Durham University, Durham.

3. An unidentified larva sent to me by the Musee Royale de L'Afrique Centrale was labelled "Intestin, Potamochere [probably Potamochoerus porcus, the red river-hog] I. 1938, Malela". The larva possessed anal pads similar to those of Tricyclea, but I could not identify it.

CHAPTER TEN

IDENTIFICATION OF SPECIMENS

10.1 Introduction

It is extremely difficult to give a watertight definition of a Calliphorid larva. It is not difficult, however, to distinguish Calliphorid larvae from most other Calypterates (except, perhaps, Sarcophagidae and Anthomyiidae), since the larvae of Tachinidae, Oestridae, Rhinophoridae, Muscidae, Fanniidae, Gasterophilidae, Hypodermatidae and Cuterebridae are very distinctive and usually easily recognisable for what they are (see Chapter 11 for brief characterisations of these families).

The Sarcophagidae and Anthomyiidae, however, present problems, as there is no set of characters that can easily separate them from Calliphoridae. Even the oft-repeated characters that are claimed to separate Sarcophagidae from Calliphoridae in the literature (e.g. Teskey, 1981) have been found during this study to be ill-founded. For example, it is often stated that the Sarcophagidae possess a deep incision in the third instar dorsal cornu and posterior spiracles set in a deep pit, while Calliphoridae do not possess these characters. In fact, many Calliphoridae do possess one or both of these characters and, moreover, many Sarcophagidae, especially the subfamily Sarothromyiinae as already shown by Hall (1932), do not possess a deep terminal pit.

Another important problem is the fact that Calliphoridae, Sarcophagidae and Anthomyiidae not only strongly resemble one another, but also resemble the larvae of the vast assemblage of "Acalypterates". These facts make it extremely difficult to give a reliable definition of the family Calliphoridae; further detailed studies are urgently needed.

In this section identification keys are given for carrion-breeding and myiasis-causing agents only. There are two reasons for this. Firstly, the location of these larvae will immediately exclude a large number of other Cyclorrhapha and thus make the problem of identification much easier. Secondly, the larvae of the more specialised groups, such as the termitophilous species or snail-parasites are so incompletely known, that reliable identification is virtually impossible.

10.2 Examination of Specimens

When examining a larva for identification the following procedure should be followed: Whenever possible examine the larva alive; if it is very active it may be slowed down by refrigeration of its medium as recommended by Ferrar (1979). The number of lobes of both anterior spiracles can be counted much more easily in the living, than in the preserved larva; often, too, it is much easier than in a slide-mounted specimen, as the cephalopharyngeal skeleton beneath may render the spiracles opaque. Next, the larva may be killed and preserved by dropping into acetic alcohol. If the larva is required for immediate examination, dropping into almost boiling water will

kill the larva instantly; it may then be preserved in acetic alcohol. The whole larva should then be examined under the stereoscopic microscope and details of the spinal bands and posterior papillae, and the spiracle distance factor (see 4.2.6) noted. The posterior spiracles may easily be examined by pushing the larva (posterior end upwards) into wet sand in a watch-glass. A slide-mount may then be prepared by cutting off the anterior part of the larva (the first three segments) with a sharp scalpel, washing it quickly in water and placing it on a slide. For the sake of standardisation I always place the specimen on the slide facing towards the left. A drop of Berlese's Fluid may then be added on top of the specimen, after which a coverslip is placed, and gently pressed onto the specimen; further mountant may then be added around the edges of the coverslip. (Wetting the underside of the coverslip with Berleses Fluid before placing it on the specimen reduces the risk of air bubbles forming in the preparation.) It is important, when preparing a slide of the lateral aspect of the skeleton, to align the skeleton properly, in other words, both dorsal cornua, both ventral cornua and both mouth-hooks should lie precisely on top of one another so that the profile of only one mouth-hook, one dorsal cornu and one ventral cornu may be seen. This may be done simply by moving the coverslip by means of pressing onto it with a pair of forceps or a seeker and pushing it up and down the slide, the latter being examined under the stereomicroscope all the while. If a preparation of a ventral view is desired, this must be performed very carefully by pressing the coverslip down very gently (the specimen is, of course, placed with the ventral side upwards); as soon as the mouth-hooks are seen to part and their tips point

laterally, then there is no danger of the specimen twisting and a firm press with the seeker will secure the specimen in position. The preparation may then be examined under the compound microscope for details of the skeleton and the spinal morphology. For the reasons stated earlier (2.3) KOH should not be used unless the larva is badly discoloured due to poor preservation (e.g. in alcohol). In such cases, dissection of the skeleton may be necessary. This operation may be done using two pairs of fine forceps to remove the rather brittle musculature around the skeleton. The latter can then be mounted as above, and parts of the cuticle may be mounted separately for examination of the spines. In all larvae, cutting off the rear portion of the twelfth segment and slide-mounting as above will reveal details of the posterior spiracles, e.g. the sun-ray structure.

As regards puparia, it is essential to find and examine the opercula, as one of these will contain the third instar skeleton which must be examined. The opercula may be mounted in Berlese's fluid as above. Live, intact puparia may be dissected or, of course, reared out to the adult stage.

When using Berlese's Fluid it is important to use the correct formula, as several incorrect ones have been used in the past, resulting in badly mounted specimens. The following is the correct formula (adapted from Lewis, 1973):

Gum Arabic, picked lumps	12gm
Chloral hydrate crystals	20gm
Glacial acetic acid	5ml
50% w/w glucose syrup	5ml
Distilled water	30-40ml

The constituents are dissolved at room temperature in the order shown, and filtered over glass wool to remove dust. The mixture is allowed to evaporate at not more than 30°C till it reaches the required consistency. Glyceel is a trouble-free ringing medium.

10.3 Key to British Carrion-breeding Calliphorid Genera

The following keys should enable reliable separation of all genera of British carrion-breeding Calliphorids.

First Instars

1 Hairs on 12th segment strong and well-pigmented, visible under low power (Fig. 73)

Calliphora

\- Hairs on 12th segment weak and almost unpigmented, visible only under very high power (Fig. 74) 2

2 Lateral plate broader than mouth-hook length

Phormia

\- Lateral plate less broad than mouth-hook length 3

3 Hypostomal sclerite and mouth-hook robust (Fig. 257)

Cynomya

- Hypostomal sclerite and mouth-hook weak (Fig. 254)

Lucilia

Second Instars

1 Mouth-hook evenly curved, not hooked; sub-mandibular sclerites present (Fig. 287)

Phormia

- Mouth-hook definitely hooked; sub-mandibular sclerites absent (Fig. 237) 2

2 Mouth-hook tooth long before area of curvature (Fig. 258)

Lucilia

- Mouth-hook tooth short before area of curvature (Fig. 236) 3

3 Mouth-hook tooth very abruptly curved (Fig. 259)

Cynomya

- Mouth-hook tooth not so abruptly curved (Fig. 238)

Calliphora

Third Instars

1 Oral sclerite almost wholly pigmented (Fig. 126) 2

\- Oral sclerite unpigmented, or at most only at base of rod (Fig. 145) 3

2 Mouth-hook tip curving abruptly (Fig. 262)

Cynomya

\- Mouth-hook tip more smoothly curved (Fig. 224)

Calliphora

3 Dorsal margin of mouth-hook (in lateral view) with distinct node at base of tooth (Fig. 289)

Phormia

\- Dorsal margin of mouth-hook smoothly curved

Lucilia

Puparia

1 Posterior papillae very prominent and posterior spiracles set in deep pit (Fig. 97); puparium almost black in colour

Phormia

- Posterior papillae at most only slight swellings and posterior spiracles not set in pit; puparium dark-brown or reddish-brown 2

2 Oral sclerite unpigmented or at most pigmented only at base of rod; pupal respiratory horn at most 70 µ in length (usually only 60-65 µ) and smooth (Fig. 85)

Lucilia

- Oral sclerite almost wholly pigmented; pupal respiratory horn well over 100 µ in length and with carunculations and pits (Figs. 78 and 84). 3

3 Mouth-hook tip abruptly curved (Fig. 262); pupal respiratory horn with 2 or 3 distinct lobes (Fig. 84)

Cynomya

- Mouth-hook tip more smoothly curved (Fig. 225); respiratory horn without well-defined lobes (Fig. 79)

Calliphora

10.4 Key to World Genera of third instar larvae causing Myiasis in Mammals, including Man.

Zumpt (1965) gave keys to myiasis-causing larvae, using many unreliable characters that often made the keys difficult or impossible to use. He also keyed out many species on biological information alone; e.g. He keys out Elephantoloemus indicus as "Parasitic on Indian Elephants". This is not good practice because, although E. indicus is not known to parasitise anything other than Indian Elephants, Indian Elephants are known to be parasitised by other Calliphorids. In addition, knowledge of new species gained during this study (but unknown to Zumpt) has shown that certain characters, while reliable in the range of species studied by Zumpt, can no longer be used reliably.

The keys by Oldroyd and Smith (1973) are incomplete and based largely on the keys of Zumpt (1965) and James (1947).

The following key utilises only structural features, although some supporting distributional data is given.

1 Long processes present on body segments

Chrysomya (part)

– No such processes present 2

2 Spines localised in bands along anterior and posterior margins of segments 3

- Spines distributed irregularly over whole body surface and not localised in discrete bands 9

3 Posterior spiracular peritreme complete 4

- Posterior spiracular peritreme incomplete 6

[Note: Individuals keying out at 4 may occasionally have a weakly pigmented button area. The button, however, is always distinct in these species, even if weakly pigmented, which is not the case with the species keying out at 6.]

4 Spines robust, with rounded tips (Figs. 41 and 48)

Calliphora (part)

- Spines small, with pointed tips (Figs. 40 and 56) 5

5 Mouth-hook tooth much longer than depth of base (Fig. 265)

Lucilia and Hemipyrellia

- Mouth-hook tooth only slightly longer than depth of base (Fig. 224)

Calliphora (part)

[NOTE 1: The traditional method of separating Calliphora from Lucilia in the literature is the pigmentation of the oral sclerite (stated as the presence or absence of the oral sclerite; see 5.6). It has been shown in this work, however, that some Lucilia spp. do possess at least partly pigmented oral sclerites and that some Calliphora spp. possess unpigmented ones. However, the species of Calliphora outside New Zealand always possess a pigmented oral sclerite, and in the Western Palaearctic and Nearctic regions it is, in practice, possible to separate Calliphora from Lucilia on the basis of the fact that the former possess a pigmented oral sclerite and the latter an unpigmented one. The only species of Lucilia from these regions that is known to have a partly pigmented oral sclerite is L. ampullacea.

NOTE 2: Lucilia and Hemipyrellia are very difficult to separate as larvae. However, the only two-species of Hemipyrellia whose larvae are known both have partly pigmented oral sclerites, whereas most Lucilia species have unpigmented ones. Zumpt (1965) included Hemipyrellia in his adult key although it was not known to cause myiasis, but he included it because it "may yet be found to be involved in myiasis". Pont (in Crosskey, 1980) regards Hemipyrellia as a common myiasis agent, although the only record I know of a species of Hemipyrellia acting in this way is the record cited in this thesis (see. 6.11)] .

6 Posterior papillae long and prominent

Phormia

- Posterior papillae of normal shape 7

7 Peritreme at button area with distinct bifurcation

Chrysomya (part)

- Peritreme ending abruptly at button area 8

8 Spines very large and rounded, never forked (Fig. 63); Old World Tropics only

Chrysomya bezziana

- Spines smaller and often forked (Figs. 64 & 65) New World only

Cochliomyia

9 Posterior spiracular apertures sinuous (Fig. 302)

Cordylobia

- Posterior spiracular apertures straight (Fig. 204) 10

10 Dorsal cornu deeply incised (Fig. 304); parastomal bars present

Auchmeromyia

- Dorsal cornu not incised; parastomal bars absent 11

11 Spiracles inverted (i.e. button dorsal) and situated dorsally

Elephantoloemus

- Spiracles not inverted and situated posteriorly

Booponus

In addition to the above, the Nearctic species Paralucilia wheeleri (Hough) has been recorded from myiasis wounds(Hall, 1948). No material was available for study, but, according to Hall's illustration, the third instar possesses a heavily pigmented oral sclerite. The adult description is very similar to that of Cochliomyia hominivorax with which it is probably congeneric.

10.5 Key to the British Species of Calliphora

First Instars

1 Lateral plate as broad as, or broader than, median tooth (Fig. 247)

vomitoria

- Lateral plate narrower than length of median tooth (Fig.246) 2

2 Dorsal arch with distinct ventral curve (Fig.248)

uralensis

- Dorsal arch without such a curve 3

3 Anterior spinal bands complete on segs. 2-8 only

loewi

- Anterior spinal bands complete on segs. 2-9 4

4 Basal section of hypostomal sclerite thicker than depth of median tooth 5

- Basal section of hypostomal sclerite narrower than depth of median tooth

subalpina

5 Lateral plate width greater than length of mouth-hook tooth

vicina

- Lateral plate width less than length of mouth-hook tooth

alpina

Second Instars

1 Mouth-hook tooth wider at area of curvature than at base (Fig. 236) 2

- Mouth-hook tooth not wider at area of curvature than at base 5

2 Anterior spinal bands complete on segs. 2-9 3

- Anterior spinal bands complete on segs. 2-8 only

loewi

3 Patch of spines present dorsal and ventral to anus 4

- Patch of spines present only dorsal to anus

alpina

4 P_2 closer to P_3 than to P_1

vicina

- P_1, P_2 and P_3 equidistant

subalpina

5 Width of mouth-hook tooth at area of curvature approx. equal to width at base

uralensis

- Width of mouth-hook tooth at area of curvature less than width at base

vomitoria

Third Instars

1 Anterior spiracles with 9-12 lobes 2

- Anterior spiracles with 5-8 lobes 4

2 Spiracle distance factor below 1 3

- Spiracle distance factor 1 or more

vicina (part)

3 Spines robust, with rounded tips (Fig. 41); arrangement of anal spines as in Fig. 206)

vomitoria

- Spines normal, with pointed tips, each spine often with two teeth (Fig. 42); arrangement of anal spines as in Fig. 207

uralensis

4 Anterior spinal bands incomplete only on segs. 10-12 5

- Anterior spinal bands incomplete on segs. 8-12 or 9-12 6

5 Spiracle distance factor 1-1.2; posterior spinal band incomplete on seg. 9; spiracle size 0.23-0.28mm

vicina (part)

- Spiracle distance factor 1.3-1.67; posterior spinal band complete on seg. 9; spiracle size 0.17-0.19mm

loewi

6 Spiracle distance factor 1-1.2

subalpina

- Spiracle distance factor 1.70 or over

alpina

Puparia

1 Anterior spiracles with 9-12 lobes 2

- Anterior spiracles with 5-8 lobes 4

2 Spines robust, with rounded tips (Fig. 104)

vomitoria

- Spines normal, with pointed tips 3

3 Spiracle distance factor 0.48–0.52

uralensis

– Spiracle distance factor 0.77–1.38

vicina (part)

4 Spiracle distance factor well below 1 (0.6–0.8) 5

– Spiracle distance factor higher, above 0.8 6

5 Anterior spinal bands on segs. 10–12 incomplete; posterior spinal bands on segs. 7–8 incomplete

vicina (part)

– Anterior spinal bands on segs. 9–12 incomplete; posterior spinal bands on segs. 7–8 complete

subalpina

6 Anterior spinal band on seg. 8 incomplete; spiracle distance factor high (1.55–1.58)

alpina

– Anterior spinal band on seg. complete; spiracle distance factor lower (at most 1.47) 7

7 Posterior spinal band on seg. 9 incomplete; spiracle distance factor low (0.77-1.11); spiracle size 0.20-0.25mm

vicina (part)

- Posterior spinal band on seg. 9 complete; spiracle distance factor high (1.43-1.47); spiracle size 0.15-0.18mm

loewi

10.6 Key to African Calliphora

The only Calliphora species endemic to Africa is C. croceipalpis (Zumpt, 1956a). However, Pont (in Crosskey, 1980) includes C. vicina in the Catalogue of Afrotropical species, and it is also possible that C. vomitoria may be introduced from time to time. For these reasons, a key is here presented for separation of these three species.

First Instars

1 Lateral plate as broad as, or broader than, length of median tooth

vomitoria

- Lateral plate narrower than length of median tooth 2

2 Basal section of hypostomal sclerite thicker than greatest depth of median tooth; posterior spinal bands complete on segs. 7-11

vicina

- Basal section of hypostomal sclerite narrower than greatest depth of median tooth; posterior spinal bands complete on segs. 10-11

croceipalpis

Second Instars

1 Mouth-hook tooth thicker at area of curvature than at base (Figs. 236 and 242) 2

- Mouth-hook tooth narrower at area of curvature than at base (Fig. 237)

vomitoria

2 Posterior spinal bands complete on segs. 7-11

vicina

- Posterior spinal bands complete on segs. 10-11 only

croceipalpis

Third Instars

1 Spines large, with rounded tips (Fig. 41)

vomitoria

- Spines smaller, with pointed tips (Figs. 40 and 50) 2

2 Anterior spinal bands complete on segs. 2-9; posterior spinal bands complete on segs. 9-11

vicina

- Anterior spinal bands complete on segs. 2-10; posterior spinal bands complete on segs. 8-11

croceipalpis

10.7 Key to Carrion-breeding Phormiinae

This group comprises all Phormiinae other than the bird blood-sucking species of Protocalliphora i.e. the genera Phormia and Boreellus, with two species in the former genus and only a single species in the latter. Unfortunately, only third instars of Boreellus were available for study and so this genus cannot be included in the keys to the early instars.

First Instars

1 Anterior spinal bands complete on segs. 2-7; posterior spinal bands all incomplete

Phormia terraenovae

- Anterior spinal bands complete on segs. 2-10; posterior spinal band complete on seg. 11

Phormia regina

Second Instar

1 Posterior spinal bands all incomplete

Phormia terraenovae

- Posterior spinal bands complete on segs. 10-11

Phormia regina

Third Instars and Puparia

1 Posterior spinal bands all incomplete

Phormia terraenovae

- At least some posterior spinal bands complete 2

2 Anterior spinal bands complete on segs. 2-9 (often 2-10)

Phormia regina

\- Anterior spinal bands complete on 2-11

Boreellus atriceps

10.8 Genus Chrysomya

Ten species of Chrysomya are known to cause myiasis in Man and animals (Zumpt, 1965), but only nine are known in the immature stages (Ch. inclinata Walker is unknown). Zumpt keyed out eight species in his key, but several pairs of species are made to key out together; these pairs of species have been found to be separable during the present study. Oldroyd and Smith (1973) repeat Zumpt's key and erroneously state that it includes all species known to cause myiasis. Kitching (1976b) and Kitching and Voeten (1977) described and keyed certain Australian species of Chrysomya as a result of S.E.M. examination. It is most unfortunate, however, that these authors misinterpreted the spinal bands, referring to the anterior bands of segments as posterior bands (presumably referring to the segments anterior to these bands). This misinterpretation may cause great confusion unless this error is understood.

In this section keys are given to separate certain pairs of very similar species.

10.8.1 Ch. albiceps and Ch. rufifacies

Hairy maggots have been found parasitising mammals in the New

World (Gagne, 1982), although the genus Chrysomya does not occur naturally in that part of the World. Several species of Chrysomya have been introduced into Brazil (Guimaraes, 1976). For these reasons it is desirable to be able to identify the larvae in order to determine from which part of the World the flies are being introduced.

The third instars of Ch. albiceps and Ch. rufifacies may be separated as follows:

1 Spines present on stalk of process 1 (Fig. 115); spiracle distance factor 0.36-0.059

rufifacies

- Spines absent from stalk of process 1 (Fig. 114); spiracle distance factor 0.22-0.24

albiceps

10.8.2 Ch. marginalis and Ch. megacephala

These two species are distinctive Chrysomya in that they are the only species of the genus known to possess a partly pigmented oral sclerite in the third instar. Although they only overlap in a small part of their range, a key to separate them may be helpful.

1 Spines rounded and unforked (Fig. 58); anterior spinal bands complete on segs. 2-11

marginalis

- Spines round and often forked (Fig. 59); anterior spinal bands complete on segs. 2-8

megacephala

10.8.3 Ch. putoria and Ch. chloropyga

It is not yet certain whether these two forms actually do represent two different species (see comments under these species in 7.2). The third instars are, however, separable as follows:

1 Spines present dorsal and ventral to anus, but not between anus and anal lobes (Fig. 211); spines 3- pointed, but narrow (Fig. 61)

putoria

- Spines present all around anus (Fig. 212); spines 3- pointed and broader (Fig. 60)

chloropyga

10.9 Genus Lucilia

Five species of Lucilia are known to cause myiasis in mammals. These are L. sericata, L. cuprina, L. caesar, L. ampullacea and

L. illustris (Meigen). Unfortunately, no material of the last-named species was available for study.

However, L. sericata and L. cuprina are the only two species of economic importance and they are the only Lucilia species known to attack sheep in the southern hemisphere. Waterhouse and Paramonov (1950) and Zumpt (1965) gave keys to separate these two species, using characters of the posterior spiracles and posterior papillae. However, these characters are unreliable, and I was unable to separate the two species using these keys.

The following keys are based on a study of material from Australia and South Africa (where these species are particularly important as sheep-strike agents). British, North American and Japanese material of L. sericata was also studied.

First Instars

1 Dorsal arch weak and parastomal bars long (Fig.254)

sericata

- Dorsal arch robust and parastomal bars short (Fig. 255)

cuprina

Second Instars

1 Mouth-hook tooth thick at area of curvature (Fig. 258)

sericata

- Mouth-hook tooth narrow at area of curvature (Fig. 260)

cuprina

Third Instars

1 Very few spines present dorsal to anus (Fig. 210); spiracle distance factor 1-1.8

sericata

- Strong patch of spines present dorsal to anus (Fig. 209); spiracle distance factor 0.67-0.75

cuprina

[NOTE: No puparia of L. cuprina were available for study. However, the spinal character used in this key may be expected to be retained in the puparium and should enable reliable separation of the two species.]

10.10 Key to Third Instars of Cochliomyia

Laake, Cushing and Parish (1936) published on excellent comparative account of Co. hominivorax (as Co. americana Cushing and Patton) and Co. macellaria. Their descriptions enable reliable separation of the two species, and in the following key the spinal character is used. They have the advantage of being easy to see, as well as being reliable.

1 Spines forked, with rounded tips (Fig. 64)

macellaria

- Spines pointed, and sometimes cleft at the tip (Fig. 65)

hominivorax

10.11 Key to third Instars of Cordylobia

Zumpt (1965) gave a reliable key to the species of Cordylobia. In the following key, however, characters that can also be seen in the puparium are used.

1 Posterior spiracular apertures very tortuous (Fig. 302)

rodhaini

- Posterior spiracular apertures only slightly sinuous (Fig. 303)

2

2 Spines short and thick; mouth-hook long (Fig. 299)

anthropophaga

- Spines distributed in 'clumps' (Fig. 76); mouth-hook short (Fig. 301)

ruandae

10.12 Nomenclature

During the course of this work, it was noticed that the names of several species, often of medical importance (e.g. Auchmeromyia luteola), were recently changed. While name-changes are often justified, most of the names in question were changed on the basis of primary junior homonymy i.e. on the basis of the fact that the name used to be a homonym when in the genus in which it was originally described, but ceased to be a homonym (in any real sense) when it was transferred to its present genus. It is, nevertheless, still regarded as a homonym by the International Code of Zoological Nomenclature and, according to the Rules, must be changed.

This is not the place to enter into a detailed discussion of the Code; my aim is simply to point out that this sort of Rule is not conducive to nomenclatureal stability and, moreover, is very much against the spirit and purpose for which the International Commission for Zoological Nomenclature was originally founded.

CHAPTER ELEVEN

EVOLUTION AND PHYLOGENY

I will set down a tale...It may be history, it may be only legend...It may have happened, it may not have happened: but it could have happened.

Mark Twain

The Prince and the Pauper

11.1 Introduction

Although much has been published on the evolution and phylogeny of Diptera as an Order, notably by Hennig (1973), Rohdendorf (1974), Oldroyd (1977) and Hackman and Vaisanen (1982), remarkably little detailed work has been done on the Calypterata or its constituent groups. Moreover, most of the work done has been largely speculative, with little detailed analysis of evidence. Exceptions are the works of Roback (1951) on the Calypterates as a whole, Papavero (1977) on the Oestridae and Griffiths (1972) on the entire Cyclorrhapha. Phylogenetic works concerned with larvae have been mentioned earlier (Chapters 4 and 5). All these works, and other less important ones, will be discussed at the appropriate points below.

The purpose of this chapter is twofold. Firstly, to present evidence supporting certain hypotheses of evolutionary trends, both within the Calliphoridae and in the Cyclorrhapha as a whole. Secondly, to analyse phylogenetic relationships within the Calliphoridae, and between it and other groups of the Cyclorrhapha.

11.2 Materials and Methods

The methods used in the following phylogenetic analysis are those expounded by Hennig (1965, 1966a). This is not the place for a full treatment of Hennig's methodology, but a few comments are here made and a few terms are defined.

In any group of closely related species, a certain number of characters will be shared among them. Any one of these characters will be found to exist in a somewhat different state in each species. E.g., in a group of closely related fly species, some may have long wings, others short wings, and yet others no wings at all. A basic task of phylogenetic analysis is to determine which of these character states is the ancestral or primitive (plesiomorphic) condition, and which is the derived or advanced (apomorphic) condition.

The fact that two species share a common character state does not necessarily mean that they are closely related. This is the case if the shared state is the plesiomorphic condition. It is also the case if the character state arose more than once independently (convergence). Only if it can be shown that the character state is a true shared apomorphy can we postulate that the two species are closely related. Such a shared derived state (synapomorphy) must be shown to have arisen only once in the shared ancestry of the two species.

In order to be able to analyse the character states within a family, it is necessary to study groups related to it, especially the sister-group. A sister-group is a group which shares a common ancestor with another group, the common ancestor being unique to these

two groups. There are sound reasons for believing that the sister-group of the Calliphoridae is the Sarcophagidae.

The following are the species of Cyclorrhapha (other than Calliphoridae) that were studied in the immature stages for comparative purposes.

Sarcophagidae

Sarcophaga argyrostoma

Sarcophaga carnaria

Brachicoma devia

Parasarcophaga knabi

Parasarcophaga ruficornis

Parasarcophaga similis

Parasarcophaga misera

Parasarcophaga crassipalpis

Parasarcophaga albiceps

Tricharaea brevicornis

Hybopygia varia

Oxysarcodexia thornax

Oxysarcodexia confusa

Patonella resona

Ravinia belfordi

Chaetoravinia advena

Chaetoravinia almeidai

Engelimyia ionops

Adiscochaeta abnormis

Boettcherisca peregrina

Boettcherisca septentrionalis

Helicophagella melanura

Leucomyia cinerea

Wohlfahrtia vigil

Tachinidae

Argyrophylax aureiventris

Phryxe vulgaris

Zygobothria ciliata

Plesiocyptera sp.

Medina egregia

Metagonistylum minense

Therobia abdominalis

Mycteromyia phasmatophaga

Actia painei

Schistocercophaga dampfi

Oestridae

Oestrus ovis

Cephenemyia trompe

Tracheomyia macropi

Hypodermatidae

Hypoderma bovis

Hypoderma diana

Hypoderma lineatum

Gasterophilidae

Gasterophilus intestinalis

Gasterophilus pecorum

Gyrostigma pavesii

Platycobboldia loxodonta

Cuterebridae

Cuterebra chiquibulensis

Cuterebra sp.

Dermatobia hominis

Alouattamyia baeri

Muscidae

Musca domestica

Muscina pabulorum

Hydrotaea dentipes

Polietes lardaria

Anthomyiidae

Hylemya brassicae

Drosophilidae

Drosophila melanogaster

Drosophila funebris

Drosophila simulans

Sphaeroceridae

Leptocera cambrica

Leptocera caenosa

Leptocera heteroneura

Leptocera zosterae

Copromyza sp.

Piophilidae

Piophila casei

Lonchaeidae

Lonchaea chorea

Tephritidae

Tephritis bordanae

Dryomyzidae

Dryomyza anilis

Agromyzidae

Phytomyza ilicis

Sciomyzidae

Sepedon sp.

Coelopidae

Coelopa frigida

Milichiidae

Milichia ludens

Ephydridae

Ephydra afghanica

Teichomyza fusca

Conopidae

Physocephala sp.

Syrphidae

Myathropa florea

The above list includes only those species studied in detail. Many other species, only superficially examined, are not included in the list.

11.3 The Taxonomic Value of Characters of Immature Stages

The taxonomic value of characters of immature stages has long been a matter of dispute (Hennig, 1966), and many workers still believe that such characters should not be considered in taxonomic or phylogenetic research. There appear to be two reasons for this point of view. Firstly, it is argued that, because insect larvae (especially among the Holometabola) are caenogenetic, i.e. secondary forms not resembling the ancestral condition, the characters of these early ontogenetic stages cannot be seen to recapitulate phylogeny (van

Emden, 1957). Therefore, it is concluded that "larval characters cannot be regarded as a general rule to be of overriding importance for the taxonomy" (van Emden, (1957). This view has persisted for a long time, perhaps because of the partial truth it contains. Certainly the larvae of Holometabola are caenogenetic; no-one, as far as I know, has seriously suggested that the ancestral blowfly resembled a maggot. But this is missing the point. The point is that comparative studies of modern-day maggots will give us a good idea of what the ancestral maggot looked like, and thus will tell us a good deal about the evolution of a group.

The second reason put forward for ignoring immature characters was brought to my attention by Dr L. Davies (pers. comm.). Although not subscribing to this view himself, he informs me that some workers hold this view because immature stages do not reproduce. This strikes me as a startling hypothesis, since it seems to imply that immature stages are separate organisms having a gene-flow of their own, which is clearly not the case. All animals, to a greater or lesser extent, change in appearance during their ontogenetic development; in Holometabolous insects this change happens to be great and sudden, but this is hardly a reason for ignoring the pre-adult characters. In any case, immature stages do reproduce eventually and are themselves reproduced by the adult. These well-known facts seem to have caused confusion in the past. For example, van Emden (1957) states that the structure of the egg chorion reflects the shape of the follicular cells in the ovariole and that, therefore, chorionic structure is, in reality, an adult character. He distinguishes such characters from what he calls the "truly embryological egg characters". In my opinion,

this is a meaningless distinction, since both sets of characters are ultimately derived from the adult.

In principle, therefore, the characters of immature stages are equal to those of the adults in value. In practice, however, it is usually found that either the adults or the larvae of a group better characterise that group. For example, Crowson (1970) states that, of the two Coleoptera families Elateridae and Carabidae, the subdivisions of the former are more clearly expressed in the larval stages, whereas the reverse is true of the latter family.

Much is often made of the fact that a classification based on larval characters will almost always be different from one based on adult characters. As Hennig (1966a) points out, "In many cases the asserted incongruence between larval and imaginal systems is based on the fact that only degree of similarity is considered, without raising the question of whether the similarity rests on symplesiomorphy [shared primitive character states] or synapomorphy." One may add that convergence is another question that ought to be raised.

Of course, many entomologists do recognise the value of immature stages in taxonomy. Nevertheless, the use of these stages in taxonomic work remains a minority activity. However, several works have appeared in which immature stages have been critically studied from the taxonomic and phylogenetic viewpoints, e.g. Davies (1965) on Simuliidae and Disney (1983a) on Dixidae.

Regarding the Calliphoridae, the major sub-divisions of the family seem to be more evident in the adult stage, but many of the generic or sub-generic groupings, and even species, seem more clearly expressed in the third larval instar. In the following phylogenetic

analysis only immature characters will be used to infer relationships, but this is not meant to reflect an opinion that adult characters are not useful in this respect, but simply that adult taxonomy is largely out of the scope of this thesis, although reference will be made to the work of others in this field.

Finally, it is possible that the longevity of a particular stage may be related to its taxonomic use. In the Coleoptera examples cited above, Crowson (1970) states that it may not be accidental that the larvae are long-lived and the adults are short-lived in the Elateridae, whereas the reverse is true of the Carabidae. In my own limited studies on the Oestridae, which have very long-lived larvae, Crowson's point finds strong support.

The same may be true of Tachinidae, many of which overwinter as full-grown larvae (Clausen, 1940). It is well-known that the identification of Tachinids is not easy, but it has hardly ever been thought worthwhile to question whether this is because the species features may be more clearly expressed in the larval stages. In a largely overlooked paper, Thompson (1922) makes the following remarks: "It sometimes happens that species belonging to this group [i.e. Tachinidae] , though easily separated by constant and well marked characters in the larval stage, are in the adult stage so similar that it is only possible to separate them by characters whose value in the group as a whole is so open to question, that to admit their validity in general would be to plunge the taxonomy of the family into inextricable disorder." He goes on to describe three larval species parasitising Pyrausta nubilalis (Lepidoptera: Pyralidae). Each of these three species consistently developed into one adult 'species'.

Paraphorocera senilis Rondani. The identification of the adults was carried out by Villeneuve.

In spite of these observations, Tachinidae specialists have continued to ignore the larvae in their definitions of species. In a group whose biological importance (to man, at any rate) lies in the activities of the larvae, such neglect is extraordinary.

11.4 Lines of Evidence

In this section the various lines of evidence used to deduce the plesiomorphic and apomorphic states of characters are discussed. Lines of evidence that are of potential, if little actual, use are also briefly discussed.

11.4.1 Evidence from Palaeontology

Very few fossil Calypterates are known. According to Rohdendorf (1974) only about twenty species of "not exactly distinct representatives" of the group are known from the Tertiary. Rohdendorf's work is restricted to fossil adult forms, but, in addition, about six or seven different finds of fossil puparia have been made (Gautier, 1974; Kitching, 1980).

The oldest alleged fossil puparia known are a few specimens from the Late Cretaceous (70 million years B.P.) of Alberta. These were originally described by McAlpine (1970) as Cretaphormia fowleri. These remains were sent to me on loan by Dr McAlpine, initially with the intention of S.E.M. examination. Unfortunately, the rock to which

these fossils are attached was too large to fit into the vacuum chamber, and permission to cut it was not forthcoming. The specimens were, therefore, examined under a stereomicroscope at magnifications of up to X320; in addition, photographs at X50 magnification were taken and photographic slides made, which were projected at much greater magnification onto a screen. The following are the results as compared with McAlpine's description.

The four specimens were designated A,B,C and D by McAlpine. Specimens A and C are elongate structures (Fig. 186 is of C). Specimen B is a hollow in the rock and specimen D is a broad, flattened object (Fig. 187).

Specimens A and C were described by McAlpine as possessing twelve "body" segments. Although the specimens undoubtedly have an annulated appearance, I could not count a definite number of rings. McAlpine described certain granulations on the surface as "traces of integumental spines"; high magnification failed to reveal any structure for these granulations, being simply larger incrustations with which the specimens are covered. He further states that specimen C (the holotype) possesses three posterior papillae; I could detect none.

On the other hand, the lengths of these specimens (about 12-13mm) is within the range of blowfly puparial size. Furthermore, the Shape Factor for the holotype (0.39) is typical for a Calliphorid puparium, although McAlpine did not use this measurement in his description. A further supporting piece of evidence is the break at the (presumably) anterior end of the 'puparium' (the left hand side in Fig.186). This may represent the broken-off caps of the puparium, the upper one being absent.

Specimen B, the hollow, was described by McAlpine as being the inner surface of a puparium and possessing pharyngeal sclerites that were "clearly evident". I could find no trace of such sclerites.

Specimen D (Fig. 187) is described by McAlpine as a puparium. I cannot agree with this as it is quite the wrong shape. It does, however, resemble the abdomen of an adult fly. It measures 6mm at its broadest part and about 5.5mm in length; these are almost exactly the dimensions of the abdomen of a modern blowfly species.

Apart from his evaluation of these specimens as fossils, McAlpine makes two other statements that require comment. Firstly, he states that specimen C is lying on its side, i.e. the uppermost surface is lateral while the side nearest the camera (in the phologragh) is ventral. If it is a puparium then this can hardly be the case, since the manner of breaking of the caps (one dorsal and one ventral) indicates that the uppermost surface would be dorsal (or possibly ventral), but certainly not lateral. Secondly, McAlpine's statement that twelve body segments are apparent is curious, since, although it is true that Cyclorrhaphous larvae have twelve apparent segments, only eleven are normally visible in the puparium, due to the contraction of the cephalic segment into the first thoracic.

In conclusion, all that can be said is that these remains possibly represent the puparia and abdomen of a Cyclorrhaphous fly. Size would indicate that it was a Calypterate. However, I find no features to justify McAlpine's statement that they are Calliphoridae as opposed to any other group of Calypterates. It is possible that they represent an ancestral species to these modern groupings. Finally, I see no value in giving these remains a formal name.

The second oldest fossils examined by me were from the Pliocene/Pleistocene boundary (i.e. the Tertiary/Quaternary boundary) of the Makapan Valley, South Africa, associated with remains of Australopithecus Dart. These fossils are puparial internal casts, i.e. no external features were visible. They were thought to be fly puparia because a few well-preserved specimens with external features present (spines, spiracles etc.) were found among them (Kitching, 1959 and 1980). Regrettably, none of these well-preserved specimens were available for examination.

The only features that could be used to attempt an identification of these rather nondescript remains were size and the Shape Factor. In size they varied from 10-15 mm in length. The Shape Factor ranged from 0.44-0.57. These measurements fall within the range of many blowfly species and cannot be used to suggest any particular genus or species. The remains are about 1.9 million years old.

The most recent fossils examined were remains associated with the bones of the Woolly Rhinoceros (Coelodonta antiquitatis) and the Steppe Bison (Bison priscus) from the Late Pleistocene (about 75,000 years old) of Belgium. These were studied by Gautier and Schumann (1973) and Gautier (1974), who arrived at the conclusion that they were the remains of Phormia terraenovae. Their conclusion was based on the shape of the mouth-hook and the size of the posterior spiracle, and their illustrations show these features clearly. These structures, however, were not represented in the material sent to me, which was mostly pieces of cuticle. The spines show the occasional bifurcated ones typical of Ph. terraenovae (among others) (Fig. 185). The peripheral row of smaller spines is also typical of this species

(compare Figs. 184 and 69). These results support the findings of the above authors.

Regarding phylogeny, these fossils tell us little. If they are indeed all fossil puparia (there is no doubt about the Belgian specimens) then all we can say is that, in size at least, these insects have changed little since the late Cretaceous. If the Canadian specimens are true puparia, then this is the only evidence of Calypterate flies existing in the Mesozoic.

A word of caution is necessary regarding the drawing of phylogenetic conclusions from fossils. As Eldredge and Cracraft (1980) point out the presence of a character state in an ancient fossil does not necessarily mean that this is the plesiomorphic condition, since that lineage may simply have died out after evolving a derived character state, while the truly plesiomorphic condition may have persisted in the lineage that survives to the present day. As proposed by Hennig (1981), the starting point of phylogenetic research should be the Recent Animal Kingdon, and the fossils should be analysed in the light of knowledge gained in this way, rather than vice versa. This does not mean, of course, that fossils in their own right cannot tell us a good deal about the history of a group, but in terms of attempting to establish the plesiomorphic expression of a character they should be used with caution.

Puparia are very durable objects, while adult flies are particularly fragile. It is likely, therefore, that many fossilised puparia exist in Nature but are overlooked, and it is also likely that future palaeontological research on the Cyclorrhapha will depend on finds of puparia. There are several areas of the World that would

repay investigation in this field; in Britain the interbasaltic Ardtun Leaf Beds (Eocene) of the Isle of Mull, Scotland, seem promising. Their age (about 60 million years B.P.) indicates that this may be a likely area for remains of early Calypterates. A well-preserved Tipulid and a Bibionid were discovered in these beds (Zeuner, 1941).

11.4.2 Evidence from Parasitology

The parasites (or hosts) of animal groups have often been used to infer their relationships (Crowson, 1970). The basic principle is that the evolution of a group of parasites will parallel that of its hosts to a greater or lesser extent. This principle has been set up formally as Fahrenholz's Rule, which is discussed at length by Hennig (1966). However, before looking at the hosts of the Calliphoridae with the purpose of learning something about the evolution of the group, it is necessary to answer a more fundamental question first.

The Calliphoridae are divided into obligate parasites and obligate saprophages, with a vast array of normally saprophagous species that can also act as facultative parasites. The question is whether parasitism or saprophagy is the primitive, ancestral habit. The question may be applied to the whole of the Cyclorrhapha.

Keilin (1915) noted that Cyclorrhapha larvae are very uniform in structure, but exhibit a very great diversity in life-habit, whereas Orthorrhapha larvae exhibit great structural diversity which is not accompanied by great biological diversity. Keilin asks how, then, can one explain the great diversity of Cyclorrhaphous larval habits coupled with such uniformity of structure? He concluded that the

ancestral Cyclorrhaphan must have followed a life-habit from which the later great diversity was derived. He further concluded that this ancestral habit must have been parasitism. His reasons for holding this view are as follows:

1. A very large number of parasitic species are known among the Diptera, but they are almost all Cyclorrhapha, not Orthorrhapha. Parasitism among the Orthorrhapha is extremely rare.

2. Larviparity and pupiparity, both adaptations to the parasitic habit, are again limited exclusively to the Cyclorrhapha and are absent from the Orthorrhapha.

3. Only in the Cyclorrhapha are found an enormous fauna of saprophagous and myiasis-causing species. The latter may be considered to be a sort of transition between parasitic larvae with a long, terminal saprophagous period, and truly saprophagous larvae.

Therefore, so Keilin argued, all free-living Cyclorrhaphous larvae are secondarily so. The peculiar form of the free-living Cyclorrhaphous maggot is an example of the irreversibility of evolution.

Zumpt (1965) held the opposite view, believing that the parasitic habit in myiasis-causing species is derived from the free-living saprophagous habit. He saw the ancestral species of myiasis-causing flies as being very unspecialised feeders like the modern Muscina stabulans (Fall.) (Muscidae) which is saprophagous on dead vertebrates and insects, a scavenger in wasps' nests, a predator on other maggots and, occasionally, a myiasis agent.

He hypothesised two roots to myiasis: a saprophagous and a sanguinivorous root. He saw the saprophagous root as beginning with

species that bred in carcasses, which later became facultative parasites of suppurating wounds. This was then followed by a facultative parasitic habit on unwounded tissues, which eventually became an obligate parasitic habit. Zumpt saw intestinal parasites as arising from larvae accidentally swallowed in food.

The sanguinivorous root arose from larvae that preyed upon other maggots. Such larvae may have accidentally pierced the skin of a bird or mammal in its nest or burrow, thus obtaining a blood meal; these larvae would have evolved into obligate bloodsuckers. Zumpt offers no evidence to support his hypotheses.

My own view, like Zumpt's, is that saprophogy was the ancestral habit, both among the Calliphoridae and the Cyclorrhapha as a whole. In response to Keilin's three points cited above, the following answers can be made:

1. While it is true that an enormous number of Cyclorrhapha are parasitic, it is also true that at least an equal, if not greater, number are saprophagous. Parasitism, while not as common in the Orthorrhapha, is certainly not rare in that Suborder; the very large family Bombyliidae, and also the Nemestrinidae, Acroceridae and many Asilidae are parasitic as larvae.

2. The occurrence of larviparity and pupiparity in the Cyclorrhapha does not in itself indicate that the ancestral habit was parasitic.

3. Keilin's third point may be argued both ways; in other words the myiasis habit can easily be derived from the saprophagous habit, as shown by Zumpt.

Points in support of Zumpt's view are:

1. The parasitic habit among Calypterates is often linked with features that are obviously derived, e.g. the reduction of adult mouthparts and the lack of adult feeding in the Oestridae.

2. The widespread saprophagous habit among the Cyclorrhapha, even in many families that contain parasitic species, would indicate that this habit is primitive.

3. Parasitism is an all-embracing term that covers many different phenomena. For example, the parasitoid habit of Tachinidae is a very different phenomenon from the myiasis-causing habits of blowflies, and it is difficult to see how one habit could have arisen from the other. It is, however, easy to see how a generalised feeder like Muscina stabulans (see above) could have developed any of the life-habits covered by the term 'Parasitism'. It is very likely, therefore, that parasitism arose independently many times in the evolution of the Cyclorrhapa as a whole and probably in the Calliphoridae as well.

Regarding the peculiar form of the Cyclorrhaphous larva, this must have evolved in response to the saprophagous habit, and does not indicate that the ancestral habit was parasitic. It simply shows that the 'maggot-form' is so successful that it enabled the Cyclorrhapha to invade a wide variety of habitats.

In this thesis, therefore, the hypothesis is that saprophagy is the plesiomorphic habit and parasitism the apomorphic. Keilin's view is not accepted, although it has long been accepted by many parasitologists (e.g. Rothschild and Clay, 1952).

The second question to answer is: What can the actual hosts of

the Calliphoridae tell us about the evolution of the group?

The following groups are known as hosts of Calliphoridae:

1. Mammalia. Most known Calliphorid parasites are parasites of Mammals. They are recorded from a large number of wild and domestic mammals (Zumpt 1965).

2. Aves. The genus Protocalliphora is a blood-sucker of many bird species.

3. Reptilia. Very few records known. Zumpt (1965) cites a case of a gecko (Naultinus elegans Gray) as a host of Calliphora stygia in Australia. Specimens from parasitised tortoises (Testudo hermanni) kept in captivity in Vienna, Austria, and sent to me proved to be Lucilia ampullacea and Calliphora vicina.

4. Amphibia. Lucilia bufonivora and L. prophyrina are known as obligate and facultative parasites respectively, of Anura.

5. Mollusca-Gastropoda. A few species are known as parasites of snails.

6. Annelida-Oligochaeta. Pollenia rudis is recorded as a parasite of earthworms.

7. There are few known true insect parasites. But there are many termitophilous and myrmecophilous species, and also some are predatory on locust egg-pods.

It is obvious from the above that Mammals are the main host-group and, as pointed out by Hennig (1981), it would be a fascinating task to study how far the Cyclorrhapha parallelled the evolution of the Mammalia and flowering plants during the Tertiary. As noted above, many kinds of mammals, including wild ones, may be parasitised, both by obligate and facultative species. However, the

interesting point is that there are very few records of species of Calliphora, Lucilia (except L. bufonivora) or Chrysomya parasitising wild mammals in the wild state. All records known to me are either from zoo animals or animals in an urban situation. Domestic mammals are frequently parasitised by blowflies, however. Even the obligate parasite Chrysomya bezziana has never been recorded from a wild mammal in the wild state, while it is recorded from twenty-one zoo mammal species from kangaroos (Macropus rufa) to Polar bears (Thalarctos maritimus) by Spradbery and Vanniasingham (1980). During many years of collecting Zumpt (1965) has never recorded Ch. bezziana from a wild African mammal, in spite of the abundance of this species in Africa.

What does this indicate? I suggest that these species may have evolved the parasitic habit in association with Man. Further evidence in support of this view is that, of the six British species of Calliphora, the only two known to cause myiasis in any animal are the two synanthropic species C. vicina and C. vomitoria.

The endemic species of Calliphora in Australia include some, e.g. C. augur and C. stygia, that are known to be important agents of sheep myiasis, yet none of these species has ever been recorded as a parasite of any indigenous marsupial, bat, or dingo. This would suggest that the parasitic habit evolved after the arrival of Man with his flocks of sheep to Australia, and that prior to this these flies must have bred exclusively in animal carcasses. This seems to support strongly the view that parasitism in these species arose in association with Man, and in response to the attraction of the unhygienic conditions prevailing in human dwellings and barns. It is possible that Calliphorids do not parasitise wild animals both because

of their generally cleaner condition (in the wild) and because that niche has already been filled by the Oestridae and Gasterophilidae.

If this proposal is true, it would probably follow that the parasitic habit evolved after Man became settled in communities. In this connection, a paper by Pierce (1945) is interesting. He describes some fossil puparia, which he named Protochrysomyia howardi, from the remains of an extinct vulture, Teratornis merriami, from the Pleistocene of California. He describes the association as 'a case of myiasis'. While this is possible, there seems to be nothing to indicate that it was anything other than saprophagy.

Further investigation of this point would be of great interest.

11.4.3 Evidence from Comparative Morphology

This is one of the most important lines of evidence. The method of Outgroup Comparison, in particular, has been widely used in phylogenetic work (Eldredge and Cracraft, 1980; Wiley, 1981). The basic principle of this method is that, if a character exists in, say, two conditions within a taxon, the condition which occurs in related forms outside that taxon is probably plesiomorphic within it.

The related forms usually compared in this manner are comprised within the sister-group. However, strong supporting evidence may be found by studying related groups as well as the sister-group. The reason for doing this is that a character may occur in two states in both sister-groups. In such cases it is necessary to treat both these sister-groups as one group and analyse the characters of its sister-group, if known. A great deal may be learnt by looking at a wide range

of related forms (in the present case, the Cyclorrhapha) and noting how widespread a character-state is. A very widespread character-state is probably primitive.

Much use of this line of reasoning will be made in the following phylogenetic analysis.

11.4.4 Evidence from Ontogeny

As was seen above (11.3), the larvae of Holometabolous insects are caenogenetic and their features cannot, therefore, be seen as recpitulating the features of the ancestral adult. Nevertheless, it must be seen that during the ontogenetic development of the larva itself, the features expressed during the early stages might shed some light on what the ancestral larva looked like. In other words, the plesiomorphic expression of a character should appear before the more specialised, apomorphic expression.

Some use will be made of this kind of reasoning, although it will always be used in support of other evidence.

11.4.5 Evidence from Genetics

Species are not morphologically, but genetically defined populations. Although not a watertight definition, the biological species may be defined as a group of populations that may freely interbreed, but which are reproductively isolated from other populations (Cain, 1963).

In principle, therefore, a useful method of investigating

whether two closely related forms are actually different species or not, is by hybridisation experiments. This is not always practicable.

In the Calliphoridae several pairs of such closely related forms are known. Chrysomya putoria and Ch. chloropyga are a case in point. These have been grouped together as one species by many authors, but hybridisation experiments have shown they are genetically isolated (Zumpt, 1965). No such work appears to have been carried out on another such pair of species, Ch. albiceps and Ch. rufifacies, although they were found to be quite easily separable on structural grounds during the course of this work.

Calliphora vicina and C. vomitoria were once considered to be the same species (Townsend, 1937), although this view has long been rejected. The larvae are easily separable, and attempts by me to hybridise these species in the laboratory failed.

11.4.6 Evidence from Physiology

During the course of this work a limited number of experiments on the rate of development of various species were conducted, and it was noted that certain species develop faster than others under similar conditions. Now, it is known that obligate parasites such as the Oestridae and Gasterophilidae develop slowly (have a long larval life) whereas saprophagous species such as Piophila casei develop relatively rapidly (Zumpt, 1965). Furthermore, from the above-mentioned experiments it was noted that Calliphora vicina developed faster than the more advanced (structurally) C. vomitoria. It is possible, therefore, that rapid development may be a primitive feature.

The above proposal is a very tentative one and this character will not be used in the phylogenetic analysis, since it is probably very much subject to reversion during evolution.

Another piece of physiological evidence may be found in the nutritive requirements of flies. In the vast majority of blowfly species that have been studied, it was found that a protein meal was required by the female to mature her first batch of eggs (anautogeny). The obligate parasite Chrysomya bezziana is autogenous, not requiring a blood meal in order to develop the first batch of eggs (Spradbery and Schweizer, 1970). Adult Oestridae do not feed at all (Papavero, 1977).

These facts would seem to indicate that autogeny is an advanced characteristic. This is because it is linked to the parasitic habit and, in the Calliphoridae at least, anautogeny is very widespread.

11.4.7 Evidence from Zoogeography

The taxonomy of the Calliphoridae (based on adult characters) is not yet stabilised and the World fauna has been rather patchily investigated; this applies in particular to the Neotropical, Oriental and Australasian regions. This fact makes any zoogeographical analysis difficult, since even the number of species occurring in these regions is not (at least for most genera) known. It is, therefore, not possible to hypothesise an area of origin, based upon a knowledge of the number of modern species.

However, one general comment may be made. The Calliphoridae as a whole (and also its constituent subfamilies and genera) show a

continuous pattern of distribution. This would almost certainly indicate that the group is a young one and at its most evolutionarily successful stage.

The dipterous fauna of New Zealand is a largely endemic one (Hennig, 1966b). Such a relict fauna may be expected to exhibit a number of plesiomorphic features when compared to their closest relatives. In fact, the endemic species of New Zealand Calliphora do exhibit such features which have been deduced to be primitive from other evidence. Therefore, these species may offer strong supporting evidence. It is regrettable that none of the endemic species of the Madagascan fauna were available for study.

Three genera of Calliphoridae are reasonably well-known taxonomically. The numbers of species of each genus known in each zoogeographic region are listed in the following table.

	Genus		
Region	Calliphora	Lucilia	Chrysomya
Palaearctic	11	15	4
Oriental	10	9	10
Afrotropical	1	4	12
Australasian	32	4	9
Nearctic	8	12	-
Neotropical	4	16	-

[N.B. Three species of Chrysomya have recently been introduced by Man into the Americas]

A glance at the table will show that, while it is difficult to come to any definite conclusions regarding Lucilia and Chrysomya distribution, it would be logical to propose that Australasia was probably the area of origin of the genus Calliphora. This hypothesis is further supported by the fact that some of the most primitive members of the genus occur in this region.

11.4.8 Evidence from Climatology

Fairchild (1969) discussed the possible role that climate may have played in the evolution and distribution of the Tabanidae. He begins by putting forward his belief that insects as a Class, and probably most Orders and Families, evolved in the Tropics, i.e. those areas where the temperature rarely if ever is low enough to stop insect activity. He reasons that, if this is so, then the ability to survive and reproduce outside the Tropics is an acquired adaptation, and he notes that the Diptera have been unusually successful in this respect. Cold adaptation and the consequent movement out of the Tropics would, therefore, mean movement into an environment of lower competition and lessened selection pressure. It would then follow that evolution would be slowed by cold climates, and that movement by a cool-adopted taxon back into the Tropics would be increasingly difficult. Since movement of insects would be more prevalent into cool regions from the Tropics, and evolution would be expected to be slower in cool areas, there should be a gradual accumulation of less specialised taxa in cool areas, in other words, cool areas act as traps for primitive stages in the evolution of a group.

This interesting idea is strongly supported by the present study. Those character-states that have been inferred to be apomorphic are certainly far more common in the warmer parts of the World. However, this line of reasoning cannot really be used directly, since evolution, although slow in cold areas, certainly does not cease, and many cold-adapted species do possess advanced characteristics. Rather, the results of the present study may be seen as evidence supporting Fairchild's hypothesis, rather than vice versa.

11.4.9 Evidence from Previous Taxonomic Work

Any piece of taxonomic work is built upon previous studies, and, as pointed out above (11.3) it is believed that the main subdivisions of the Calliphoridae are better expressed in the adult stage. These divisions are, therefore, accepted in the present work; their main value lies in showing that certain characters have evolved more than once in the family.

On the other hand various generic groupings will be questioned, although no formal changes of nomenclature are proposed.

11.5 Character States

In this section an analysis of a variety of characters will be made. For each character evidence will be presented to support hypotheses concerning the plesiomorphic and apomorphic expressions of that character.

All references to apomorphy and plesiomorphy made in this

section refer to the condition within the Calliphoridae alone, unless otherwise stated.

11.5.1 Characters of the Third Instar larva

11.5.1.1 Spine Structure and Pigmentation

Small fine-pointed spines are the plesiomorphic expression of this character. Large, rounded spines, and spines with more than one tooth are apomorphic expressions. Darkly pigmented spines are also apomorphic, while lightly or unpigmented spines are plesiomorphic.

Evidence: Fine, unpigmented spines are the rule in the Sarcophagidae. Such spines are also very widespread amongst other Cyclorrhapha, much more so than strong, heavily pigmented spines (see Figs. 180 & 181). In addition, the first or second instar Calliphorids examined hardly ever possessed strong, dark spines, this feature always appearing (if it does appear) only in the third instar.

11.5.1.2 Spine Banding

Dorsally incomplete banding on the posterior segments is a plesiomorphic feature.

Evidence: Many Sarcophagidae possess incomplete spinal bands, although they are complete in a few species. However, in the vast array of Acalypterates studied incomplete banding of most (not only the posterior) segments was the rule, e.g. in Drosophila melanogaster all bands are incomplete dorsally.

11.5.1.3 Number of lobes of Anterior Spiracle

A great number of lobes (12-13) is the plesiomorphic condition, with fewer lobes as an apomorphic feature.

Evidence: A great number of lobes is always exhibited by the Sarcophagidae, and is the rule among most Cyclorrhapha. However, in the Tachinidae, Muscidae and Anthomyiidae the character is as varied as in the Calliphoridae, although there is, nevertheless, a greater tendency to a higher number among the three former families than in the Calliphoridae. It seems that meristic characters tend towards a reduction in number during evolution (Crowson, 1970), although increases in number have occasionally been known.

11.5.1.4 Posterior Spiracle Size and Distance Factor

The Spiracle Distance Factor of the ancestral Calliphorid was probably between 1.2-1.8, although this character was found difficult to analyse. Among the Sarcophagidae the same range of factors exists as in the Calliphoridae, so outgroup comparison is not of much use on this occasion.

Evidence: The range of 1.2-1.8 is very common in the Calliphoridae. Highly specialised larvae have either a very low SDF (e.g. Chrysomya bezziana: 0.11-0.13) or a very high SDF (e.g. Auchmeromyia luteola: 4-5.3). Therefore, evolution seems to have gone, on occasion, in opposite directions, the primitive condition in this case being at neither extreme.

Size of the posterior spiracle is linked to the SDF; the lower

the SDF (spiracles close together) the greater the diameter of the spiracle.

11.5.1.5 Ecdysial Scar Pigmentation

Although this is a variable character which may be misleading in identification, nevertheless there is a strong tendency towards lack of pigmentation in many species. It is tentatively proposed that the unpigmented condition is plesiomorphic.

Evidence: The overwhelming majority of Sarcophagidae lack pigmentation in this area (Fig. 182). Some specialised Sarcophagids, however, do have the button pigmented, e.g. Brachicoma devia (Fig. 183) a parasite of Hymenopterous larvae. Due to the specialised nature of this species, however, one can conclude that it is the apomorphic expression in Sarcophagidae as well.

11.5.1.6 Posterior Spiracle Anastomoses

A great number of anastomoses in the spiracular slits is the plesiomorphic condition.

Evidence: The spiracular slits of Sarcophagidae possess a large number of anastomoses. Those Calliphoridae that possess only a few anastomoses are specialised parasites, e.g. Protocalliphora and Auchmeromyia.

11.5.1.7 The Sun-Ray Structure

The sun-ray structure as a well-developed feature is the plesiomorphic expression.

Evidence: The sun-ray structure is usually well-developed in the Sarcophagidae. Specialised species, e.g. Protocalliphora spp. have very much reduced sun-ray structures. In the genus Chrysomya the SR structure is well-developed in most species, except in Ch. bezziana, an obligate parasite, where it is lacking.

The interspiracular bristles of certain Cyclorrhapha, e.g. Drosophilidae and Coelopidae are probably homologous with the SR structure, as their form and arrangement is similar to the Calliphorid structure, but much more pronounced (Fig. 178).

11.5.1.8 Body Processes

The body processes of the 'hairy' maggots are clearly an apomorphic feature.

Evidence: The vast majority of Calliphorids lack such processes, and they are totally absent from the Sarcophagidae. The only comparable structures known to me among the Calypterata are the body processes of Fannia (Muscidae). Body processes probably arose independently twice in the Calliphoridae; once in the 'hairy' maggots, and once in Chrysomya varipes. The reason for this belief is that Ch. varipes possesses only two processes per segment and the skeleton is of a very different type to the one shared in common by the 'hairy' maggot species.

11.5.1.9 Posterior Papillae Size and Position

Medium-sized papillae (as e.g. in Calliphora vicina) are the plesiomorphic condition. Also, P_1, P_2 and P_3 equidistant is plesiomorphic.

Evidence: The above condition is very common within the family and is also the rule in Sarcophagidae. Furthermore, all first instars possess this character in this condition, even in those species whose third instars possess either very well-developed or very reduced papillae. This character has evolved in two directions, the plesiomorphic expression being intermediate.

11.5.1.10 Shape Factor

A Shape Factor of 0.20-0.25 is probably the plesiomorphic condition.

Evidence: This is a range typical of most Calliphoridae and Sarcophagidae. Calliphorid species with a higher Shape Factor range are specialised parasites, e.g. Protocalliphora azurea (0.29-0.34) and Cordylobia rodhaini (0.49-0.51). A lower Shape Factor is linked to the primitive curvature so widespread among the Cyclorrhapha. This primitive shape is lost in larvae with a high Shape Factor.

11.5.1.11 Mouth-Hook Length

Very long and very short mouth-hooks are apomorphic expressions of this character. The plesiomorphic condition is probably that found

in species like Lucilia sericata and Calliphora vicina.

Evidence: Very long and very short hooks are present in specialised parasites, e.g. long in Lucilia bufonivora, while in other, saprophagous, Lucilia species it is shorter. The mouth-hook is very short in Protocalliphora spp. In most Sarcophagids the condition is similar to the hypothesised plesiomorphic condition in Calliphoridae.

11.5.1.12 The Oral Sclerite

An unpigmented oral sclerite is the plesiomorphic expression.

Evidence: Most Calliphorids lack a pigmented oral sclerite. Hardly any Sarcophagidae possess pigmented oral sclerites. The oral sclerite is widespread among the Cyclorrhapha, but is hardly ever pigmented (see Figs. 174 and 175).

Skidmore (pers. comm.) suggests that the oral sclerite in Calliphoridae may have arisen from the fusion of paired oral sclerites such as are present in some Muscidae, suggesting that these paired structures are primitive. Hartley (1963) also implies that the complex structures present in Limmophora (Muscidae) are primitive. However, the widespread presence of the Calliphorid-type oral sclerite among the Cyclorrhapha is strong evidence to suggest that this is the primitive condition, and that the paired Muscid structures arose from the splitting up of the oral sclerite.

11.5.1.13 The Liguloid Arch

A broad, straight, well-pigmented liguloid arch is the plesiomorphic expression.

Evidence: The condition is widespread among the unspecialised Calliphoridae. Parasitic species tend to have modified arches. Broad, well-pigmented arches are the rule among the Sarcophagidae (Figs. 167 and 170).

This structure is very variable in the Cyclorrhapha as a whole. It is totally absent from many, e.g. Piophila casei (Fig. 176), while it is very well-developed in others. Teskey (1981) has suggested that the dentate arch of many Sciomyzidae may be homologous with the liguloid arch (Fig. 171). If this is so, then this is an extreme condition of the structure. The liguloid arch seems to be absent from most Tachinidae and Oestridae.

11.5.1.14 The Dental Sclerite

A well-developed dental sclerite, as in most Calliphora spp. is the plesiomorphic expression; its reduction or total absence is apomorphic.

Evidence: Sarcophagidae almost always possess a well-developed dental sclerite. A robust sclerite is also very widespread among the Calliphorids, and is reduced (e.g. in Chrysomya bezziana) or absent (in Protocalliphora spp.) in parasitic species.

Once again, the dental sclerite is very variable in the Cyclorrhapha. It appears to be absent from most Tachinidae (Figs. 308 and 309) and Oestridae and also from many Acalypterates, although most of the latter possess it.

11.5.1.15 The Hypostomal Plates

Weakly pigmented hypostomal plates situated close together are probably plesiomorphic expressions.

Evidence: This condition is prevalent among the Sarcophagidae (Figs. 167 and 169), although great variation occurs in this structure within the Calliphoridae. In most Cyclorrhapha the plates are not very heavily pigmented and are situated close to one another (Figs. 172 and 176). Total fusion seems to have occurred in many Tachinidae (Fig. 310) and in many Acalypterates, such as Lonchaea chorea.

In Protocalliphora spp. the plates situated close together are probably a secondary feature, since the plate apertures are anterior in this genus, whereas they are posterior in most Cyclorrhapha (see Fig. 166).

11.5.1.16 The Hypostomal Sclerite

1. A long hypostomal sclerite (i.e. only slightly shorter than the mouth-hook) is probably plesiomorphic.

2. A narrow (in lateral view) hypostomal sclerite is plesiomorphic.

3. A narrow cross-bar of the hypostomal sclerite is plesiomorphic.

Evidence for (1) and (2): These conditions are widespread in the Calliphoridae, but great variation between Sarcophagid species exists as regards this character. Long, narrow hypostomal sclerites seem to

be plesiomorphic in the Cyclorrhapha as a whole (See Fig. 173).

Evidence for (3): This condition is widespread in the Calliphoridae and Sarcophagidae (Figs. 148 and 168). Very thick cross-bars exist in such species as Chrysomya albiceps, which exhibit a great number of apomorphic features in the larva as a whole and in the skeleton in particular.

11.5.1.17 The Parastomal Bars

Narrow, elongate parastomal bars are the plesiomorphic condition. Thickened, anteriorly tapering bars, and absence of bars are apomorphic features.

Evidence: The hypothesised plesiomorphic condition is very common both in both Calliphoridae and Sarcophagidae. Those lacking bars are overall highly specialised, e.g. Stomorhina cribrata and Chrysomya sufifacies. Thick bars are present in the specialised genus Protocalliphora.

Parastomal bars are very common among the Cyclorrhapha, although they are absent from Tachinidae (Fig. 309), Muscidae and Oestridae. As a rule, they are present in the Acalypterates (Fig. 173).

11.5.1.18 The Dorsal Cornu

A dorsal cornu of medium thickness (as in Calliphora vicina) is plesiomorphic. The presence of a cleft in the cornu is apomorphic.

Evidence: With the Calliphoridae, species with much enlarged (e.g. Protocalliphora) or much reduced (e.g. Pollenia) dorsal cornua

are specialised parasites. The thickness of the dorsal cornu in Sacophagidae is similar to the hypothesised ancestral condition. Most Calliphoridae do not possess a cleft in the cornu, although most Sarcophagidae do. Nevertheless, I do not think that is a plesiomorphic feature because, in Calliphoridae, it is present only in specialised species (Stomorhina, Auchmeromyia). A cleft is absent from most Cyclorrhapha.

The dorsal cornu is narrow in most Muscidae, but is very large in Tachinidae (Figs. 308 & 309), Oestridae and Cuterebridae. It is interesting to note that these three groups are parasitic. In the distantly related parasitic family, Conopidae, the dorsal cornu is much enlarged (Fig. 319).

11.5.1.19 The Ventral Cornu

The ventral cornu varies interspecifically according to whether it is long or short in relation to the dorsal cornu. Short ventral cornua seem to be present in species with a large number of primitive features, and yet long cornua are much more widespread in Calliphoridae and Sarcophagidae and most Cyclorrhapha. It is, therefore, tentatively proposed that short cornua are the apomorphic expression.

11.5.1.20 The Lateral Plate

A lateral plate narrower than the length of the mouth-hook is plesiomorphic.

Evidence: This condition is very common in Calliphoridae and Sarcophogidae. Those Calliphorids with very broad lateral plates are specialised predatory (e.g. the 'hairy' Chrysomya spp.) or parasitic (e.g. Protocalliphora) species. The hypothesised plesiomorphic condition is also the rule among most Cyclorrhapha, especially the saprophagous species.

11.5.1.21 The Pharyngeal Ridges

Well-developed pharyngeal ridges are the plesiomorphic condition.

Evidence: This is a very widespread condition among Calliphoridae and Sarcophagidae and most Cyclorrhapha (although absent from Tachinidae). In Calliphoridae, pharyngeal ridges are lacking only in a few specialised species (e.g. Auchmeromyia).

11.5.2 Characters of the Second Instar Larva

11.5.2.1 The Mouth-Hook

A mouth-hook with a greatly thickened area of curvature is the plesiomorphic condition.

Evidence: This is a very widespread condition among the Calliphoridae. Also, it is strongly linked to a number of plesiomorphic features in the third instar. Mouth-hooks with narrow areas of curvature are almost always associated with apomorphic features in the third instar, e.g. strong spines.

11.5.2.2 The Hypostomal Process

A thin hypostomal process is plesiomorphic. Its absence or great thickening are apomorphic expressions.

Evidence: Thin hypostomal processes are very widespread in Calliphoridae. They are absent from the parasitic Elephantoloemus indicus and are greatly thickened in Protocalliphora spp.

11.5.3 Characters of the First Instar Larva

11.5.3.1 The Mouth-Hook

A strongly angled mouth-hook is the plesiomorphic expression.

Evidence: This condition is both widespread in the Calliphoridae and linked to a number of plesiomorphic features in the third instar.

11.5.3.2 The Post-Mandibular Sclerite

The presence of this sclerite is apomorphic, as it is very rare in the family. It probably arose more than once during the course of evolution.

11.5.3.3 The Lateral Plate

A lateral plate narrower than the length of the mouth-hook is plesiomorphic.

Evidence: This condition is very widespread in the

Calliphoridae. Lateral plates broader than the length of the mouth-hook are linked to various apomorphic features in the third instar.

11.5.3.4 The Posterior Hairs

The presence of well-developed hairs is an apomorphic feature.

Evidence: The absence of these hairs, or the presence of very fine hairs, is widespread in Calliphoridae. They seem to be totally absent from the Sarcophagidae.

11.5.4 Characters of the Egg

11.5.4.1 The Median Area

An anteriorly forked median area is the apomorphic expression.

Evidence: The eggs of all Sarcophagidae and Muscidae examined did not have an anteriorly forked median area. This seems to be the rule in most Cyclorrhapha (Hinton, 1981).

11.5.4.2 The Hatching Pleats

Raised, well-developed hatching pleats are the apomorphic expression.

Evidence: This condition is the minority condition within the Calliphoridae. It is absent from the Sarcophagidae examined. This feature seemed to have evolved many times in the Cyclorrhapha, e.g. it is present in many Muscidae (Ferrar, 1979).

11.5.4.3 Plastron Craters

The presence of these craters appears to be an apomorphic feature. It is very rare in the Calliphoridae. It is also present in some Muscidae (Hinton, 1981) and appears to be an adaptation to dry habitats. It was not present in any Sarcophagidae examined.

11.6 Phylogeny of Selected Groups of Calliphoridae

In this section a phylogenetic reconstruction of five groups of Calliphoridae is presented. These reconstructions are based entirely on larval characters, although adult characters will be mentioned occasionally in order to discuss previous authors' views on the limits of genera. Adult characters were initially taken from the literature and were not personally investigated; all such characters were, however, checked by me on specimens in the collections of the British Museum (Natural History) and, in the case of Calliphora croceipalpis, on specimens loaned by Dr L. Davies.

11.6.1 The Genus Calliphora

The phylogeny of the genus Calliphora (mainly the Australian species) has been discussed by Patton (1935), Hardy (1937) and Kurahashi (1971). None of these authors undertook any detailed analysis of character-states and their phylogenetic trees give no indication as to how their conclusions were reached. Kurahashi's tree of the phylogeny of the Calliphora-group shows four taxa originating from the same point in the cladogram.

Nevertheless, these authors did note a number of what they considered to be primitive features in the adults of some species within the group. For example, Kurahashi establishes the basal dichotomy of his tree on whether the eyes of the male are dichoptic or not. (I infer this from the text of the paper, since he does not actually make it clear which character he is using to establish the dichotomy). This basal dichotomy divides the group into Calliphora sensu stricto on the one hand, and a group of other, more primitive, genera (those with dichoptic eyes in the male) on the other. This latter group includes the genera Aldrichina, Triceratopyga, Eucalliphora and (although not dealt with by Kurahashi) Cynomya and Cynomyopsis. Although primitive in many features, these genera show a number of apomorphic features in the adult, especially in the structure of the hypopygium. The present study shows that they have a large number of primitive features in the larval and egg stages, but also show a few apomorphic features, especially in regard to the number of lobes of the anterior spiracle.

Regarding Calliphora sensu stricto, it was suggested above (11.4.7) that this genus originated in Australasia, because of the great number of species occurring there and because of the presence of many primitive features among some of the representatives in that area. For example, the pigmentation of the oral sclerite, which is such a feature of this genus, is shown at its most primitive condition in many Australasian species, especially those of New Zealand, where the pigmentation is at a minimum.

C. croceipalpis is the only species of the genus known to occur in the Afrotropical region. Zumpt (1956b) states that it is

intermediate between C. vicina and C. vomitoria. This is certainly true in the adult stage, the buccae being black, with black hairs, but the larval stages show immediately that its affinities lie with C. vicina rather than C. vomitoria. In fact, it is very difficult to separate the larvae of C. vicina and C. croceipalpis, whereas it is very easy to distinguish between them on the one hand, and C. vomitoria on the other. Hennig (1966b) quotes Seguy (1940) as saying that C. croceipalpis (as C. antarctica) evolved from C. vomitoria; I cannot agree with this.

The practical difficulty in attempting to reconstruct phylogenies based on immature characters is the small number of species known as larvae. While it is possible (as set out above) to work out the apomorphic and plesiomorphic states of characters, it would serve little purpose to present a cladogram of a group of which only a few species have been studied. A cladogram for the genus Calliphora on a World basis cannot, therefore, be constructed.

However, since all the species of Calliphora from Britain have been studied it is possible to construct a cladogram for the species of this area. The method used was to define each taxon (or clade) on the basis of at least one apomorphy unique to it in the group in question. The result is shown in Fig. 332.

It will be immediately obvious that there is a weakness in the cladogram. This occurs at the point indicated by the arrow. It is a weakness because that particular clade is defined on the basis of a plesiomorphy, not an apomorphy, and thus we are left with a residual paraphyletic group. The reason this has happened is a lack of data. Further studies, especially on adult characters should go a long way

towards solving the problem.

Two interesting points emerge from the cladogram. Firstly, C. uralensis is seen to be more closely related to C. vomitoria than to C. vicina, although it more closely resembles the latter species in the adult stage. Secondly, C. subalpina appears more closely related to C. loewi than to C. alpina, although C. alpina and subalpina were at one time grouped together in a separate genus Acrophaga.

In the case of C. uralensis, I believe that the cladogram shows that the adult characters are invalid for phylogenetic purposes, since this species is strongly linked with C. vomitoria by synapomorphies in the larval stages. In the case of C. subalpina, however, I believe that the adult characters are more significant, a belief supported by the fact that the cladogram is weak at this point.

11.6.2 The Subfamily Phormiinae

This subfamily is usually divided into three genera: Phormia, Boreellus and Protocalliphora. The latter genus is sometimes split into Protocalliphora sensu stricto and Trypocalliphora (Zumpt, 1956a).

The present study supports the view that Protocalliphora and Trypocalliphora could usefully be regarded as separate genera. Regrettably, no specimens of Trypocalliphora were available for study. However, the illustrations by Zumpt (1965) and Hakanen et al (1974) of Trypocalliphora lindneri Peus were studied and compared with the species of Protocalliphora examined. The most obvious difference was the absence of the sucker of the pseudocephalon in Trypocalliphora. This is not surprising, since the latter genus is not a bloodsucker,

but a subcutaneous parasite of bird nestlings (Zumpt, 1965). These two facts would seem to justify the splitting of the genus.

Regarding Phormia and Boreellus, it is difficult to see any justification for the existence of two genera in this case. Hall (1948) states that (on adult characters) the genus Boreellus is very distinct among the Phormiinae, since the head is elongate, the apical cell of the wing is closed and the arista pubescent. I studied adults of the two Phormia and single Boreellus species and I find that, as far as these three characters are concerned, Phormia terraenovae is intermediate between Phormia regina and Boreellus atriceps. Furthermore, the larvae of all three species are exceedingly similar and very difficult to tell apart.

A cladogram of the divisions of the Phormiinae is presented (Fig. 333).

11.6.3 The Genus Cordylobia

The three known species of this parasitic group show characters in their immature stages that enable a well-founded phylogenetic hypothesis to be proposed. This is shown in Fig. 335.

The cladogram is interesting since it shows that C. rodhaini (originally described by Gedoelst (1909) as a species of Cordylobia, but later Surcouf (1914) tranferred it to the new genus Stasisia) stands apart from the other two species. Zumpt (1965) reunited the two genera, on the basis of Fain's (1953) description of C. ruandae which is in many ways intermediate between the other two species. I see no value in retaining two generic names for the species of this group.

11.6.4 The Genus Chrysomya

Less than half the known species of this genus were studied during the course of this work. It is, therefore, not possible to produce a meaningful cladogram of species.

However, there is a great diversity among the species of Chrysomya, both structural and biological. This means that groups of species can be recognised within the genus. These are as follows:

Species Group A: The 'hairy' maggots: Saprophagous, facultative parasitic, predatory. e.g. Chrysomya albiceps.

Species Group B: 'Smooth' larvae, lacking a pigmented oral sclerite: Saprophagous, facultative parasitic. e.g. Chrysomya chloropyga.

Species Group C: Chrysomya bezziana, the only known obligate parasite in the genus.

Species Group D: 'Smooth' larvae with a pigmented oral sclerite, e.g. Chrysomya marginalis.

A cladogram (Fig. 334) has been tentatively constructed to show the relationships between these groups. It will be seen that only the basal dichotomy could be established fully on apomorphic grounds. The route leading to group B, in particular, is not well supported in this way. In fact, this is not surprising, since of all species-groups within the genus, this is the most primitive in overall morphology, and although it is always desirable to establish clades on the basis of apomorphies, it must not be forgotten that, when species split up, one of the two resulting lineages may remain fundamentally unchanged from the ancestral stock.

It has been assumed that the pigmentation of the oral sclerite, although probably evolved many times in the Calliphoridae, did not

evolve more than once in each genus. This view is held because those species that possess this feature have a number of other apomorphic features in common.

Finally, it is interesting to note that no obligate parasites among Calliphoridae possess pigmented oral sclerites, and even unpigmented ones are much reduced in some of these species. Furthermore, those species that are more successful than others as facultative parasites also do not have pigmented sclerites, e.g. Lucilia spp., although the less successful (as parasites) Calliphora spp. do possess pigmented sclerites.

11.6.5 The Genus Lucilia

The species of this genus studied during this work are too few and from too widely distant parts of the World to make an analysis possible. However, a few comments may be made.

The larvae of Lucilia spp. are remarkably uniform and retain a large number of primitive features. L. bufonivora possesses more derived features than most other species and these are doubtless associated with its parasitic habit. L. ampullacea is the only species known to have a pigmented oral sclerite. In the related genus Hemipyrellia (once submerged in the genus Lucilia) the two species studied both had pigmented oral sclerites. The two genera are separated mainly on the basis of the presence of long, erect, dense hairs on the supraspiracular convexity (between the posterior thoracic spiracle and the haltere) in Hemipyrellia; these are absent from Lucilia sensu stricta. I have examined this character, but it does not

seem to warrant the erection of a separate genus. It is possible that L. ampullacea is an intermediate form between the two 'genera'.

11.7 Affinities of the Calliphoridae within the Calypterata

A great deal of thought was given to the problem of setting up a cladogram of the Calypterata based on immature characters, but it was not possible to reach any strong conclusions based on a cladistic analysis. It would seem that the major groups of Calypterates are better defined in the adult stage, as is the case with the major divisions of Calliphoridae. Nevertheless, several interesting facts emerge.

The Calliphoridae and Sarcophagidae appear to have the most primitive larvae of all Calypterates, in that they most resemble the species of the vast assemblage of 'Acalypterates'. (The 'Acalypterata' are now seen as a number of separate groupings each equal in rank to the Muscoid Calypterata (Hackman and Vaisanen, 1982), but this subject is not pursued further here.) It also seems clear that the Sarcophagidae are the sister-group of the Calliphoridae, according to both adult and immature characters.

A rather surprising observation is that the Anthomyiidae also have primitive larvae and are very similar to the Calliphoridae and Sarcophagidae. This family is normally associated with the Muscidae, which have very different larvae, exhibiting a large number of apomorphic features; these include the loss of the parastomal bars, the loss (or reduction) of one mouth-hook and the frequent possession of complex, paired oral sclerites, although many species lack these latter (e.g. Musca domestica).

The Tachinidae, Oestridae, Gasterophilidae and Cuterebridae show the following apomorphic features: loss of parastomal bars, loss of dental sclerite and great enlargement of the dorsal cornu. The Hypodermatidae have effectively lost all trace of the skeleton. No Rhinophoridae were available for study, but the well-illustrated papers by Thompson (1934) and Bedding (1973) were carefully studied. These show that this family, as regards the skeleton, is very similar to Tachinidae, lacking as they do parastomal bars and dental sclerites.

These facts would seem to bracket Calliphoridae, Sarcaphagidae and Anthomyiidae together, with Rhinophoridae being grouped with Tachinidae and the other parasitic groups. Muscidae seems to stand alone; its larvae are without doubt the most advanced in the Calypterata.

The phylogeny of the Calypterates cannot be resolved with the available data. Further studies are needed. Previous work has not been of much assistance in this field. Roback (1951) discussed the evolution of the Calypterata using adult and larval morphology, but his phylogenetic tree is unsupported by evidence. A paper by Greene (1925) does little to resolve the issue.

Griffiths (1972) carried out a cladistic analysis of the whole Cyclorrhapha, with particular reference to the male post-abdomen. While this work is a very useful contribution to the subject, it is of little use in the present context, since he groups Tachinidae, Calliphoridae, Sarcophagidae, Oestridae, Gasterophilidae, Cuterebridae and Hypodermatidae under the name Tachinidae and considers them as one family. His study, therefore, does not analyse the affinities of these groups.

Finally, the affinities of one other group was considered. The Prosthetosomatinae are a group known only from larval forms, all of which are termitophilous (Silvestri, 1920). Hennig (1952, 1973) included them in the Muscidae, but later Pont (in Crosskey, 1980) transferred them to the Calliphoridae. During this study, I was able to examine one species of this group, Tetraplastocerus transvaalensis Silvestri from South Africa. The skeleton is very Calliphorid-like in appearance, bearing well-developed parastomal bars. The cuticle bears numerous segmented out-growths (Fig. 179) which in turn bear many hair-like projections. The Calliphorid, Tricyclea deemingi, another termitophilous species, possesses elongate antennae and feathery projections around the mouth, and it would seem that all these structures are adaptations to the termitophilous habit. I would, therefore, support Pont's view that they are Calliphoridae; in any case, they are certainly not Muscidae. It has been suggested (Smith, 1975) that, if these larvae are reared out to the adult stage, they would prove to be well-known species. All attempts to rear them have failed, however (Ferrar, pers. comm.).

11.8 Conclusion

It is clear from the above that many phylogenetic questions cannot be resolved using immature characters alone, especially in the area of the higher categories. Much, however, may be done on the generic and specific levels when the immature stages of more species become known. In addition, the phylogenetic analysis of adult characters should contribute a good deal of information towards a resolution of the problem.

CHAPTER TWELVE

CONCLUSION

12.1 Introduction

In the introduction to this thesis the value of studying the immature stages of blowflies was discussed, and the uses of such studies in the various fields of human activity enumerated. In this final chapter, it is proposed to set these studies further into context and to discuss certain indications for future work.

12.2 Taxonomy and Functional Morphology

It is often stated that the best or most useful taxonomic characters are non-adaptive ones. I must stress at the outset that I am strongly opposed to this point of view, for two reasons. Firstly, it is very difficult to know, at any rate during the early stages of a taxonomic study, which characters are adaptive and which are not. Charles Darwin, in the Origin of Species, (1859), wrote:

> ...we ought...to be extremely cautious in pretending to decide what structures now are, or have formerly been, of use to each species.

One hundred years later, Manton (1959) made the same point. She wrote:

> ...many of our so-called 'non-adaptive' characters of taxonomic usefulness may be no more than an admission of abysmal ignorance. Functional studies of arthropod morphology have shown the purposes of some fifty salient characters of the trunk region of myriapods, features which are diagnostic of classes and of their component orders, and which have hitherto had only a classificatory significance for us.

The second reason why I do not believe that adaptive characters are of no use in taxonomy (or vice versa), is the simple fact that very many groups are taxonomically defined on the basis of adaptive characters; the wings of bats, the flippers of seals, the dentition of Carnivores, the feathers of birds, the winglessness of fleas, the halteres of flies - all these are excellent classificatory characters for the groups in question, and yet no-one would seriously suggest that these features are non-adaptive.

The same is true on the specific level. In the Mammalian family Bathyergidae (the African Mole-Rats), two related species, the hairy mole-rat and the naked mole-rat, exist in East Africa. The first species burrows underground, but often comes to the surface. The second species behaves similarly, but rarely, if ever, comes to the surface. Clearly hairlessness in this species is an adaptive character - one which is also an excellent diagnostic character of the species.

The relevance of this discussion to the present work is obvious. Many characters of taxonomic use in immature Calliphoridae do suggest a functional adaptive significance, and it seems to me to be the taxonomist's duty to point out the possible functional significance of a character. This is especially true with characters whose functional significance is already known to us, e.g. the median area in the egg, and the mouth-hooks in the larva. Any deviations in these characters

from the 'normal' pattern surely must suggest to us a functional or adaptive significance. We should be prepared to erect hypotheses as to the possible function of these structures, and to test these hypotheses by further studies. Thus the presence of a very broad median area in the egg of Calliphora alpina and a very narrow one in that of Chrysomya putoria must suggest a possible adaptive significance. The first instar larvae of Amenia spp. possess a very reduced skeleton, and it is known that it is uterine and has no use for such a structure; it is thus an adaptive feature. The second instar possesses enormous mouth-hooks, and it is known that it is this stage that attacks the snail host; it is thus an adaptive feature too. These features are also highly diagnostic of the group.

All this does not mean that any feature that may serve to distinguish one species from another is necessarily adaptive, but I believe that one must not close one's eyes to such a possibility.

12.3 Biological Studies

In this section I would like to make a plea for further studies on the biology of the non-carrion feeding Calliphoridae, i.e. those that are associated with (or thought to be associated with) invertebrates. Remarkably little is known of the biology of the Ameniinae, and virtually nothing about the large subfamily Phumosiinae. These latter may be snail-parasites like Ameniinae, but this is only what is inferred from their larval structure (Ferrar, 1978). (The Phumosiinae are macro-larviparous, and all known larvae were dissected from females.) Of the six or seven known British

species of Pollenia only one has been studied biologically and nothing is known of the larval habitat of the other species. The large number of termitophilous species found in Africa should also repay study, as would the huge subfamily Rhiniinae (over 110 species in the Oriental region alone); an indication of our lack of knowledge is that we have substantial biological data for only a single Rhiniine species (Stomorhina lunata) and that from a paper published in 1935 (Cuthbertson).

The Calliphoridae are usually thought of as primarily carrion-breeders, and yet the majority of World species do not come to carrion traps. What, then, are their breeding habitats? Clearly, a rich field awaits the future researcher.

12.4 Phylogeny

In Chapter 11 the value of adult studies in phylogenetic research was stressed. I would like here to mention briefly two other fields of research.

Comparative biochemical data is almost totally lacking for Calliphorids. There is no doubt that such data would make a powerful tool in future phylogenetic research. For example Irwin (1976) used haemolymph proteins to construct an electrophoretic key for the Chironomidae of Lough Neagh in Northern Ireland.

The second field of research is genetics. This was briefly touched upon above (11.4.5), but I would like to point out here that the many studies on Drosophila genetics have shed much light on the relationships between the species (e.g. Bodmer and Ashburner, 1984).

However, I believe a word of caution is needed, for the following reason: Close genetic relationship does not necessarily imply close phylogenetic relationship. In a group of three species A, B and C, B may be more closely related genetically to C, but more closely related phylogenetically to A.

This idea is best illustrated by reference to three actual species, say, the salmon, the lungfish and the cow (Fig. 336). No-one will disagree with the phylogenetic hypothesis represented in the diagram. The lungfish is clearly more closely related genetically to the salmon. But it shares a more recent common ancestor with the cow and therefore, it is more closely related to it phylogenetically than it is to the salmon. The reason that many phylogeneticists find this idea unacceptable is because they tend to ignore the events occurring after a species splits up (point X on the diagram). What has occurred after the split in this case is that the lungfish has remained virtually unchanged since point X, whereas the other line evolved at a much faster rate to produce the cow.

12.5 The Immature Stages of other Cyclorrapha

The present study has shown that many characters do exist whereby identification of immature stages may be performed. The comparative studies on other Cyclorrhapha carried out during the phylogenetic part of the present study have shown that many characters exist that may reliably separate species of the families Drosophilidae and Sphaeroceridae, and I have used these characters successfully with material from archaeological deposits.

It is highly probable that the biometric methods discussed above (5.8) would be found useful in dealing with 'Acalypterate' larvae. At present, even the families of Cyclorrhapha are difficult or impossible to identify in the larval stages. In Teskey's (1981) recent key, up to thirteen different families of Cyclorrhapha key out at the same point.

Identification of the immature stages of Cyclorrhapha should greatly facilitate studies on the biology of these most interesting insects.

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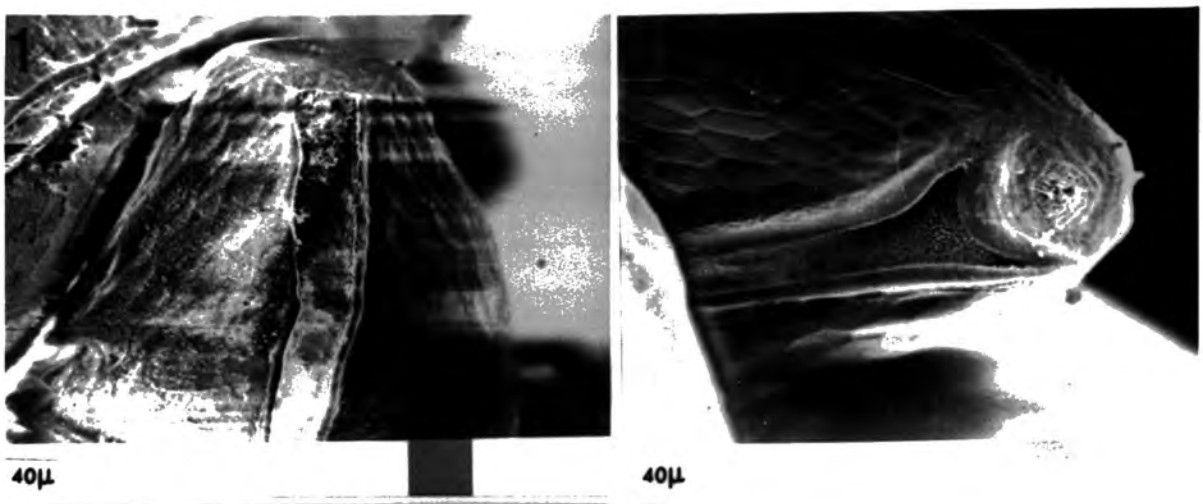
Figs. 1-8. Eggs. (1) Calliphora vicina, (2) Calliphora vomitoria, (3) Calliphora uralensis, (4) Calliphora alpina, (5) Calliphora subalpina, (6) Calliphora loewi, (7) Calliphora quadrimaculata, (8) Calliphora stygia.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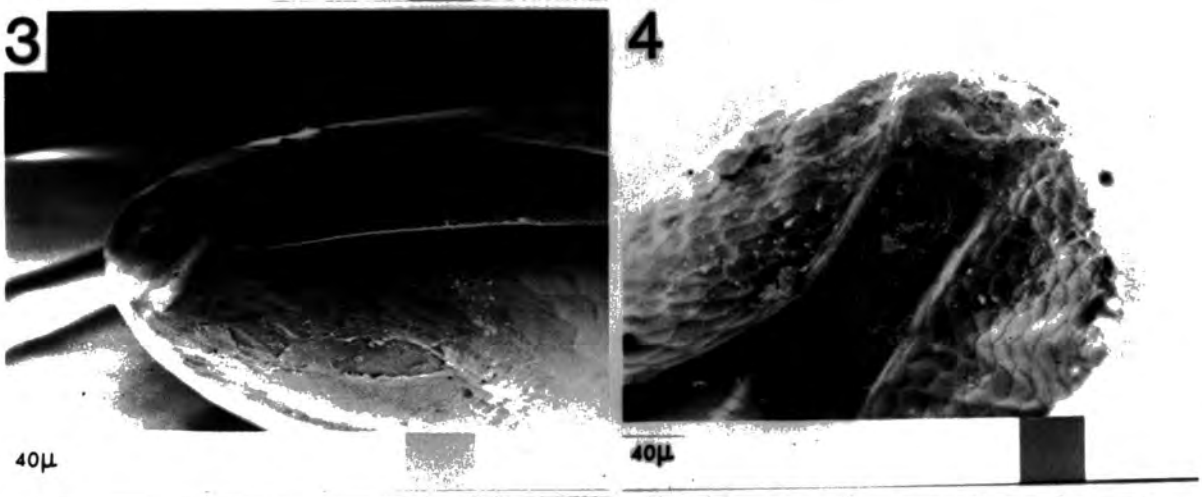
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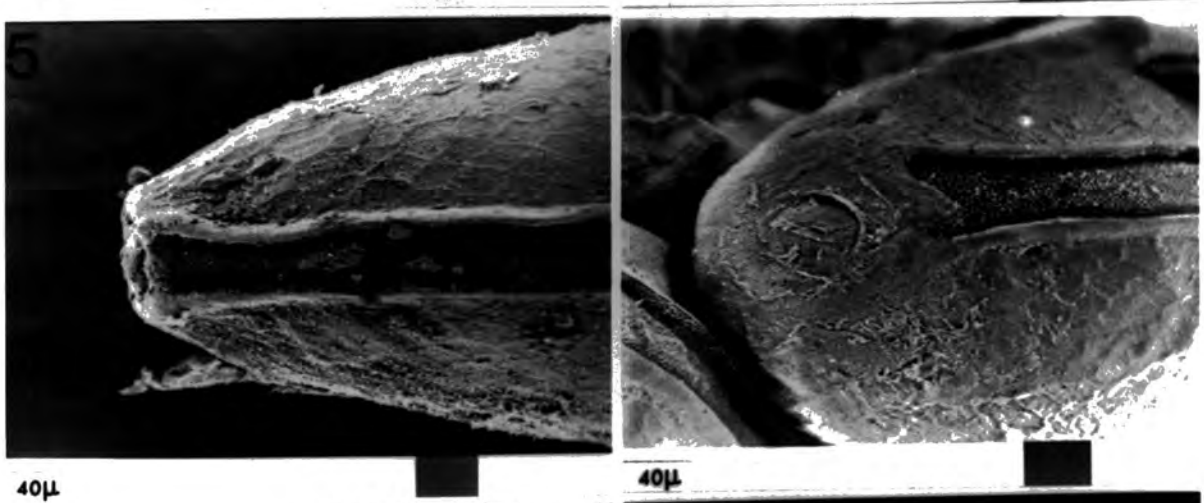
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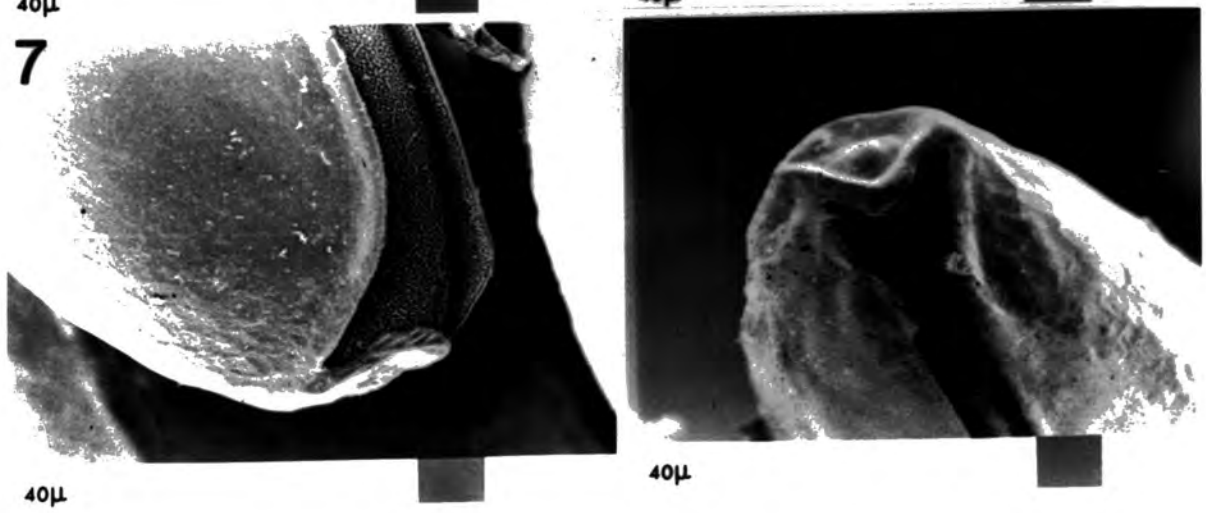
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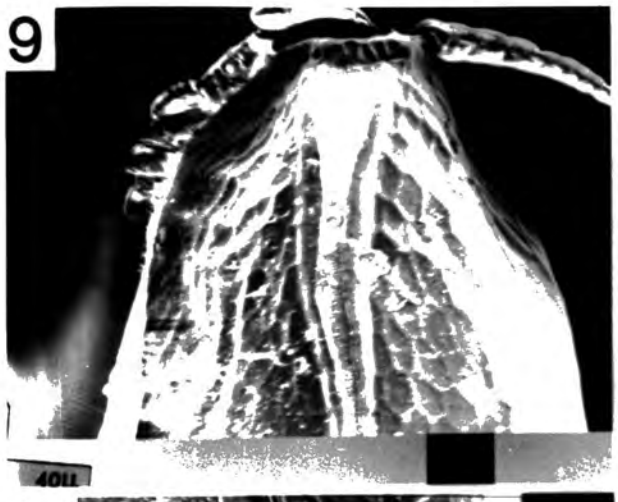
Figs. 9-16. Eggs. (9) Calliphora ochracea, (10) Calliphora stygia, (11) Calliphora ochracea (showing break in median area and plastron crater), (12) Calliphora alpina, (13) Cynomya mortuorum, (14) Triceratopyga calliphoroides, (15) Lucilia sericata, (16) Lucilia sericata.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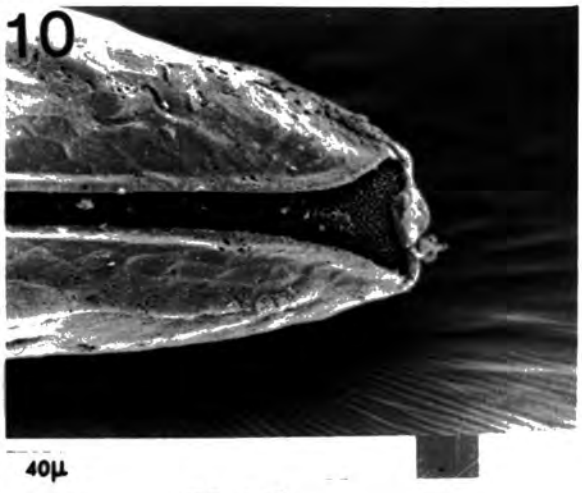
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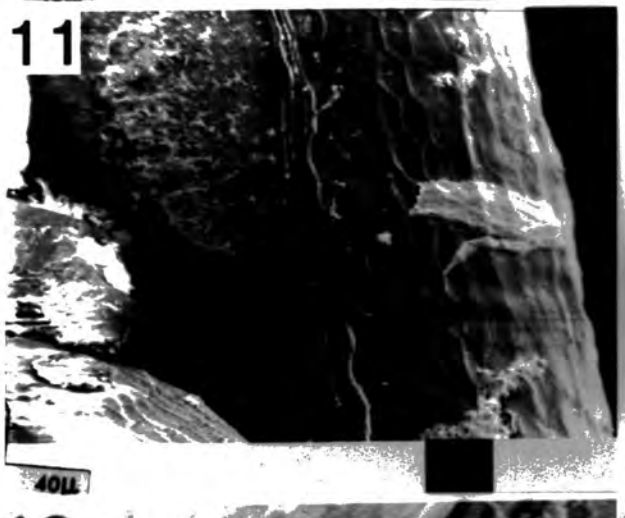
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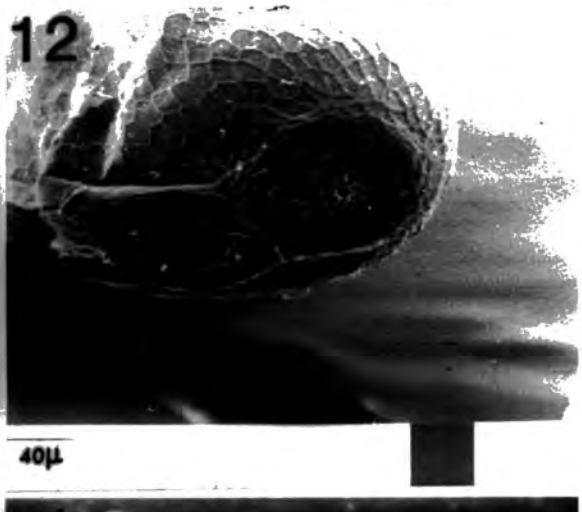
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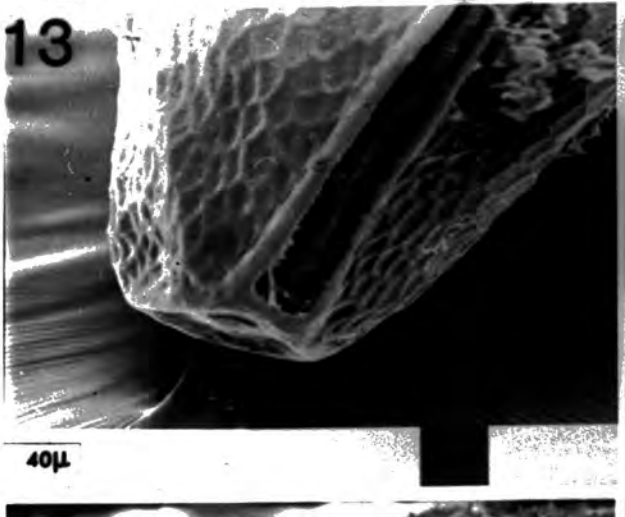
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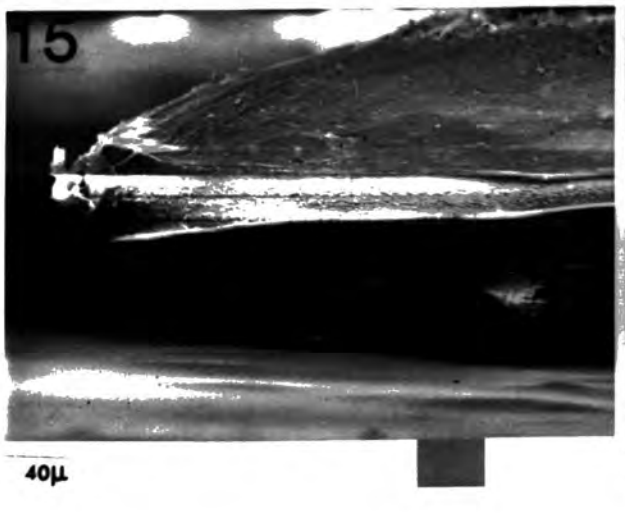
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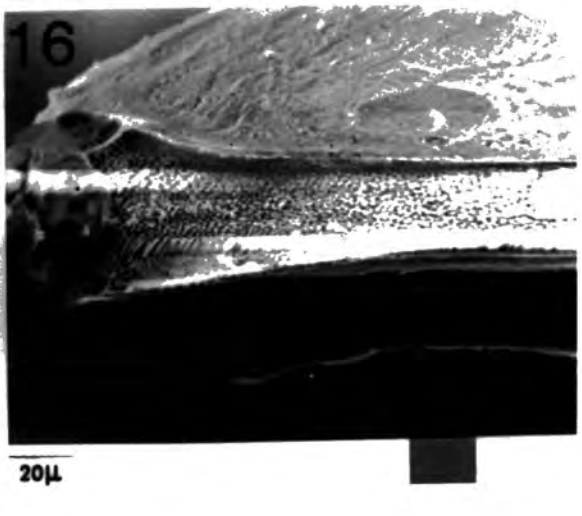
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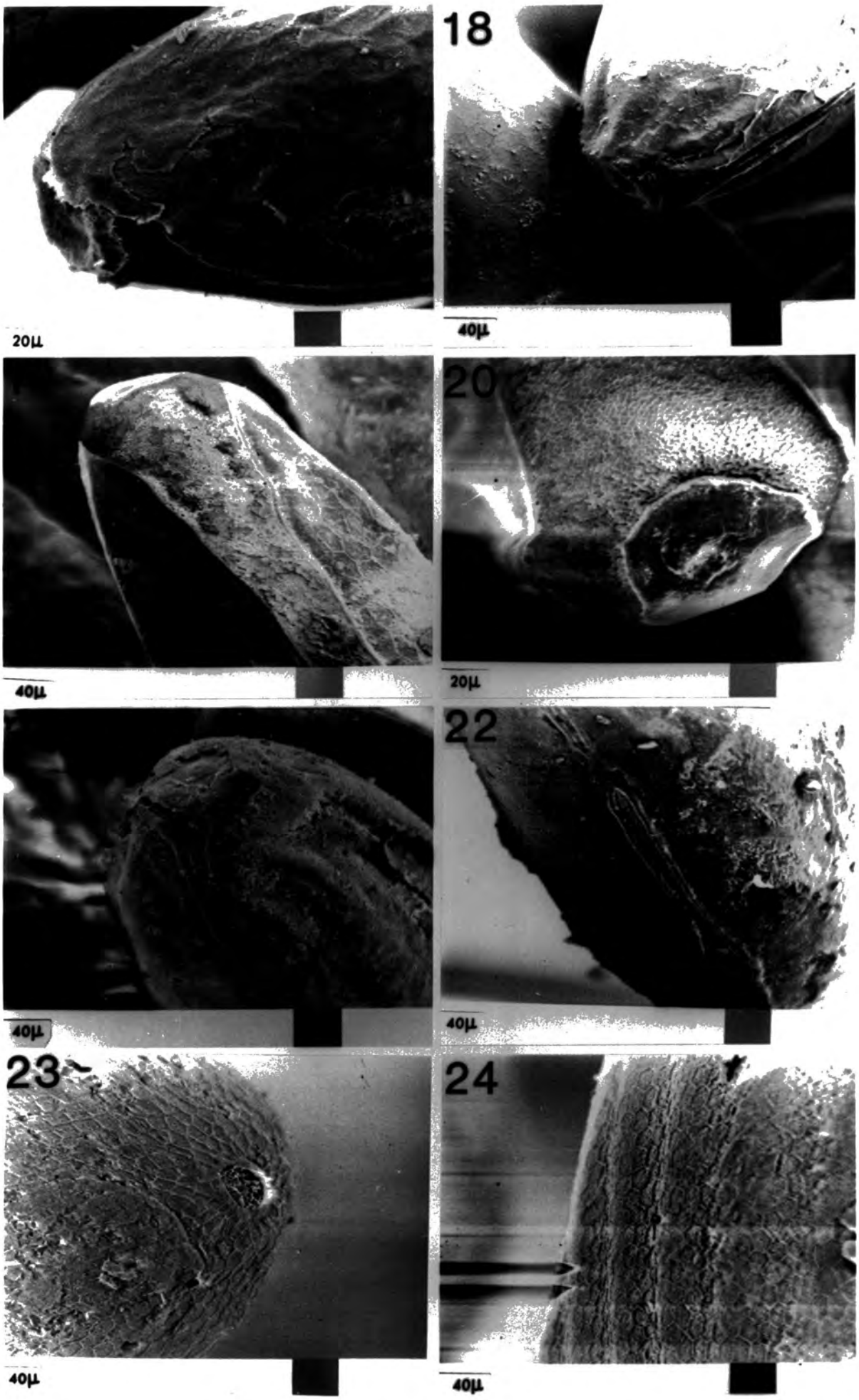
Figs. 17-24. Eggs. (17) Hemipyrellia ligurriens, (18) Phormia regina, (19) Chrysomya bezziana, (20) Chrysomya bezziana, (21) Chrysomya putoria, (22) Chrysomya putoria (showing break in median area), (23) Auchmeromyia luteola, (24) Auchmeromyia luteola (showing ridges).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Figs. 25-32. Eggs. (25) Protocalliphora azurea, (26) Protocalliphora azurea, (27) Protocalliphora azurea (median area), (28) Calliphora quadrimaculata (median area), (29) Calliphora vicina (showing hatching pleat breaking), (30) Calliphora vomitoria (showing chorion reticulations), (31) Calliphora vicina (T.S.), (32) Calliphora vicina (T.S.). Figs. 31 and 32 (x330).


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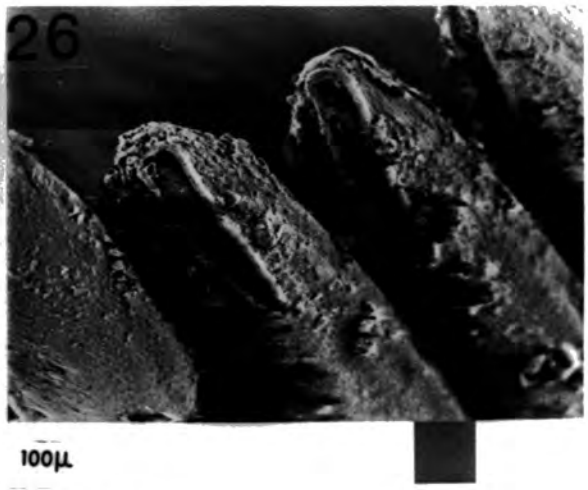
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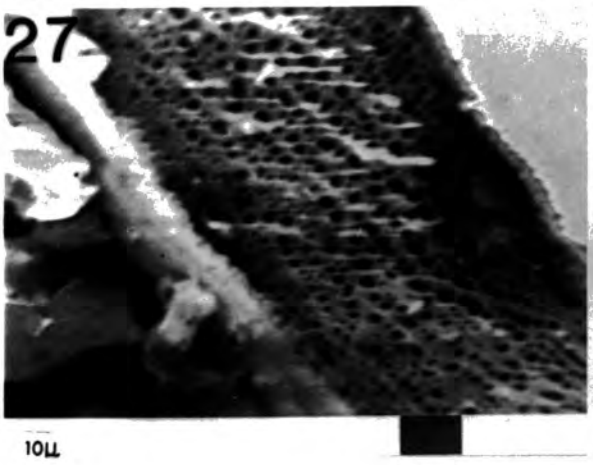
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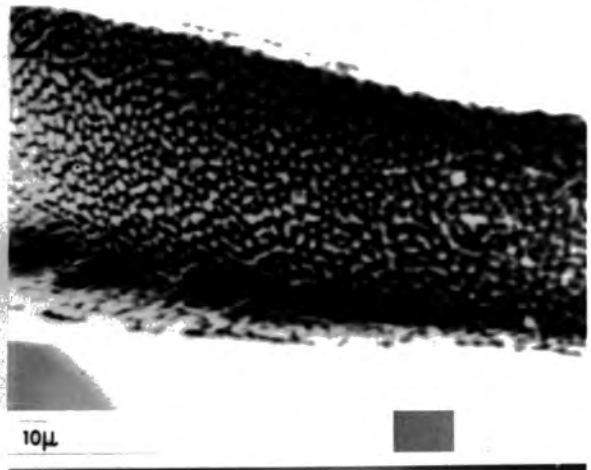
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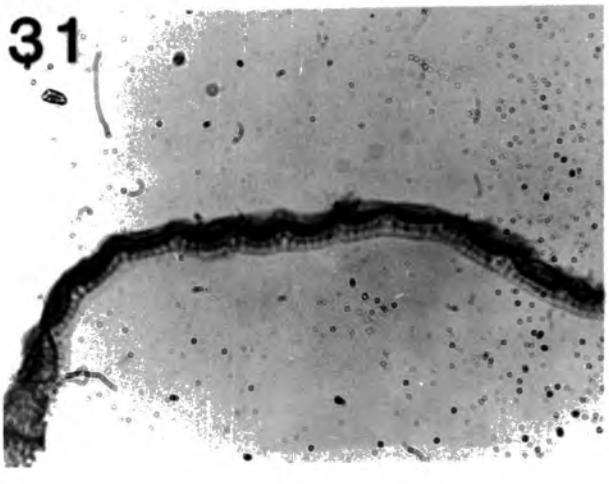
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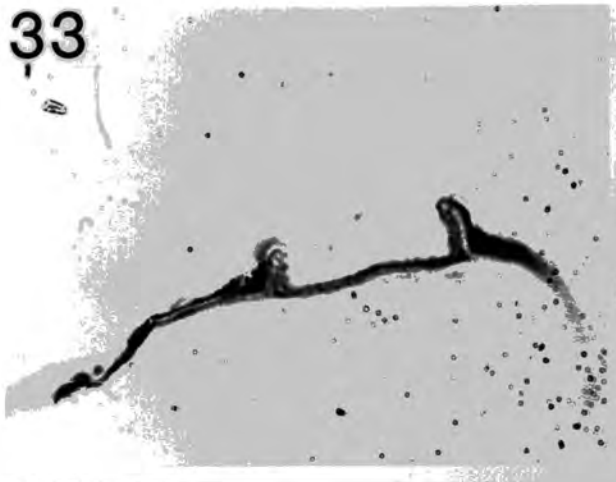
Figs. 33-39. Eggs. (33) Lucilia sericata (T.S.), (34) Cynomya mortuorum (T.S.), (35) Phormia terraenovae (T.S.), (36) Chrysomya bezziana (T.S.), (37) Muscina pabulorum, (38) Muscina pabulorum, (39) Calliphora vicina (posterior end). Figs. 33-36 (x330).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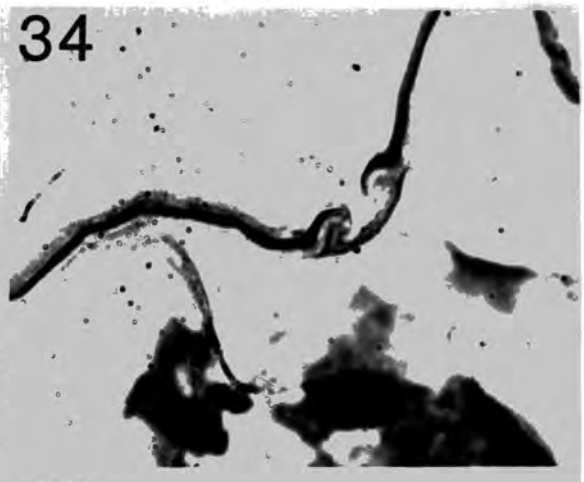
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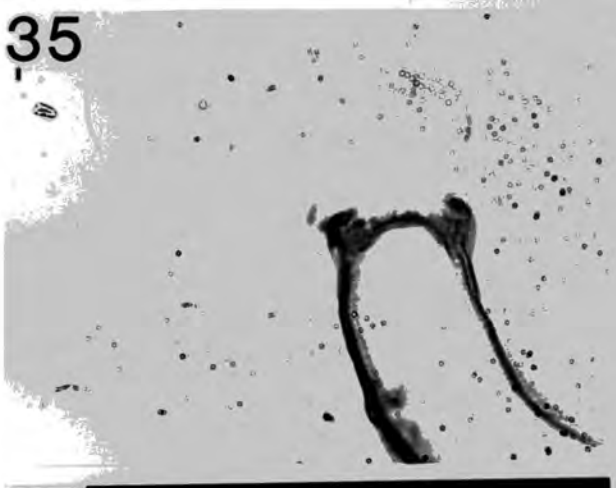
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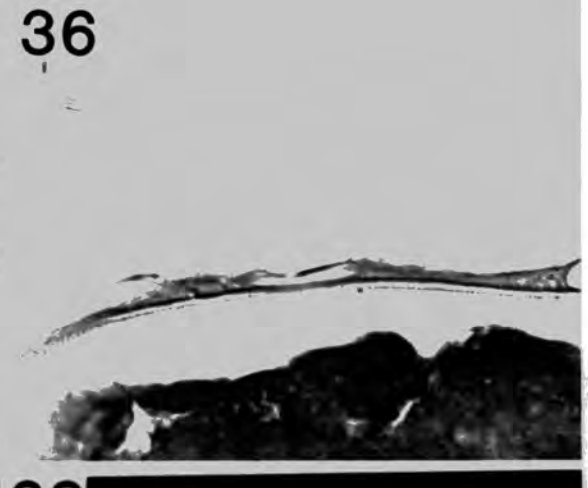
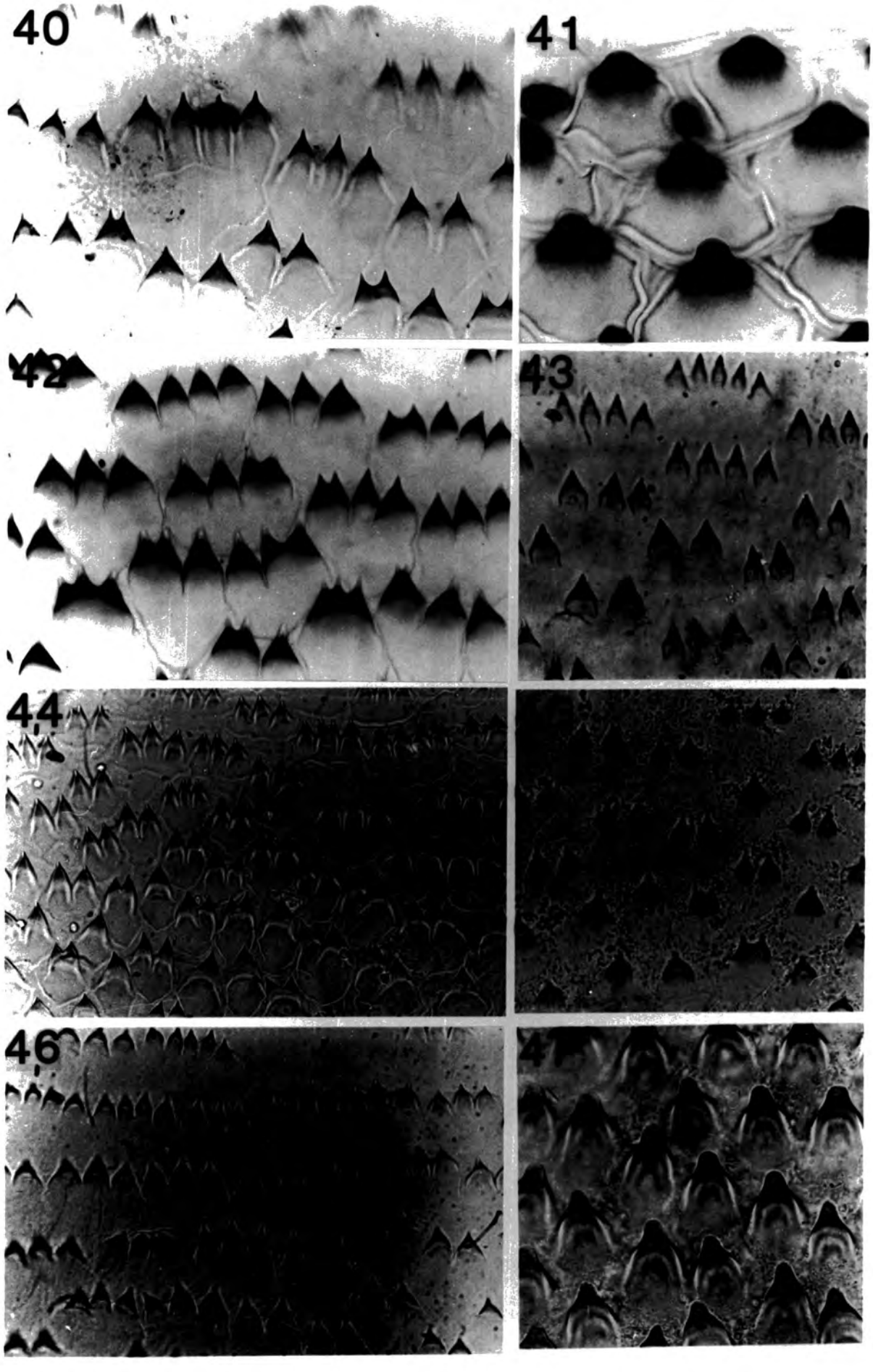

36


37
40µ

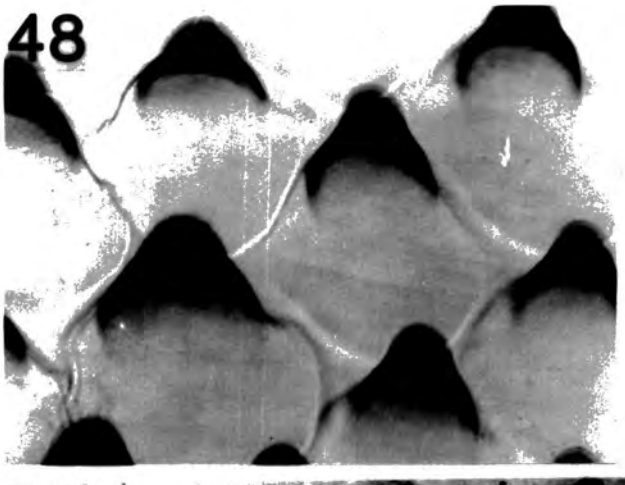

38
100µ


39
40µ

Figs. 40-47. Spines (x330). (40) Calliphora vicina, (41) Calliphora vomitoria, (42) Calliphora uralensis, (43) Calliphora alpina, (44) Calliphora subalpina, (45) Calliphora loewi, (46) Calliphora augur, (47) Calliphora stygia.


40
41
42
43
44
46

Figs. 48-55. Spines (x330). (48) Calliphora quadrimaculata, (49) Calliphora hortona, (50) Calliphora croceipalpis, (51) Calliphora lata, (52) Calliphora terraenovae, (53) Cynomya mortuorum, (54) Aldrichina grahami, (55) Hemipyrellia ligurriens.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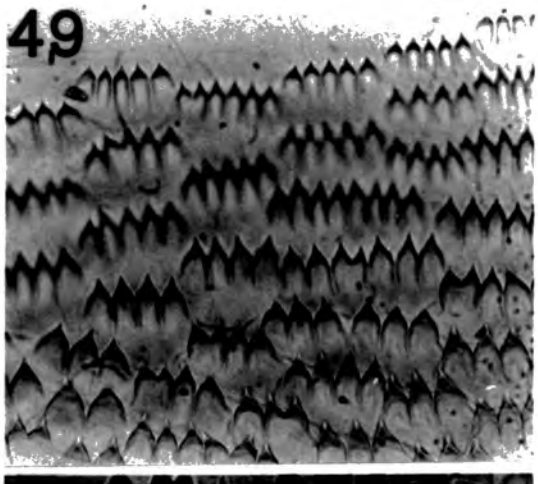
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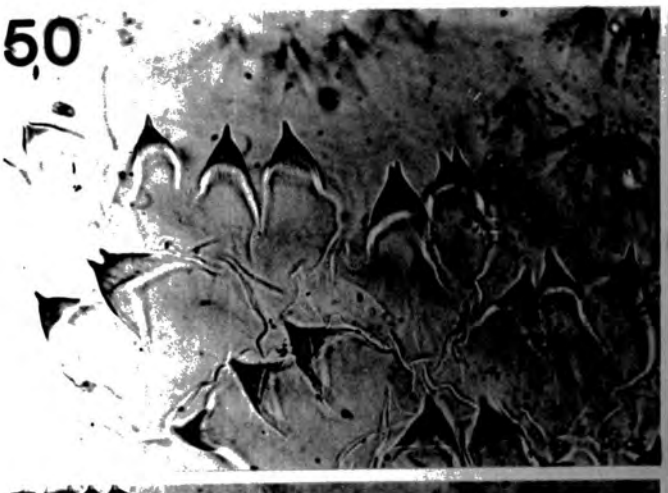
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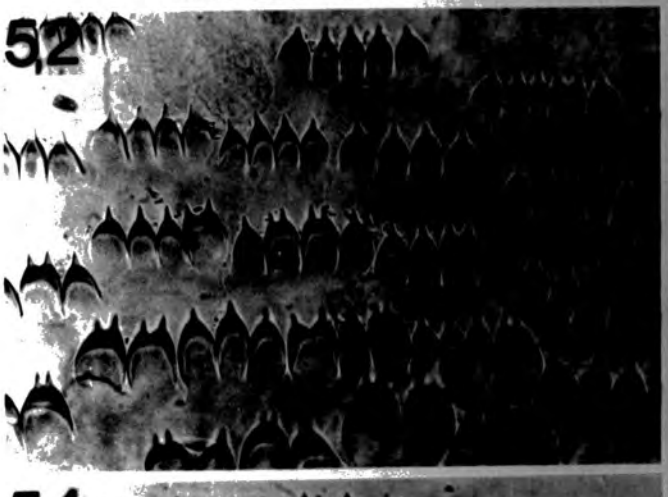
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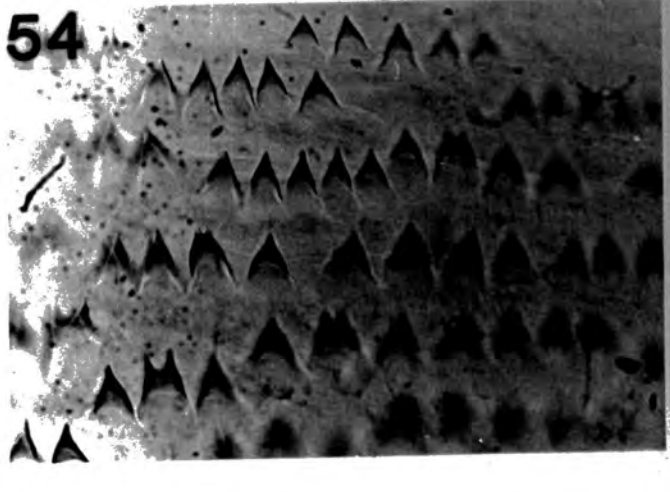
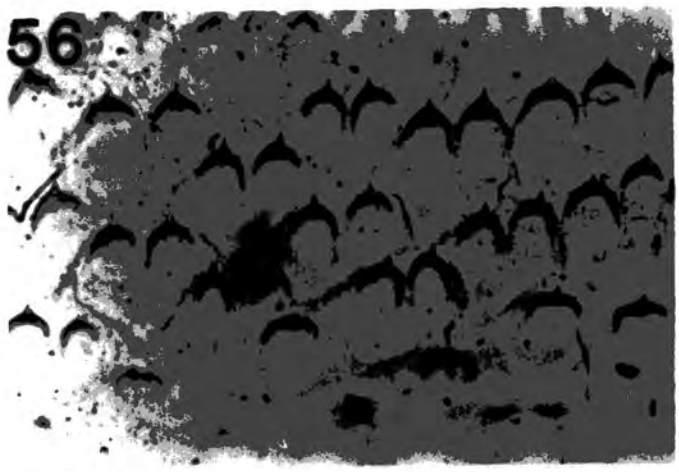
53


54


55

Figs. 56-63. Spines (x330). (56) Lucilia sericata, (57) Lucilia bufonivora, (58) Chrysomya marginalis, (59) Chrysomya megacephala, (60) Chrysomya chloropyga, (61) Chrysomya putoria, (62) Chrysomya pinguis, (63) Chrysomya bezziana.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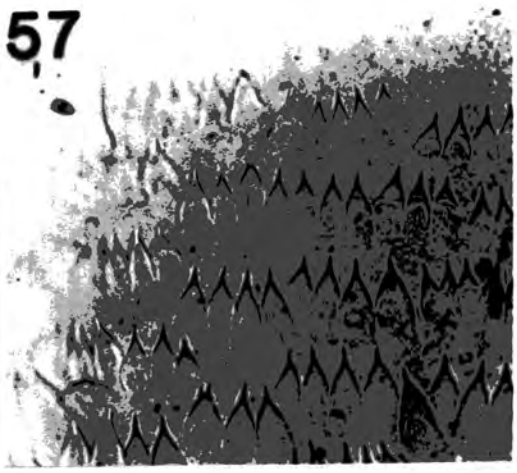
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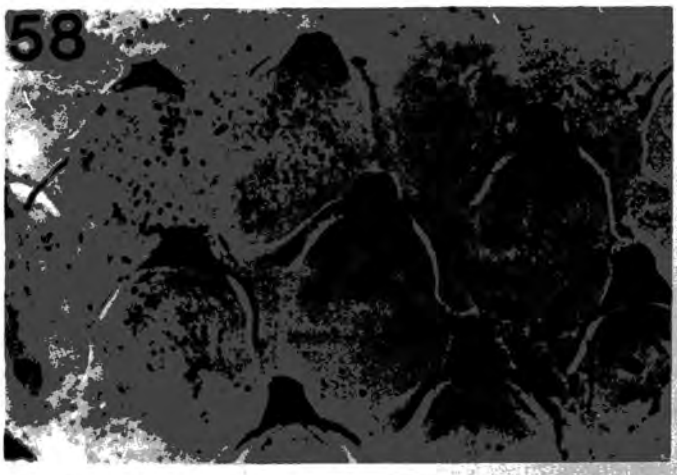
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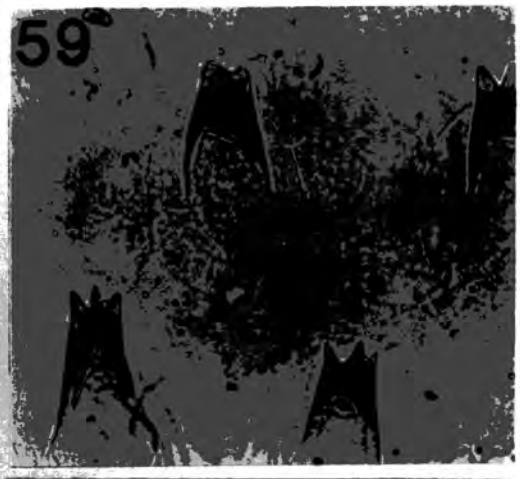
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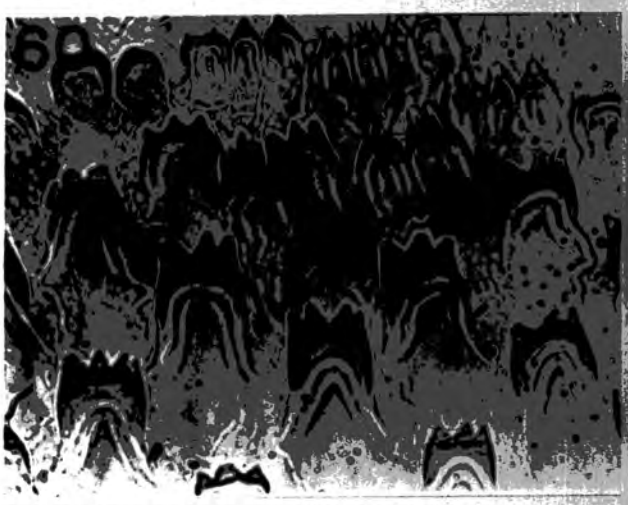
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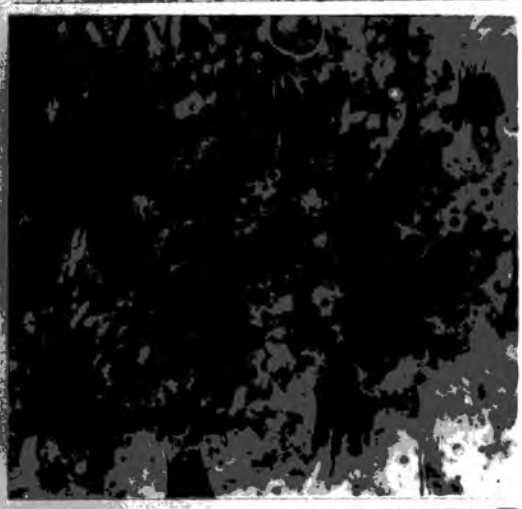
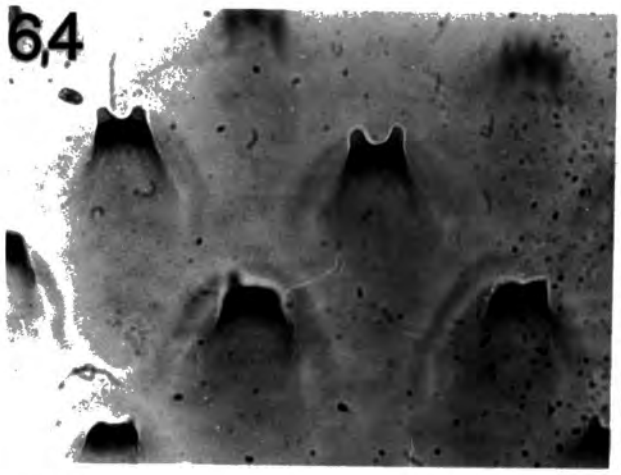



62


63

Figs. 64-71. Spines. (64) Cochliomyia macellaria (x330), (65) Cochliomyia hominivorax (x330), (66) Phormia regina, (67) Protocalliphora azurea, (68) Protocalliphora azurea (sucker hairs, x330), (69) Phormia terraenovae, (70) Amenia imperialis (2nd instar, x330), (71) Chrysomya albiceps.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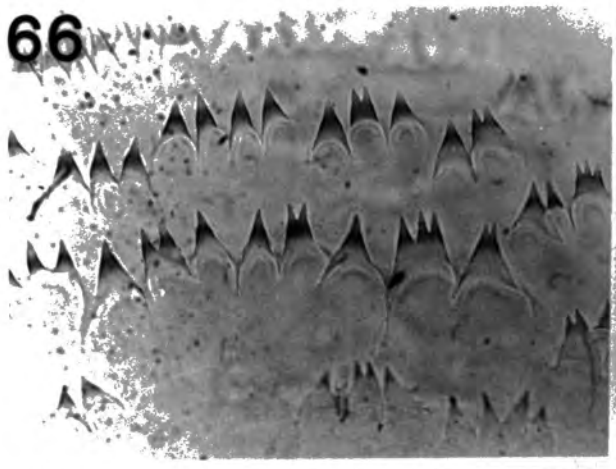
65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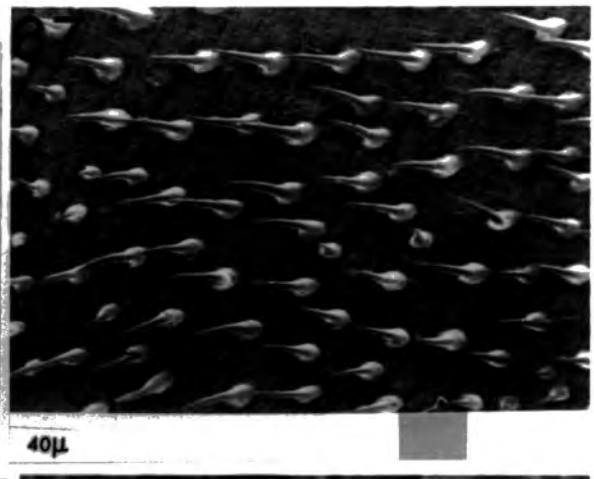
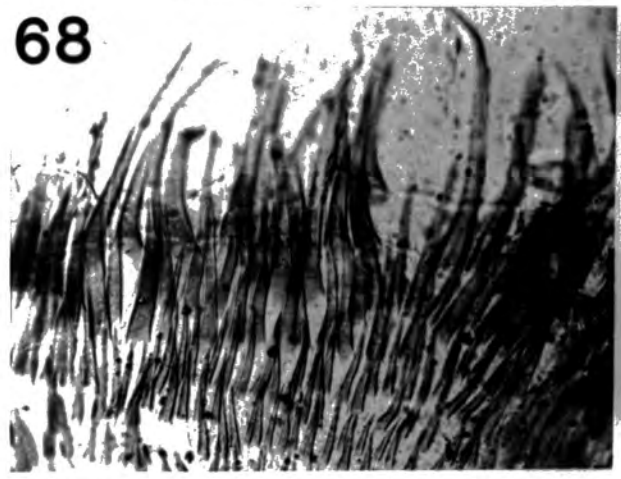
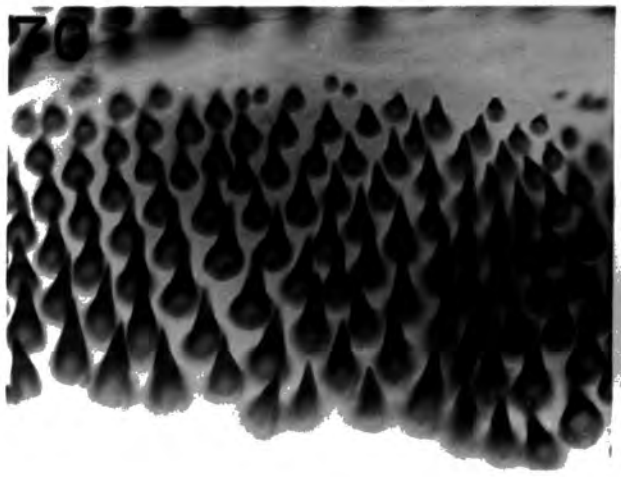

40µ


68


20µ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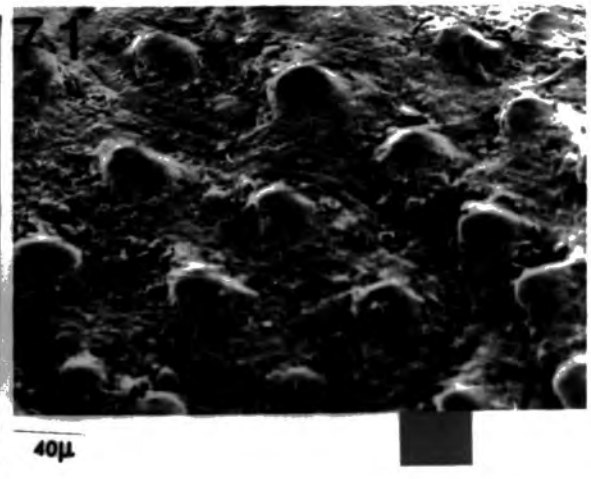
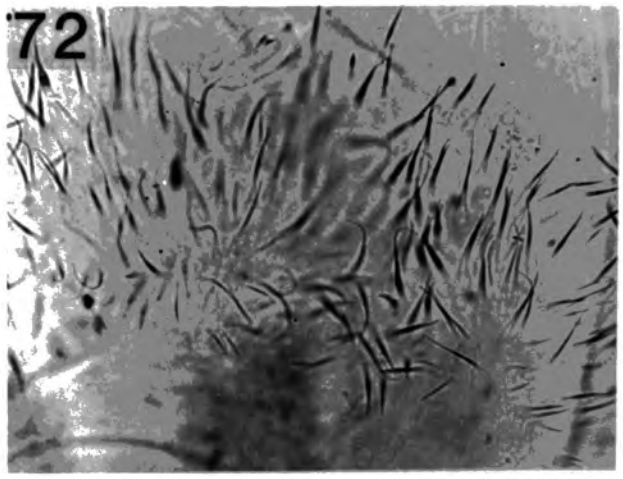

71
40µ

Figs. 72-79. (72) Posterior hairs on first instar Calliphora vicina (x500), (73) Posterior hairs on first instar Calliphora vomitoria (x500), (74) Posterior hairs on first instar Lucilia sericata (x500), (75) Posterior hairs on first instar Calliphora vicina, (76) Spines of Cordylobia ruandae (x330), (77) Spines of Lucilia sericata (cross-section, x400), (78) Pupal respiratory horn of Calliphora vicina, (79) Pupal respiratory horn of Calliphora vomitoria.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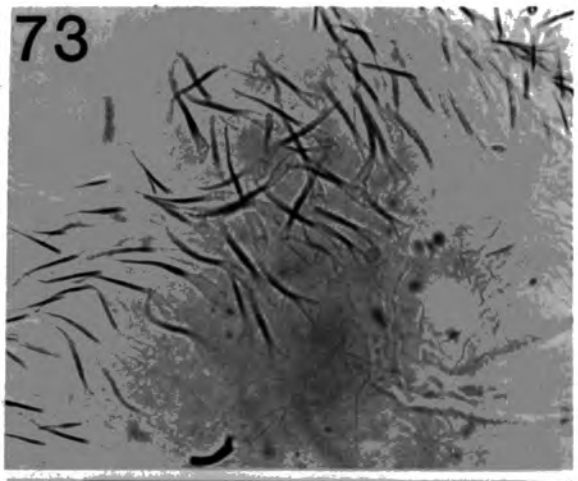
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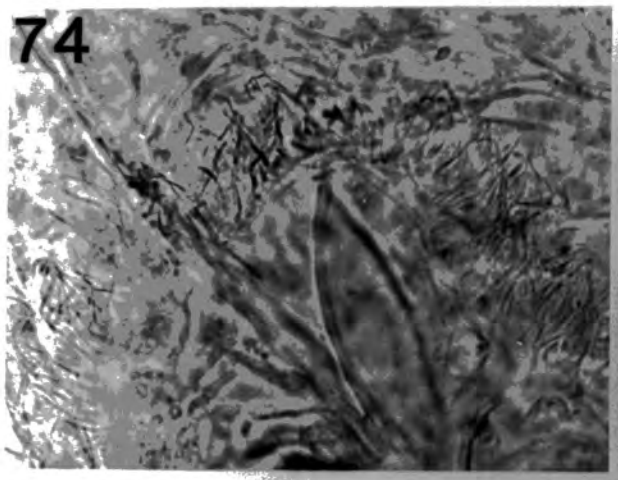
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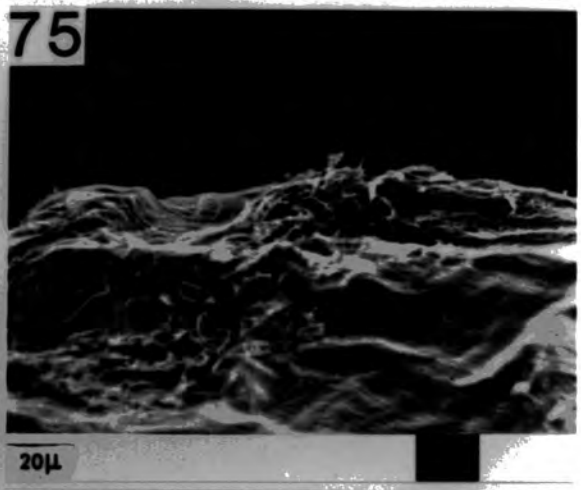
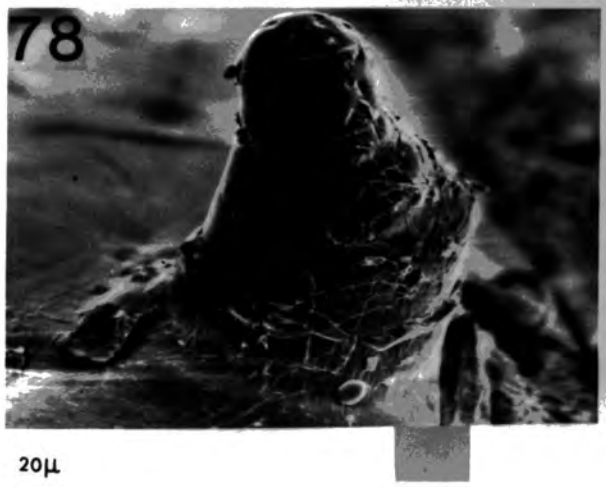
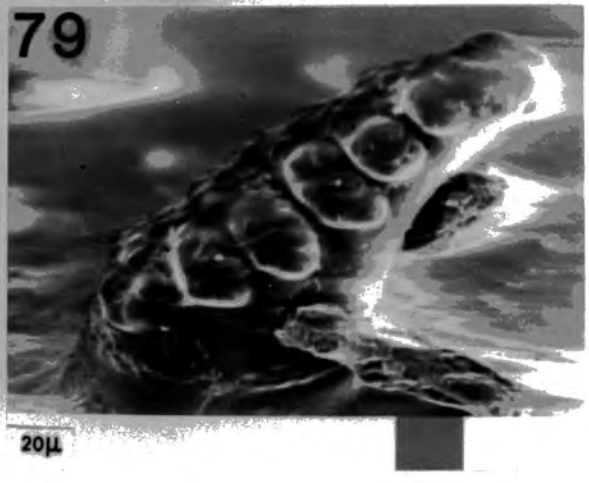

75
20μ

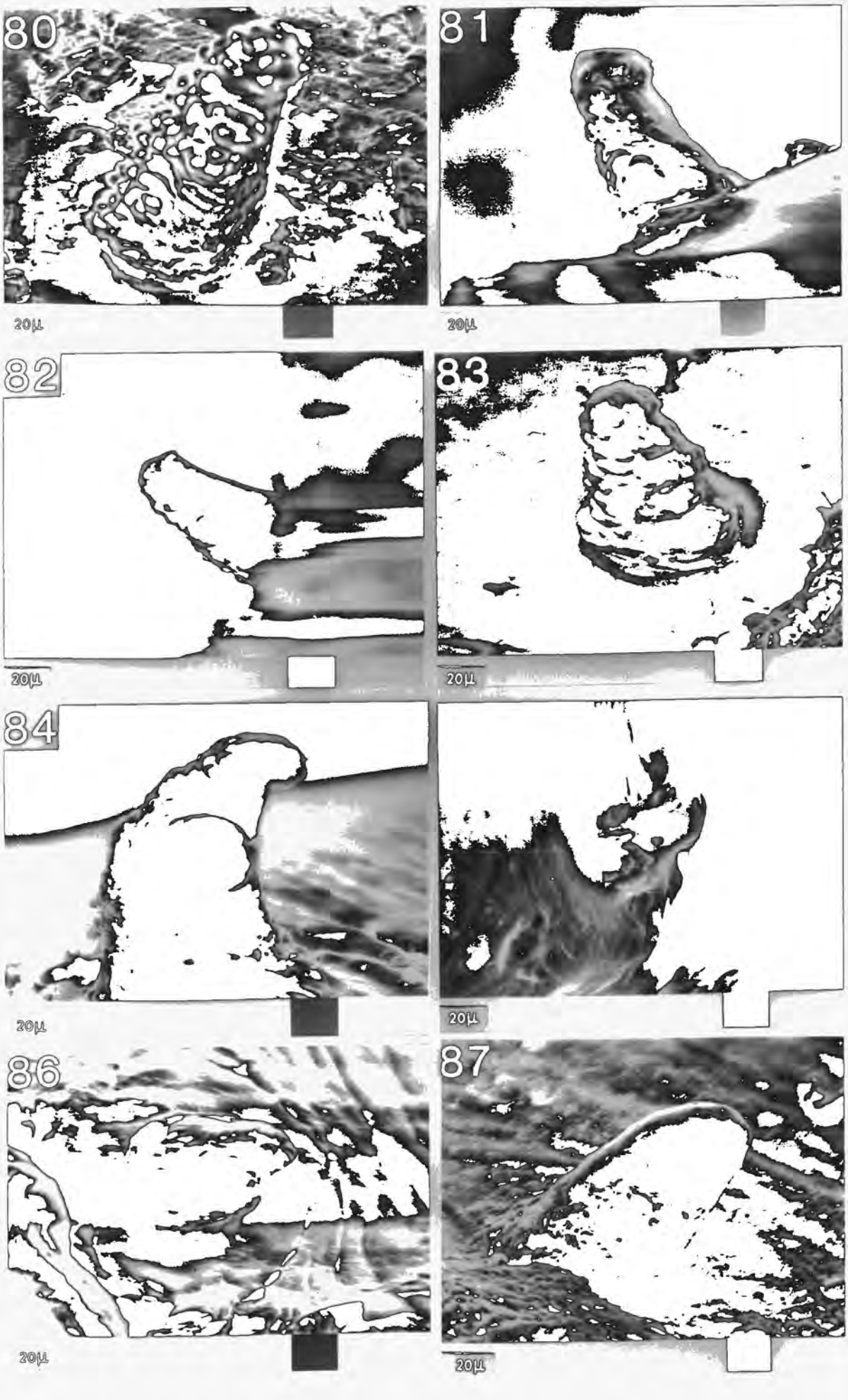

76

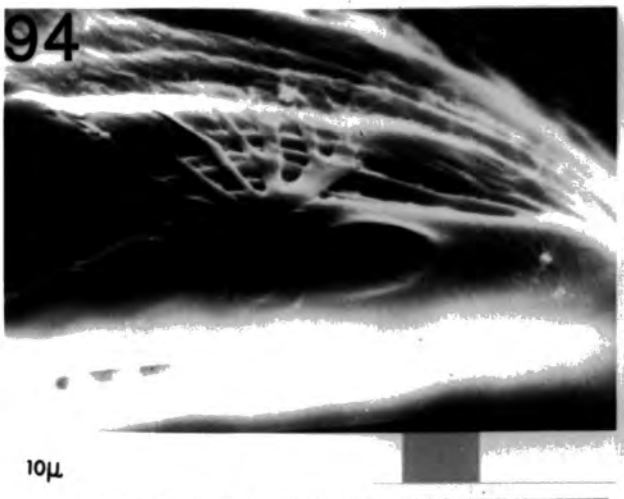

77

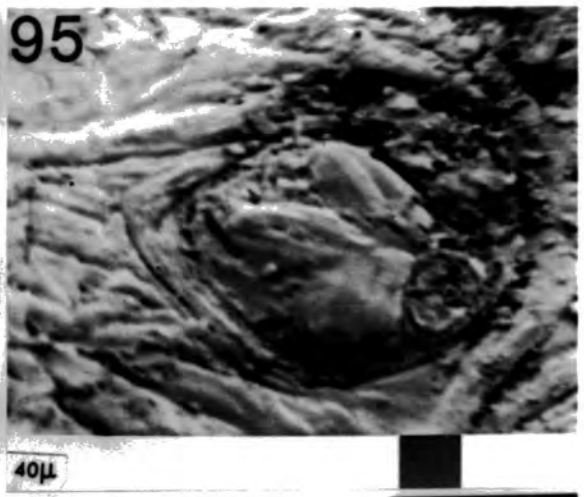

78
20μ

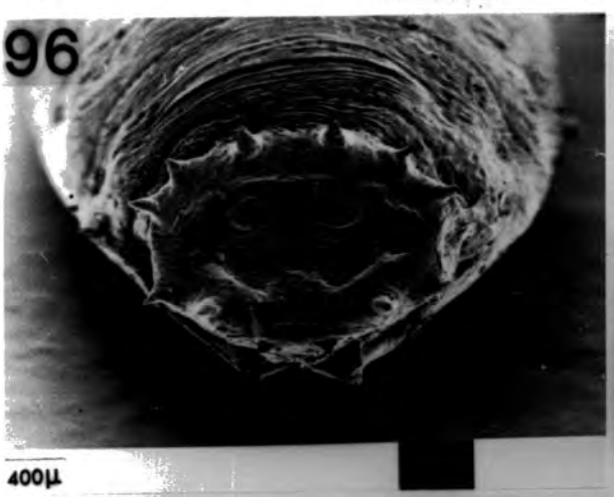

79
20μ

Figs. 80-87. Pupal respiratory horns. (80) Calliphora uralensis, (81) Calliphora alpina, (82) Calliphora subalpina, (83) Calliphora loewi, (84) Cynomya mortuorum, (85) Lucilia sericata, (86) Phormia terraenovae, (87) Chrysomya megacephala.


80
20μ
81
20μ
82
20μ
83
20μ
84
20μ
20μ
86
20μ
87
20μ

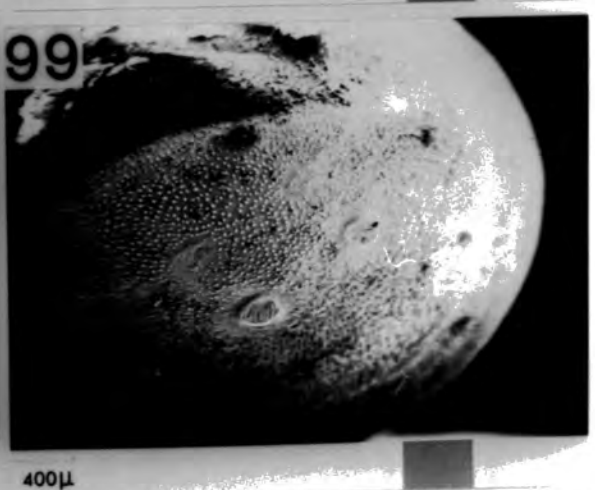

94
10μ


95
40μ

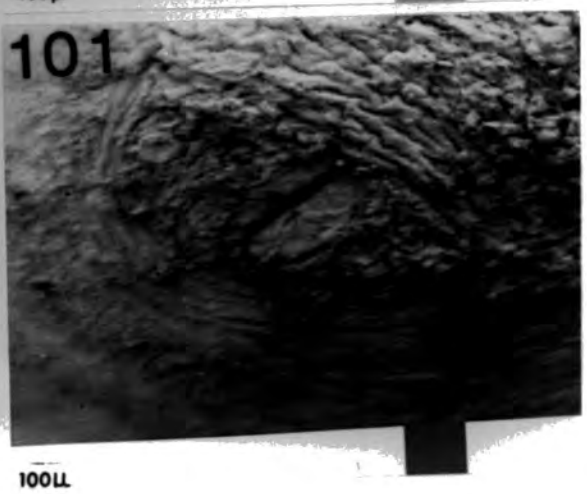

96
400μ


97
400μ

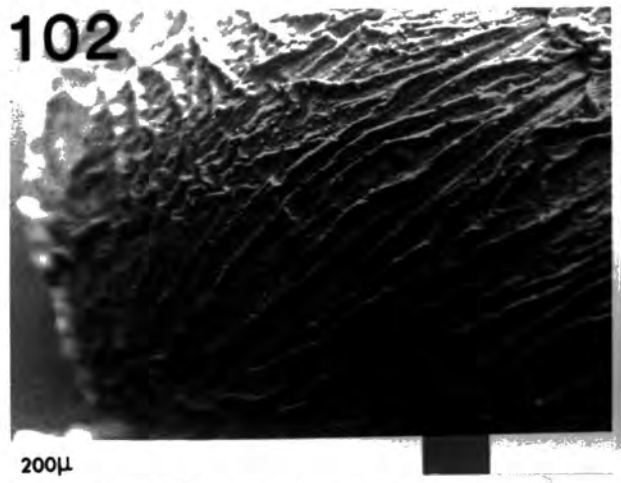

98
400μ

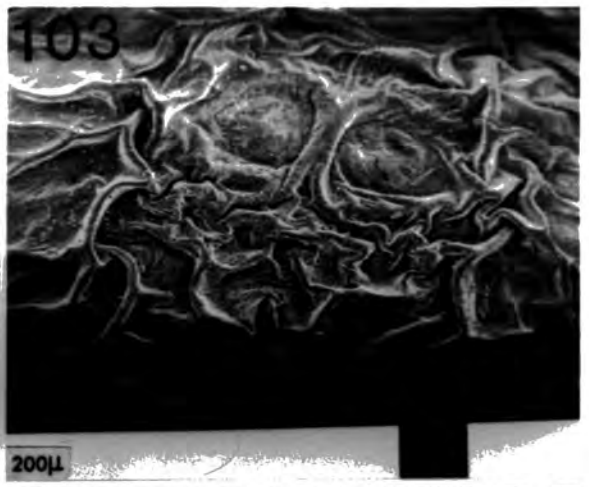

99
400μ


100
200μ

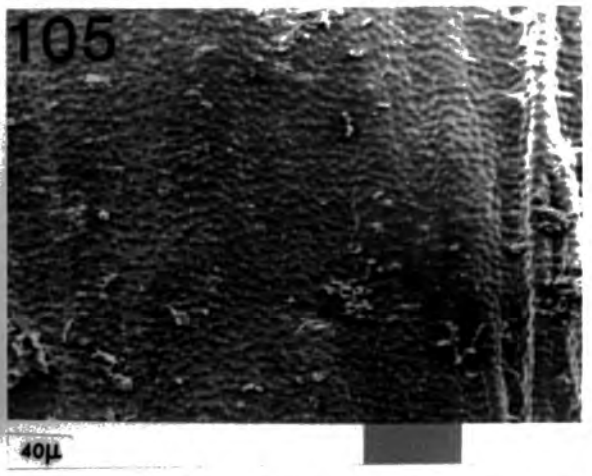

101
100μ

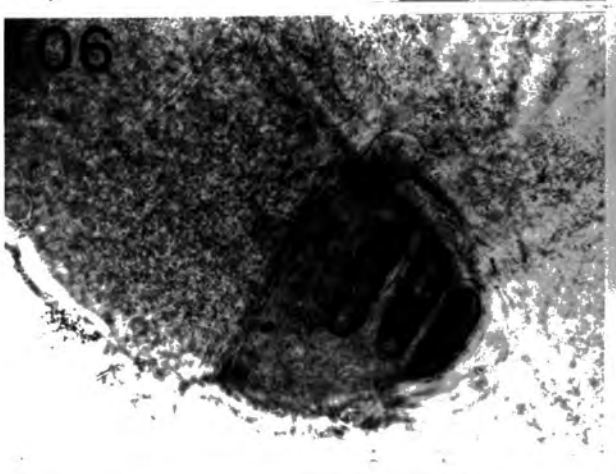
Figs. 102-109. (102) Auchmeromyia luteola puparium, (103) Cordylobia anthropophaga puparium, (104) Calliphora vomitoria spines, (105) Calliphora alpina cuticular structure, (106) Auchmeromyia luteola posterior spiracle (x330), (107) Calliphora vicina anterior spiracle, (108) Calliphora vicina papilla P_1, (109) Calliphora vicina papilla P_4.


102
200µ


103
200µ


104
40µ


105
40µ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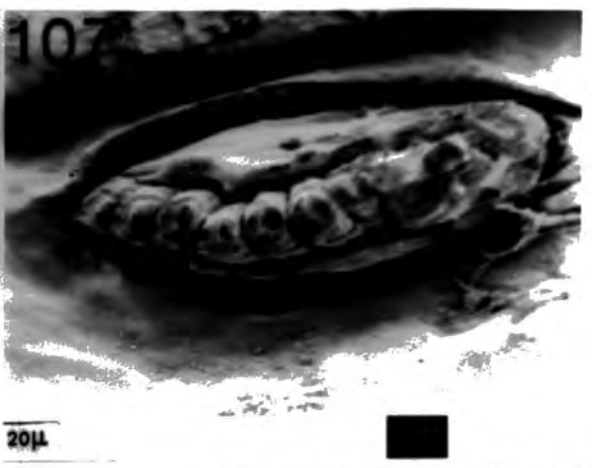
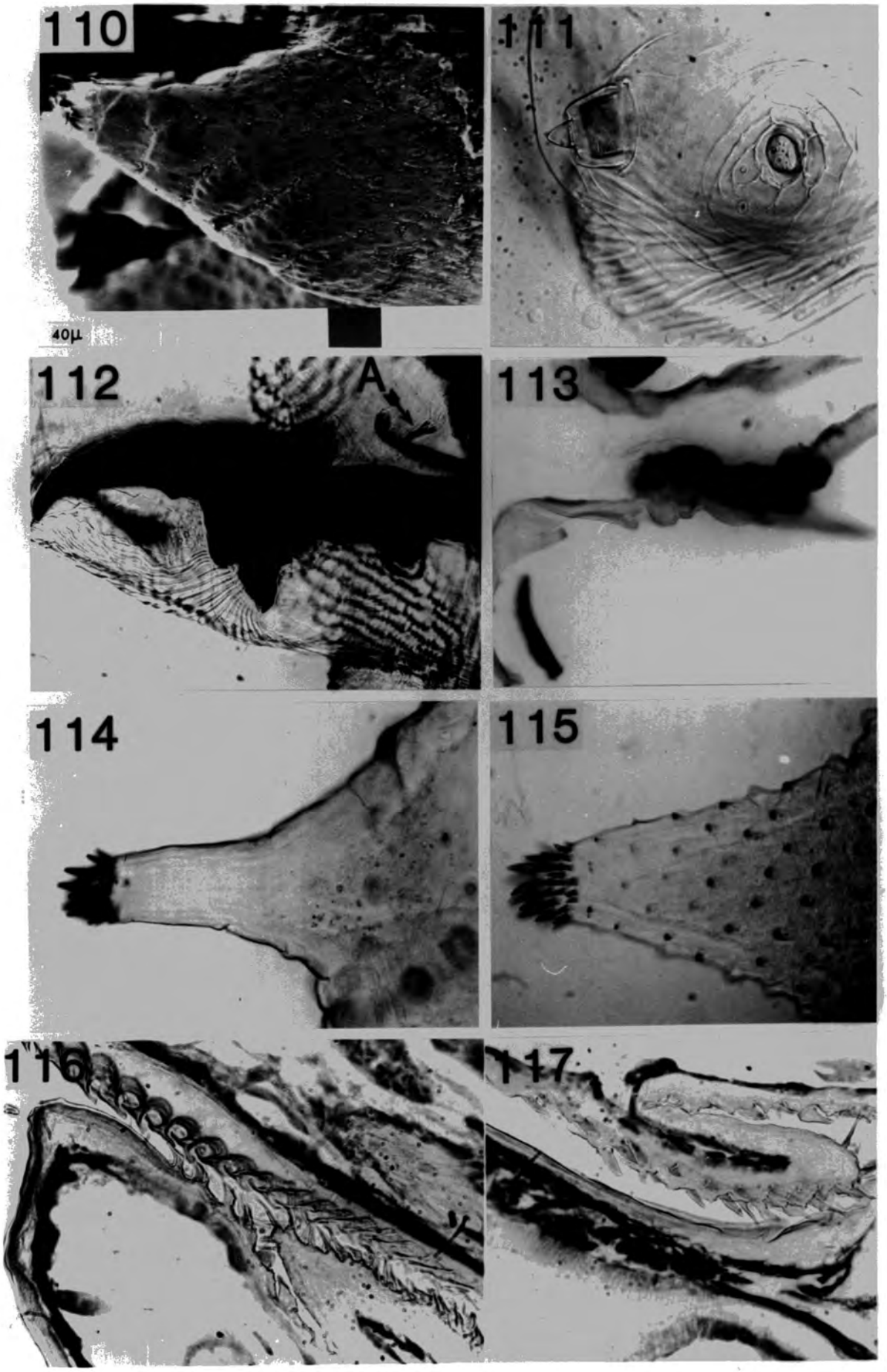

107
20µ

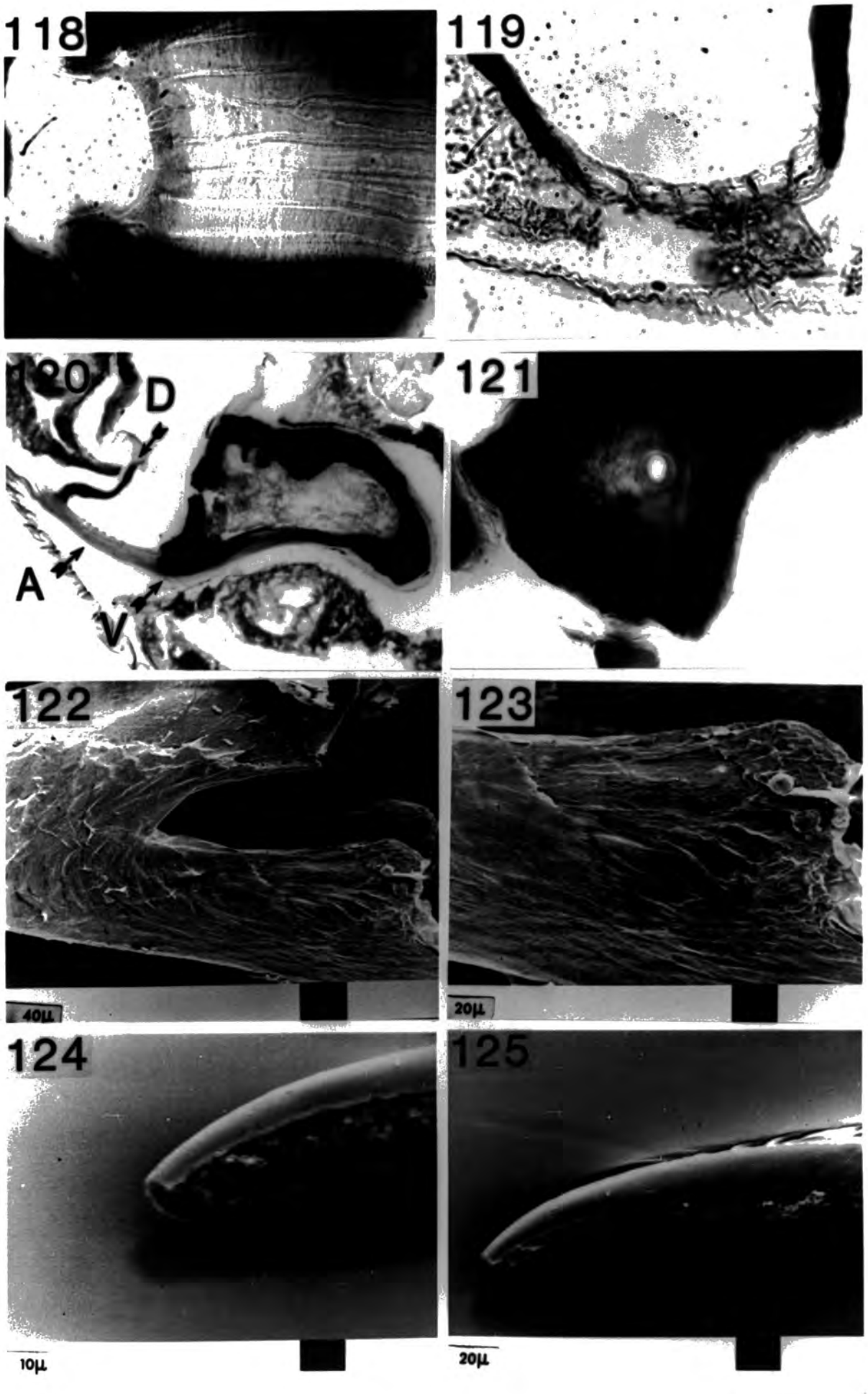

108
40µ


109
40µ

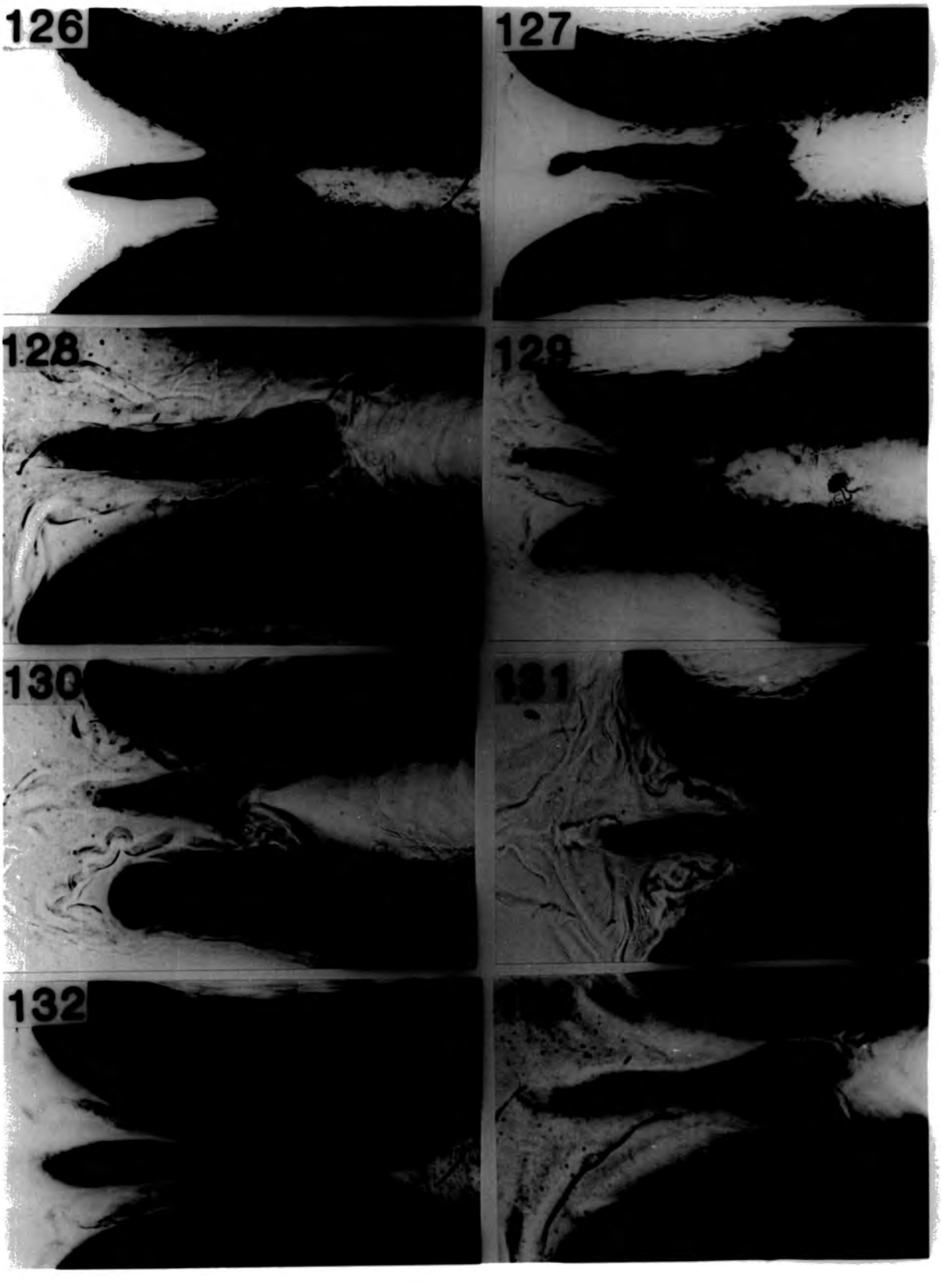
Figs. 110-117. (110) Calliphora vicina papilla P_5, (111) Chrysomya marginalis anterior sensory papillae (x330), (112) Calliphora vomitoria aciculae (A) (x150), (113) Calliphora vomitoria oral sclerite (x330), (114) Chrysomya albiceps process 1 (x200), (115) Chrysomya rufifacies process 1 (x200), (116) Calliphora vomitoria (L.S.) showing tongue-like organ (x330), (117) Same as (116) showing whole tongue-like organ.


110
111
40µ
112
A
113
114
115
116
117

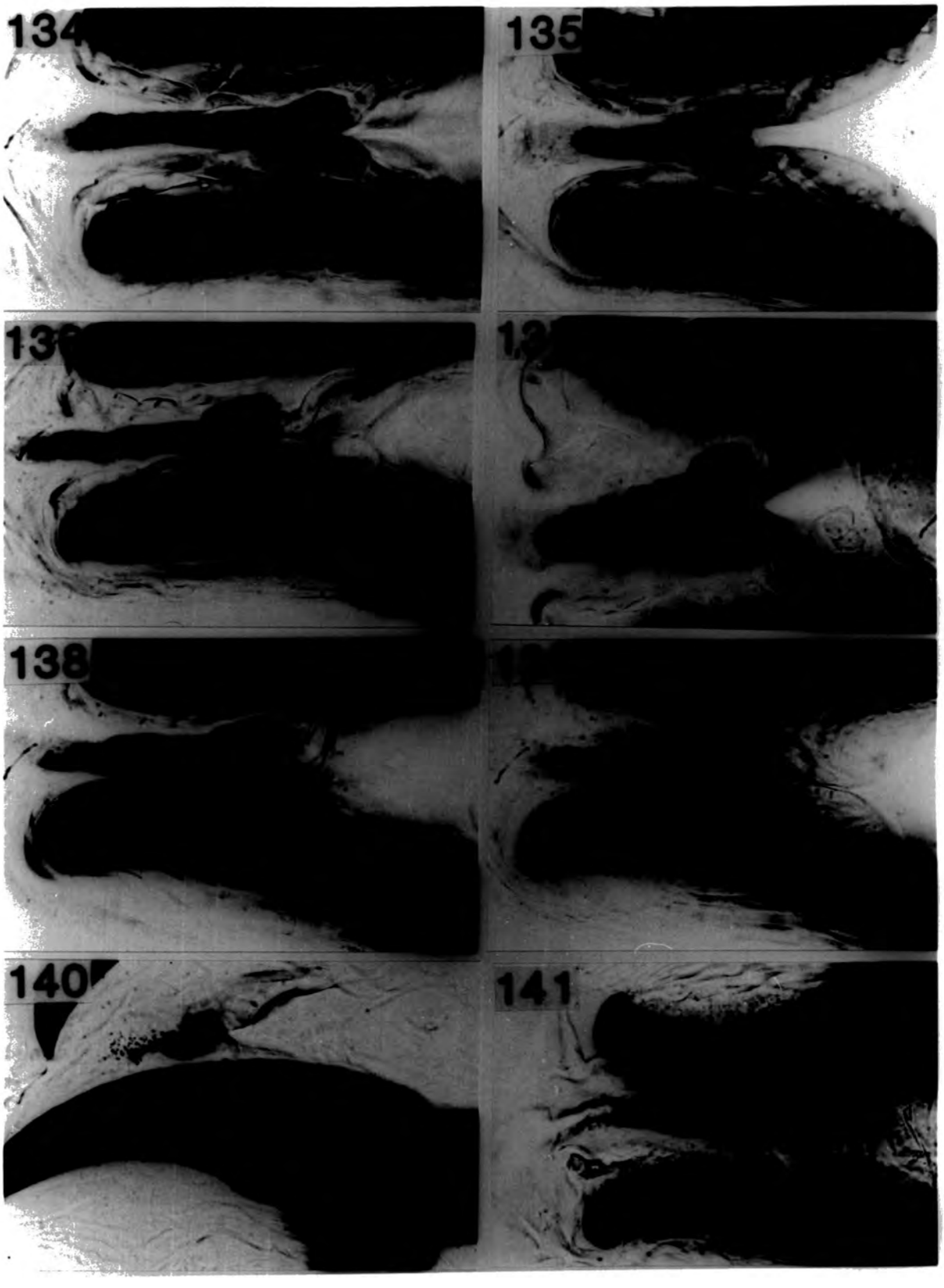
Figs. 118-125. (118) Calliphora augur pharyngeal ridges (ventral view) (x330), (119) Phormia terraenovae pharyngeal ridges (T.S. of first instar) (x500), (120) Calliphora vomitoria mouth-hook (T.S.) D = Dental sclerite, A = Apodeme, V = Ventral angle, (121) Cynomyopsis cadaverina mouth-hook showing perforation (x200), (122) Calliphora vicina skeleton, (123) Calliphora vicina ventral cornu, (124 and 125) Calliphora vicina mouth-hook.


118
119
120
D
A
V
121
122
40µ
123
20µ
124
10µ
125
20µ

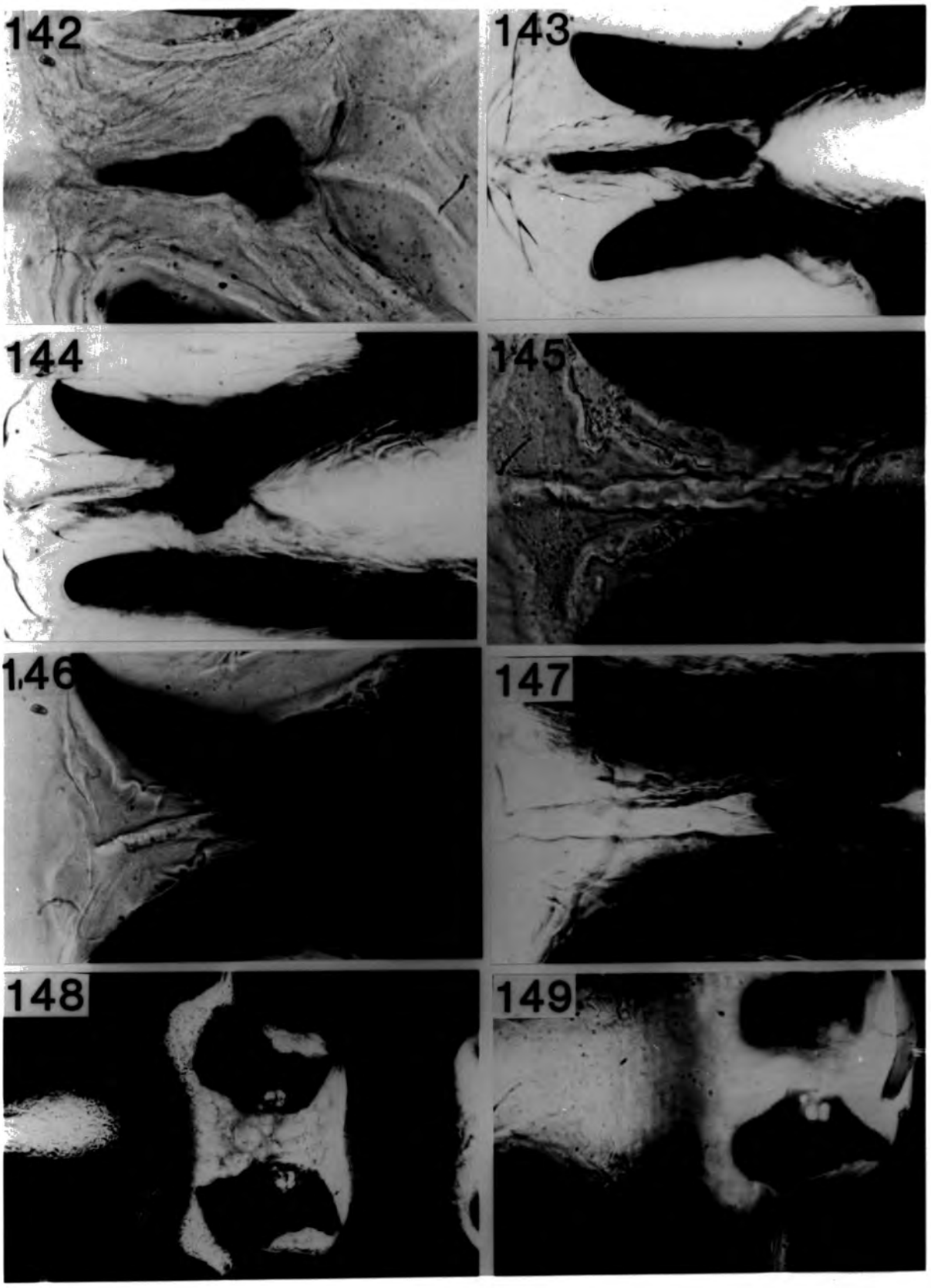
Figs. 126-133. Oral sclerites (x300). (126) Calliphora vicina, (127) Calliphora vomitoria, (128) Calliphora uralensis, (129) Calliphora alpina, (130) Calliphora subalpina, (131) Calliphora loewi, (132) Calliphora croceipalpis, (133) Calliphora lata.


126
127
128
129
130
131
132

Figs. 134-141. Oral sclerites (x300). (134) Calliphora terraenovae, (135) Calliphora livida, (136) Calliphora augur, (137) Calliphora ochracea, (138) Calliphora stygia (showing wish-bone structure), (139) Calliphora stygia (showing wing structure), (140) Calliphora hortona, (141) Cynomya mortuorum.


134
135
138
140
141

Figs. 142-149 (x300). (142) Cynomyopsis cadaverina oral sclerite, (143) Triceratopyga calliphoroides oral sclerite, (144) Aldrichina grahami oral sclerite, (145) Lucilia sericata oral sclerite, (146) Chrysomya megacephala, (147) Chrysomya marginalis, (148) Calliphora vicina hypostomal plates, (149) Calliphora uralensis hypostomal plates.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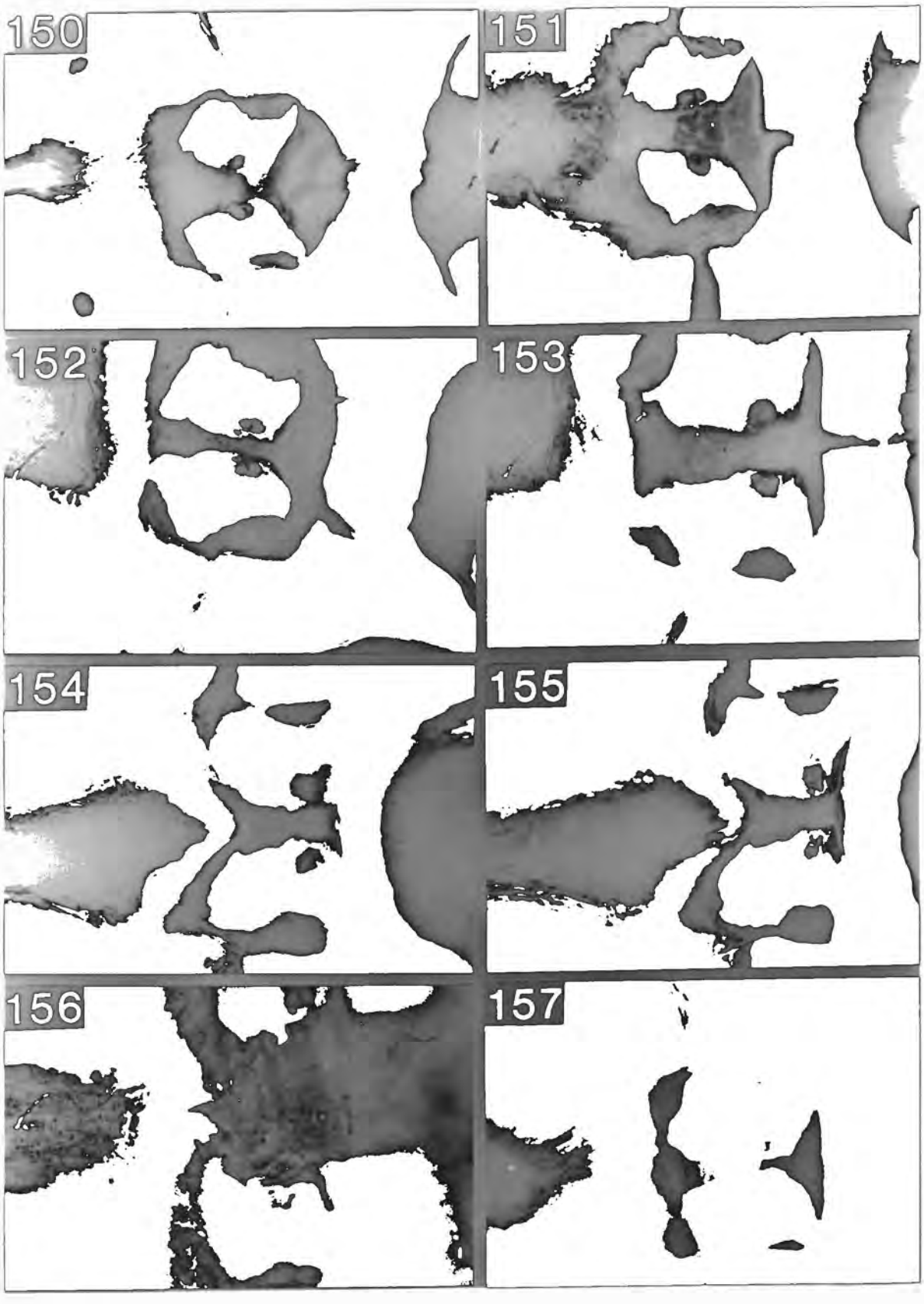
Figs. 150-157. Hypostomal plates etc. (x300). (150) Calliphora loewi, (151) Calliphora subalpina, (152) Calliphora augur, (153) Calliphora stygia, (154 and 155) Calliphora quadrimaculata, (156) Calliphora lata, (157) Calliphora croceipalpis.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Figs. 158-165. Hypostomal plates etc. (x300). (158) Calliphora hortona, (159) Calliphora ochracea, (160) Cynomyopsis cadaverina, (161) Aldrichina grahami, (162) Lucilia sericata, (163) Lucilia sericata, showing epipharyngeal sclerite (E), (164) Chrysomya albiceps, (165) Chrysomya bezziana.

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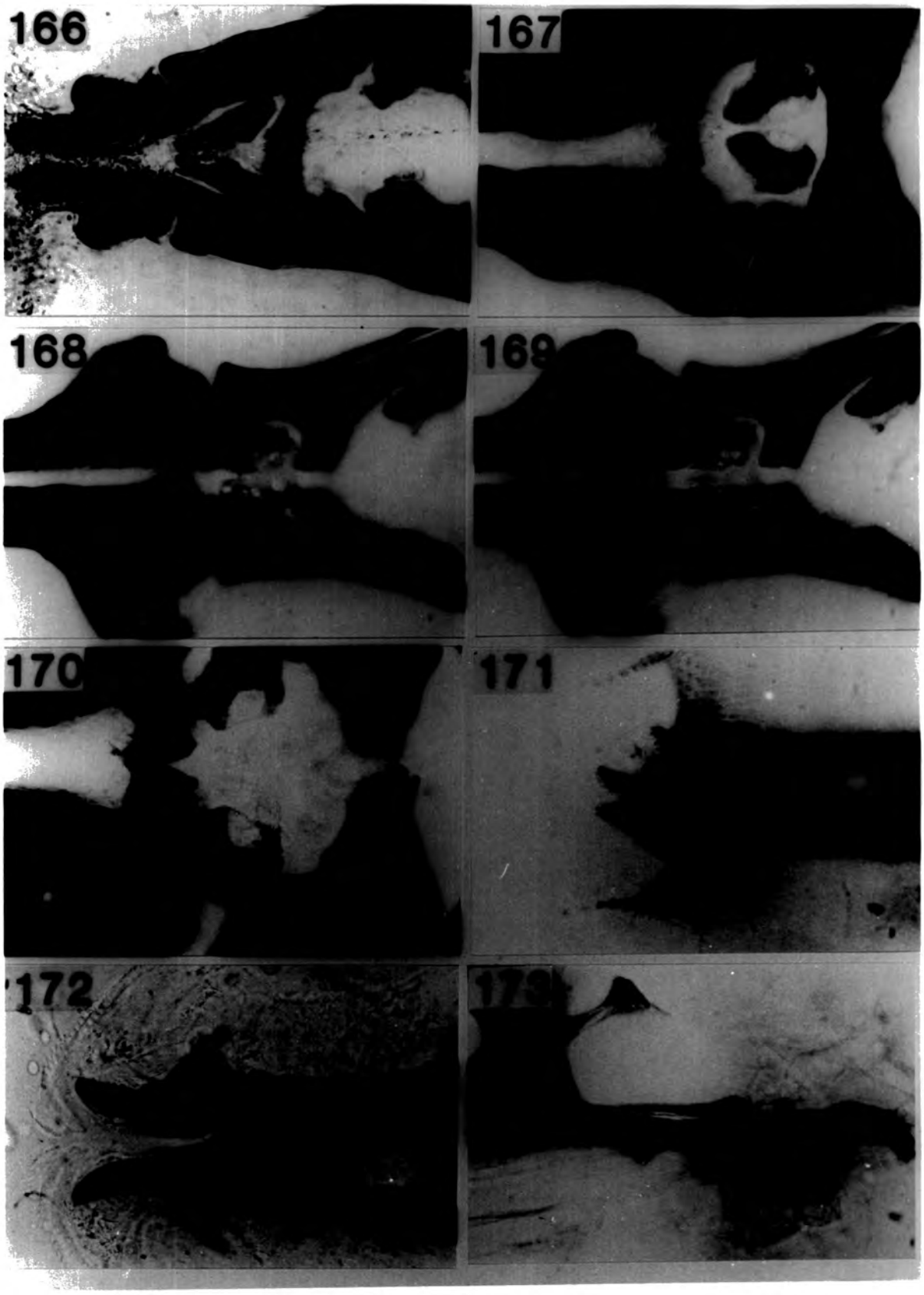
Figs. 166-173. Skeletons (x300). (166) Protocalliphora azurea, (167) Boettcherisca peregrina, (168) Tricharaea brevicornis (epipharyngeal sclerite), (169) Same as (168) showing hypostomal plates, (170) Sarcophaga argyrostoma, (171) Sepedon sp., (172) Drosophila melanogaster ventral view, (173) Drosphila melanogaster lateral view.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Figs. 174-181. (174) Dryomyza anilis oral sclerite (x300), (175) Coelopa frigida oral sclerite (x300), (176) Piophila casei hypostomal plates (x300), (177) Gyrostigma pavesii mouth-hook (x300), (178) Coelopa frigida posterior spiracle (x300), (179) Tetraplastocerus transvaalensis process (x330), (180) Muscina pabulorum spines (x300), (181) Dryomyza anilis spines (x300) (black particles are fungal spores upon which larva was feeding).


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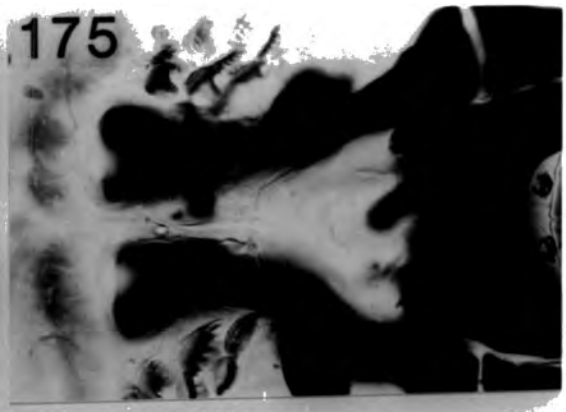
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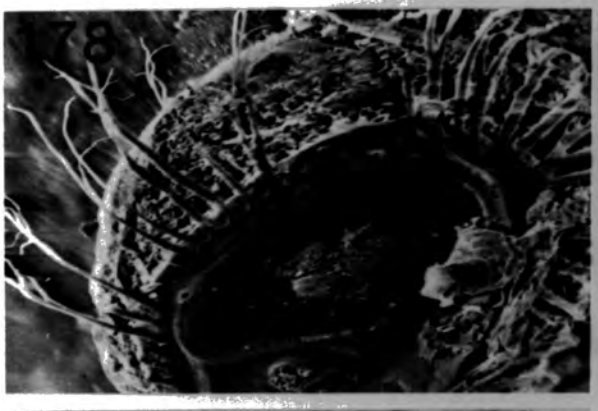
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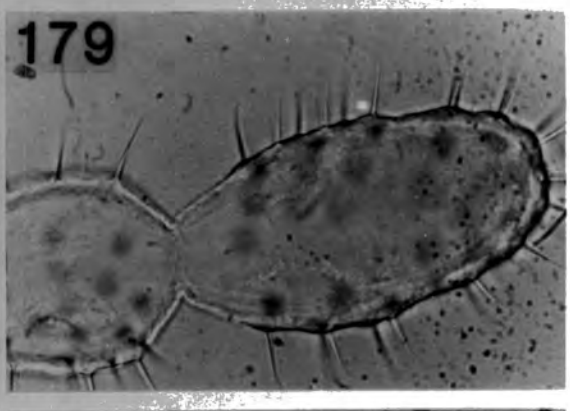
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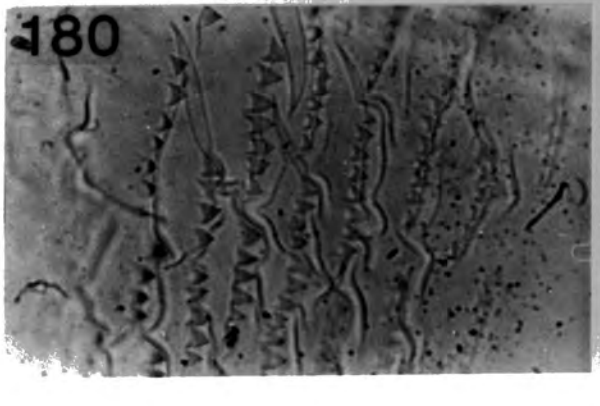
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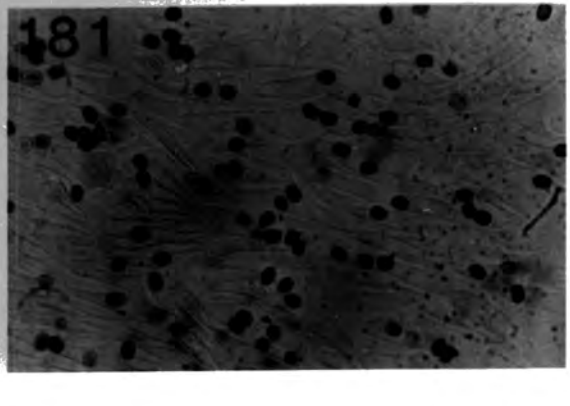
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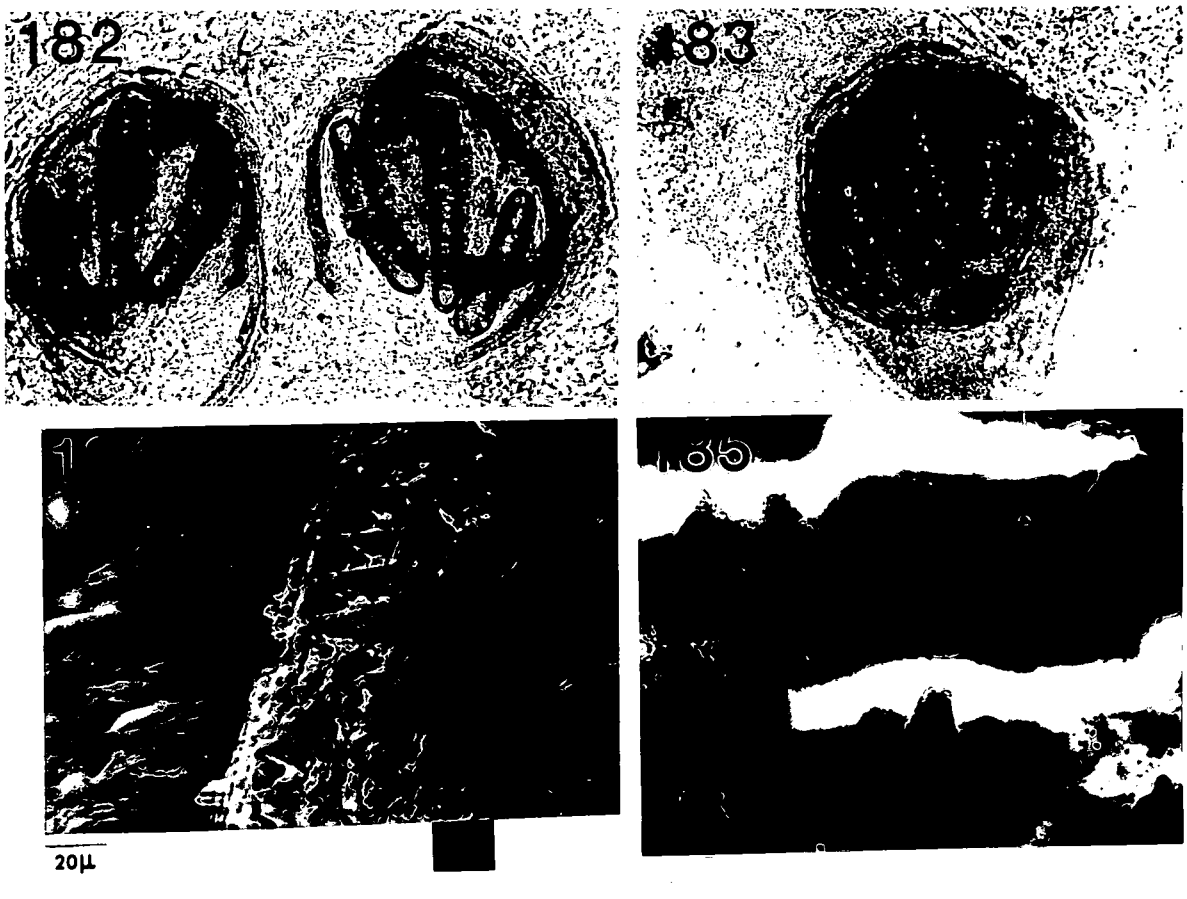
Figs. 182-185. (182) Sarcophaga argyrostoma posterior spiracle (x300), (183) Brachycoma devia posterior spiracle (x300), (184 and 185) Fossil Phormia terraenovae from Belgium.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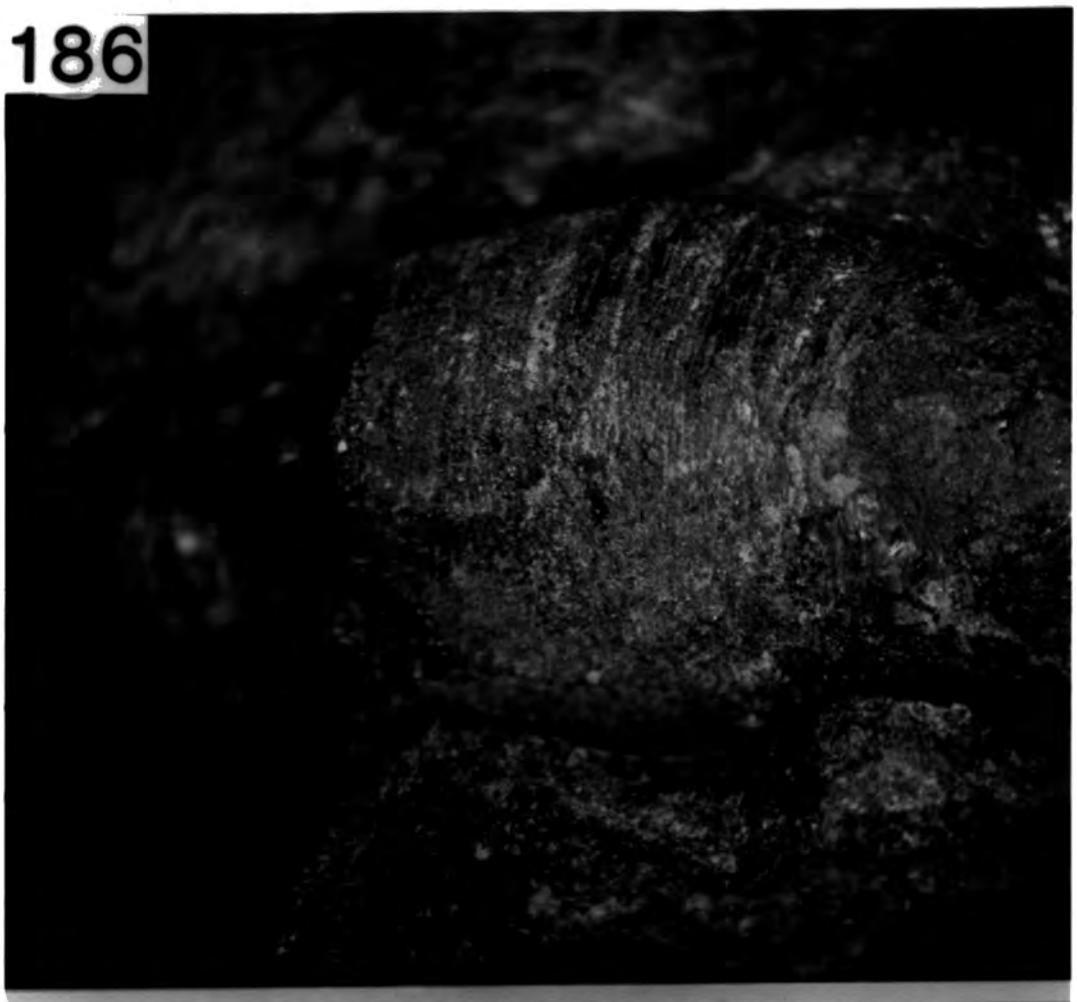
Figs. 186-187. "Cretaphormia fowleri" (x10). (186) Fossil 'C', (187) Fossil 'D'.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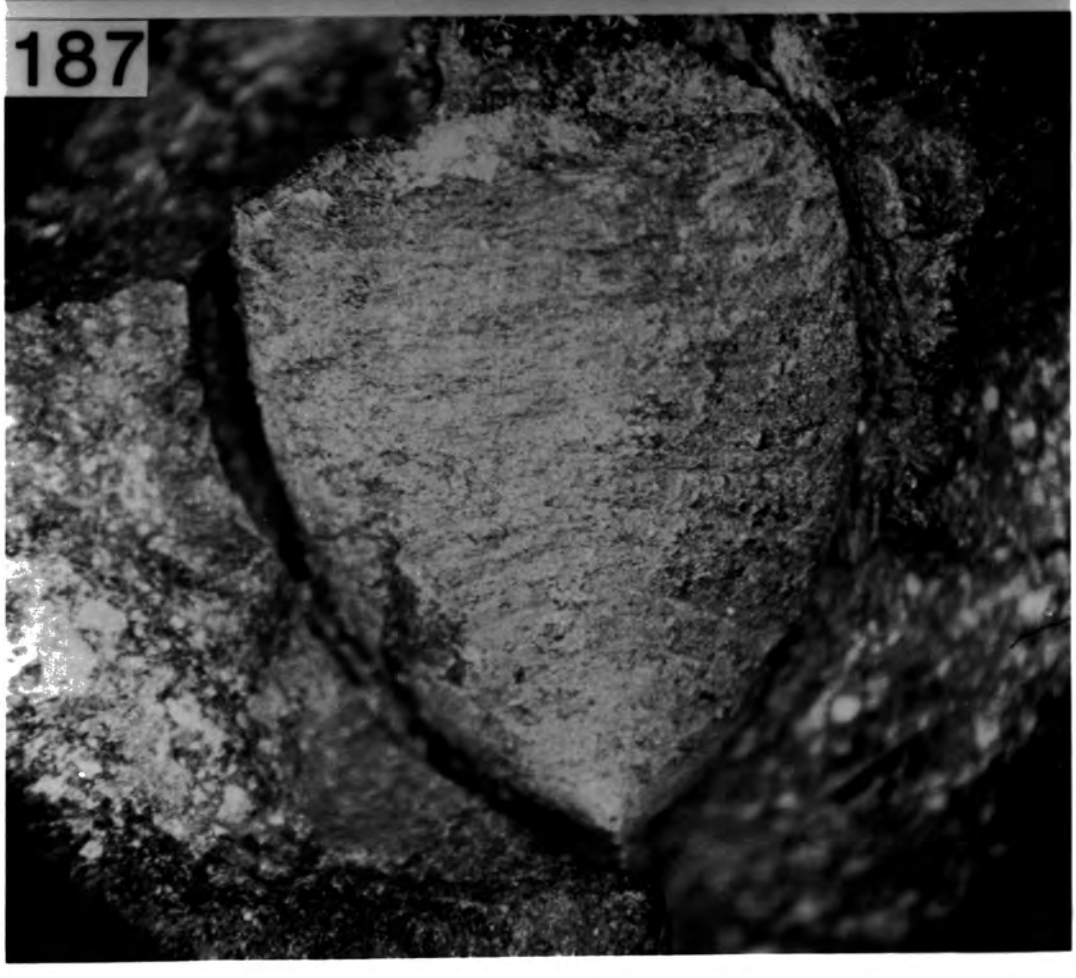
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Figs. 188-193. (188) Egg morphology (MA = Median area, MP = Micropylar plate, C = Chorion, HP = Hatching pleat), (189) Anterior part of puparium (PR = Pupal respiratory horn), (190) Anterior end of larva (A = Antenna, S = Supramaxillary papillae, MP = Maxillary palp, O = Oral papilla, M = Mouth-hook), (191) Puparial cleavage (A = Anterior spiracle, S = Skeleton, B = Main line of breakage, SL = Second line of breakage), (192) Larval curvature, (193) Spinal pattern at ventral region of segments 6 and 7.

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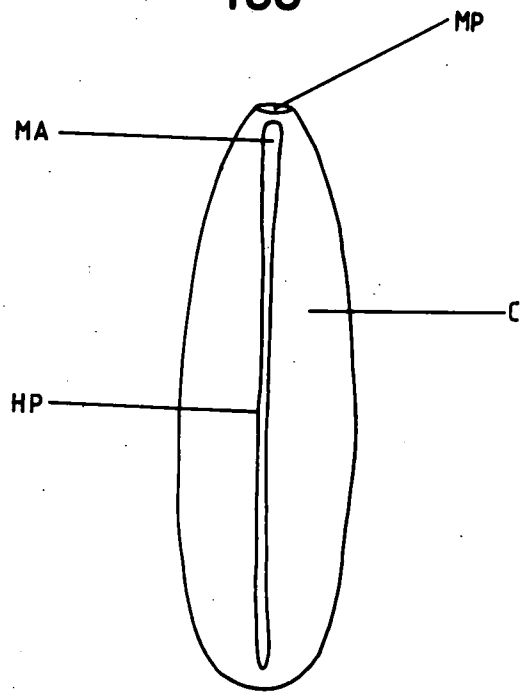

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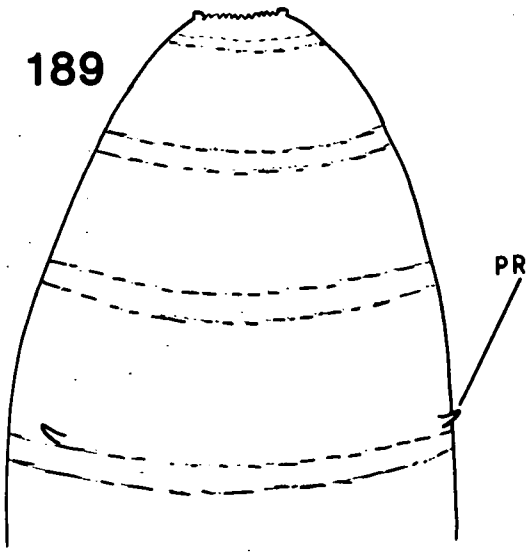

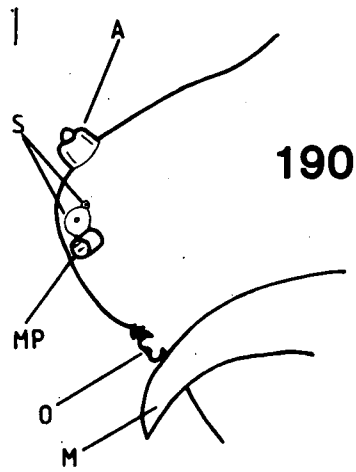

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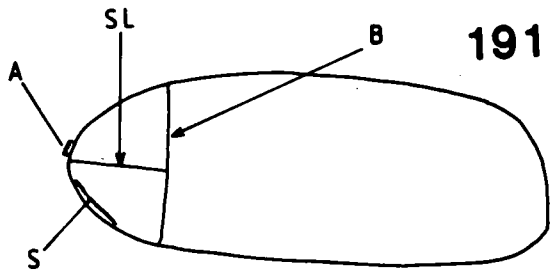

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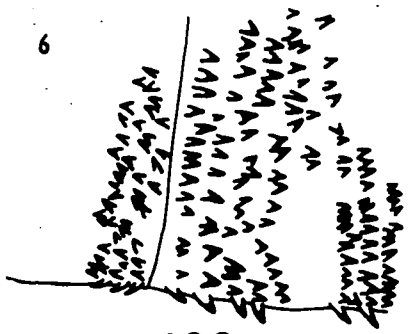

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Figs. 194-198. (194) Whole third instar, (195) Processes of "hairy" maggot, (196) Pleural band (P), (197) Posterior end of larva (S = Spiracle, WA = Wrinkled area, A = Anus, AL = Anal lobe, P_1 - P_7 = Posterior papillae), (198) Anterior end of larva (C = Cephalic segment, T = First thoracic segment, N = Newport's segment).

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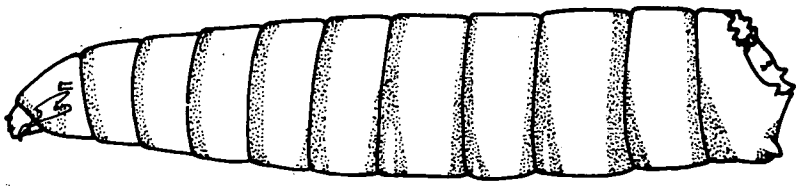

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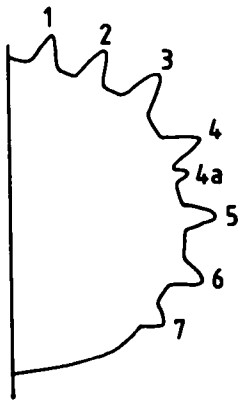

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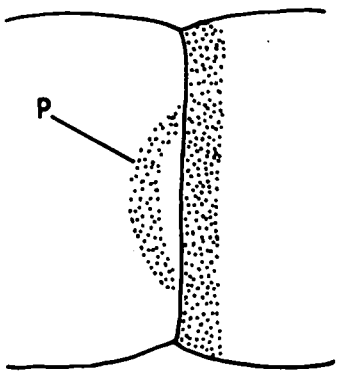

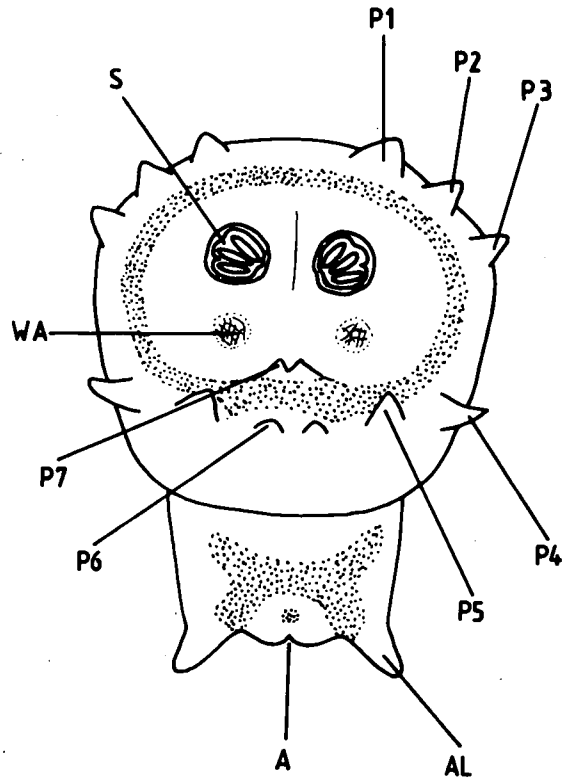

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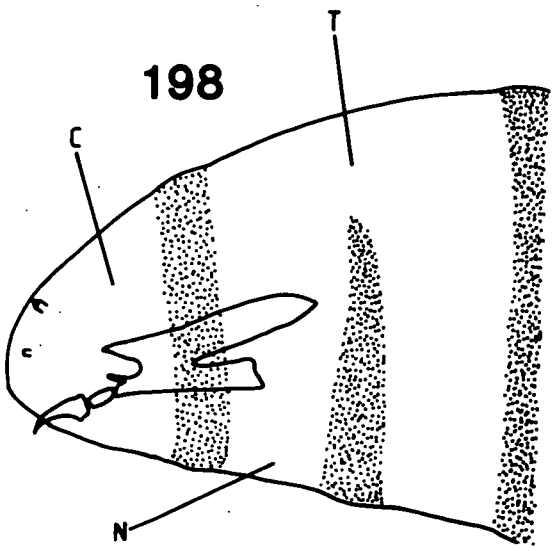
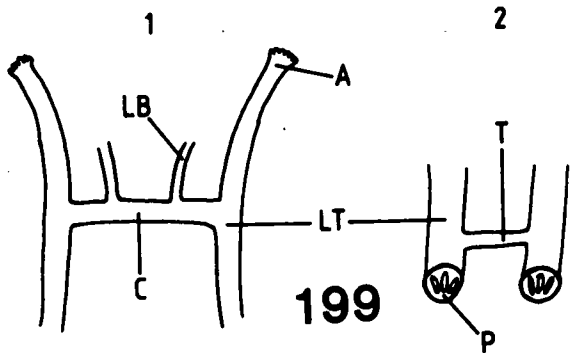


Figs. 199-204. (199) Tracheal system (1 = Anterior part, 2 = Posterior part, A = Anterior spiracle, LB = Lateral branch, C = Cervical anastomosis, LT = Lateral trunk, T = Tenth cross-branch, P = Posterior spiracle), (200) Third instar anterior spiracle, (201) First instar posterior spiracle, (202) Second instar posterior spiracle, (203) Pupal respiratory apparatus. (H = Horn, F = Felt chamber, IS = Internal spiracle, T = Trachea), (204) Third instar posterior spiracles (A = Aperture, P = Peritreme, B = Button, BS = Blister structure, IS = Intermediate structure, IPP = Internal peritremal projection).



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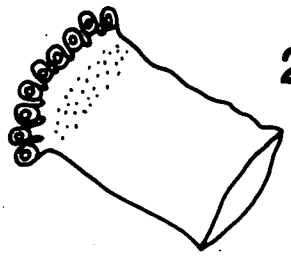

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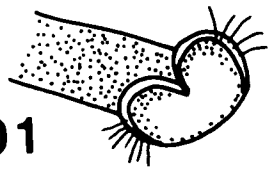

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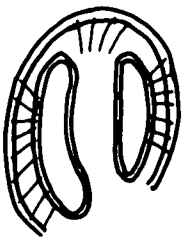

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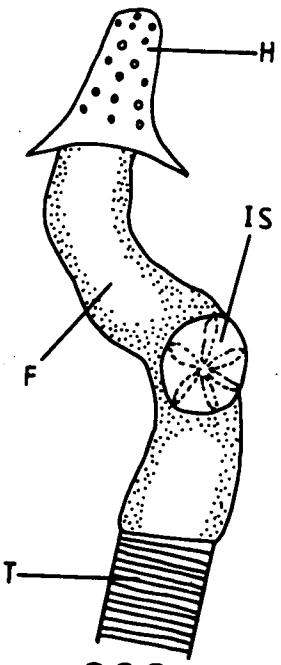

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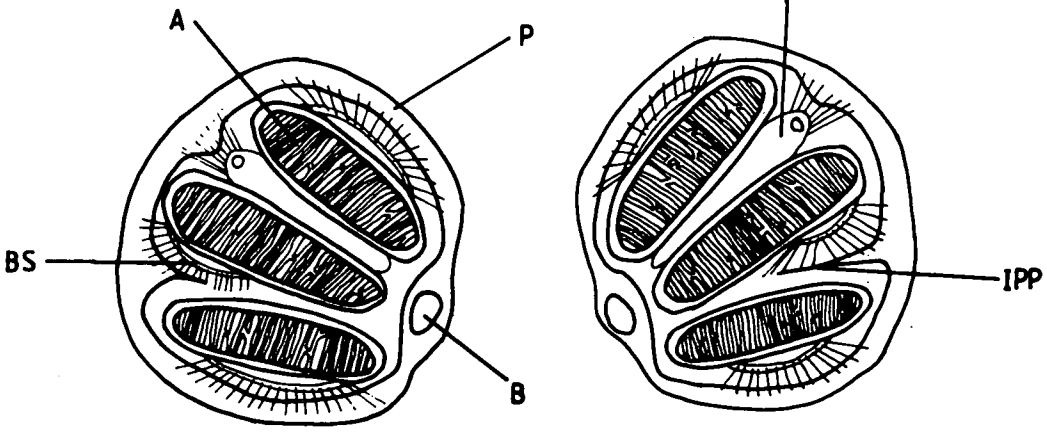
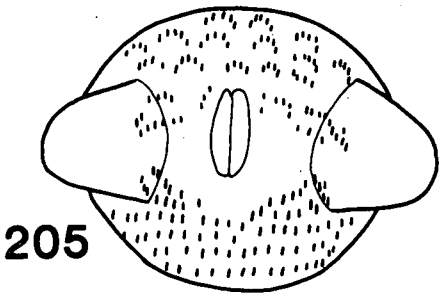


204

Figs. 205-212. Anal spine pattern. (205) Calliphora vicina, (206) Calliphora vomitoria, (207) Calliphora uralensis, (208) Cynomya mortuorum, (209) Lucilia cuprina, (210) Lucilia sericata, (211) Chrysomya putoria, (212) Chrysomya chloropyga.



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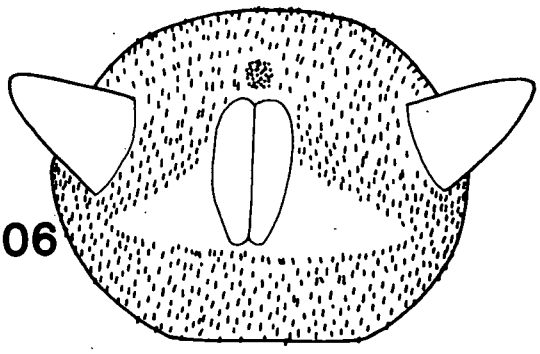

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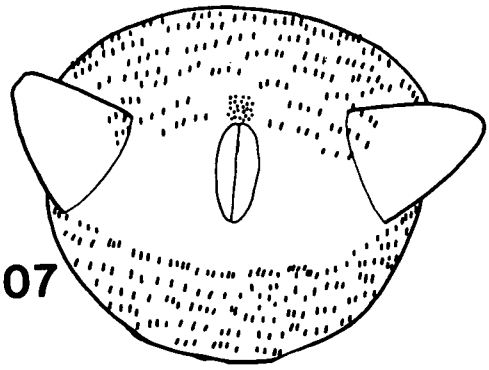

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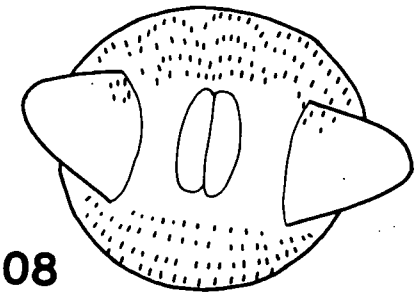

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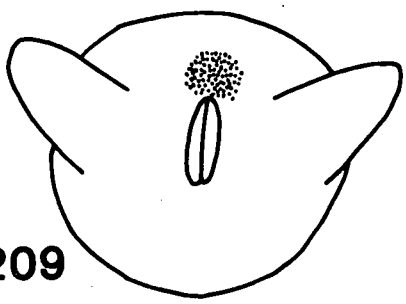

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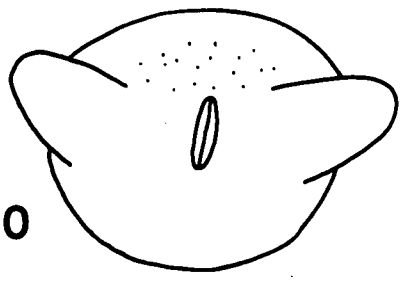

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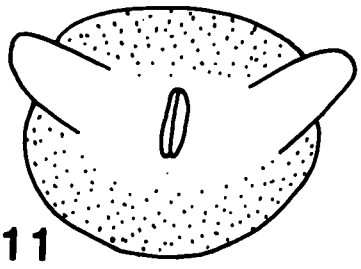

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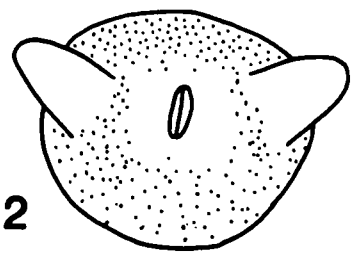

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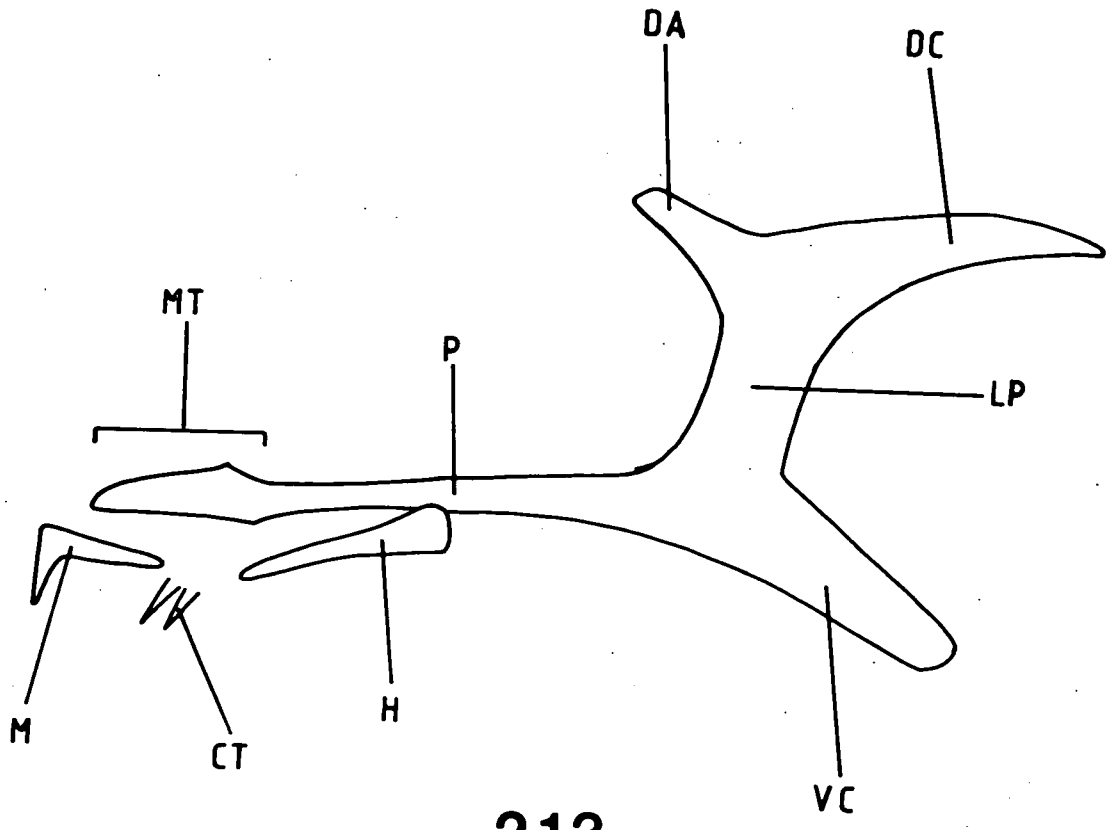
Figs. 213-214. Terminology of first instar cephalopharyngeal skeleton, (213) Lateral view, (214) Ventral view. M = Mouth-hook, MT = Median tooth, CT = Chitinised teeth, H = Hypostomal sclerite, P = Parastomal sclerite, DA = Dorsal arch, DC = Dorsal cornu, LP = Lateral plate, VC = Ventral cornu.



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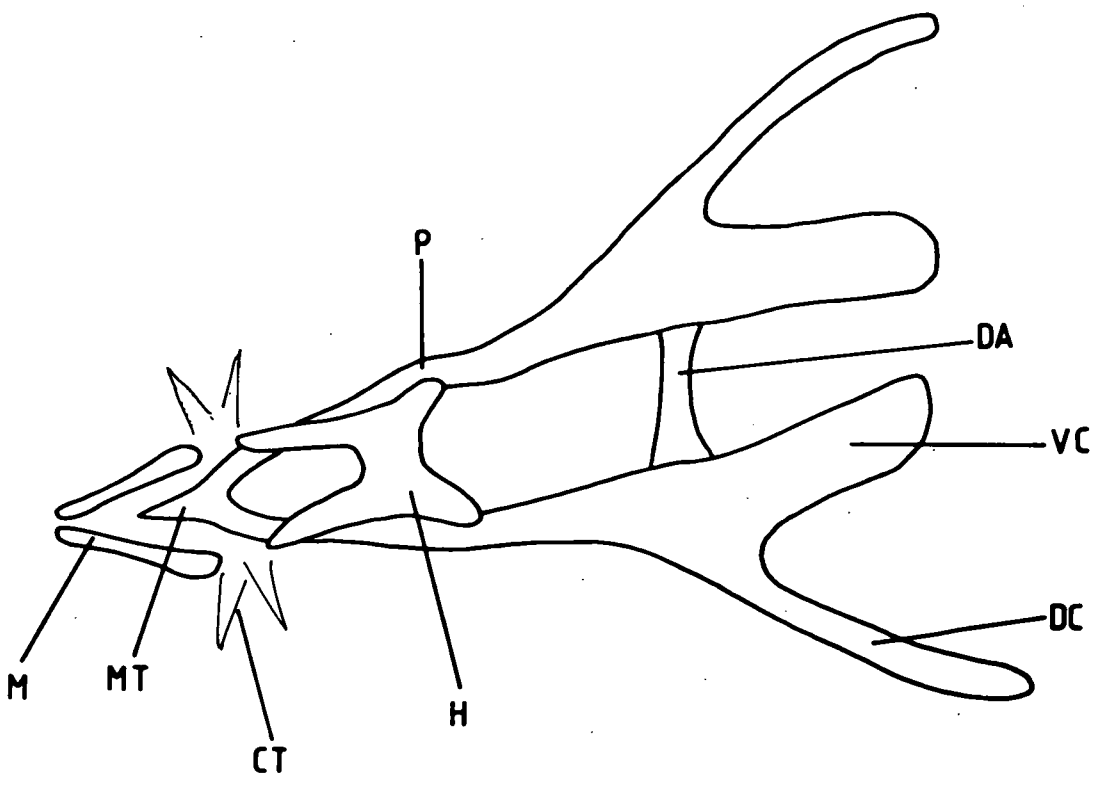

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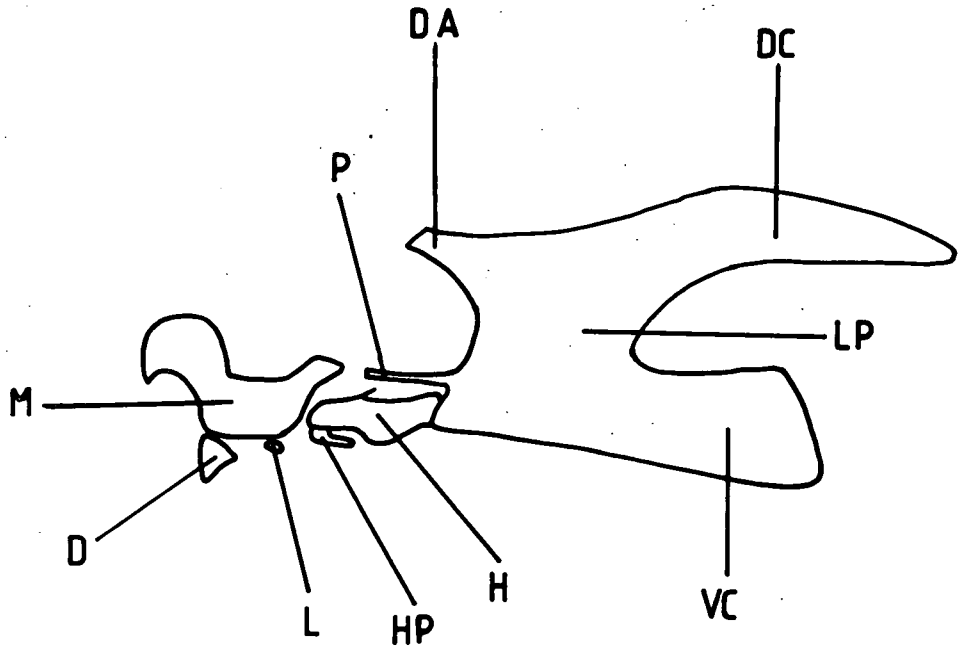
Figs. 215-216. Terminology of second instar cephalopharyngeal skeleton. (215) Lateral view, (216) Ventral view. M = Mouth-hook, D = Dental sclerite, L = Liguloid arch, HP = Hypostomal plate, P = Parastomal bar, H = Hypostomal sclerite, DA = Dorsal arch, DC = Dorsal cornu, LP = Lateral plate, VC = Ventral cornu.



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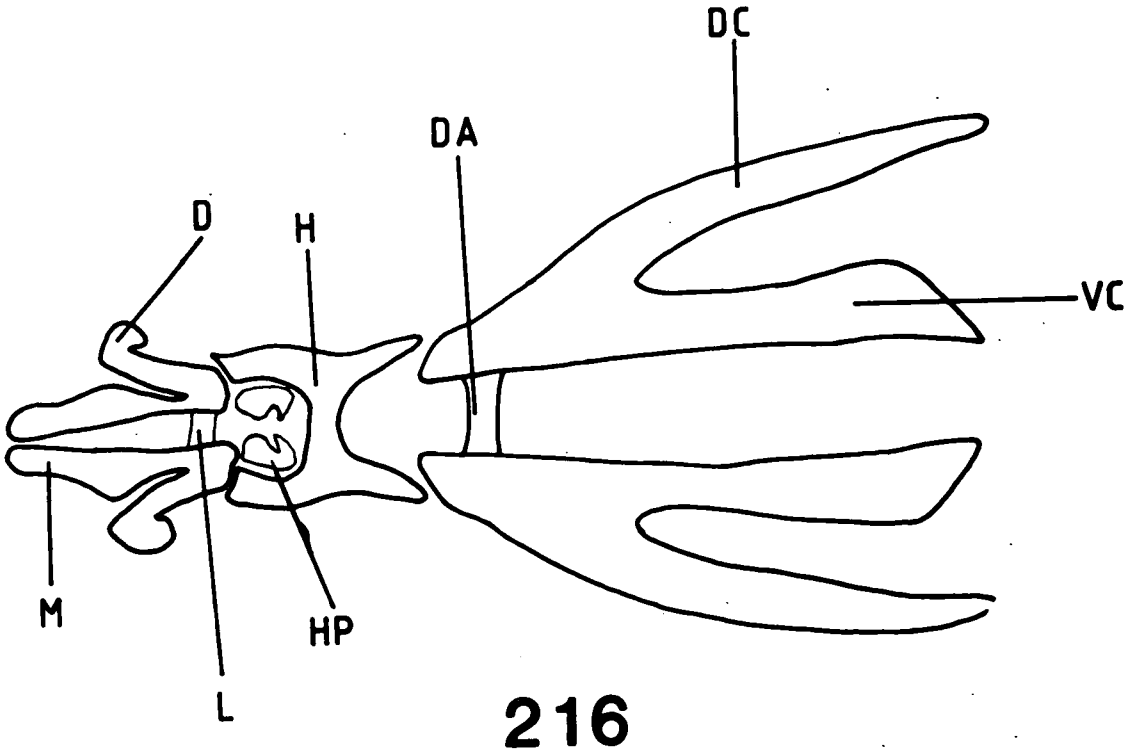

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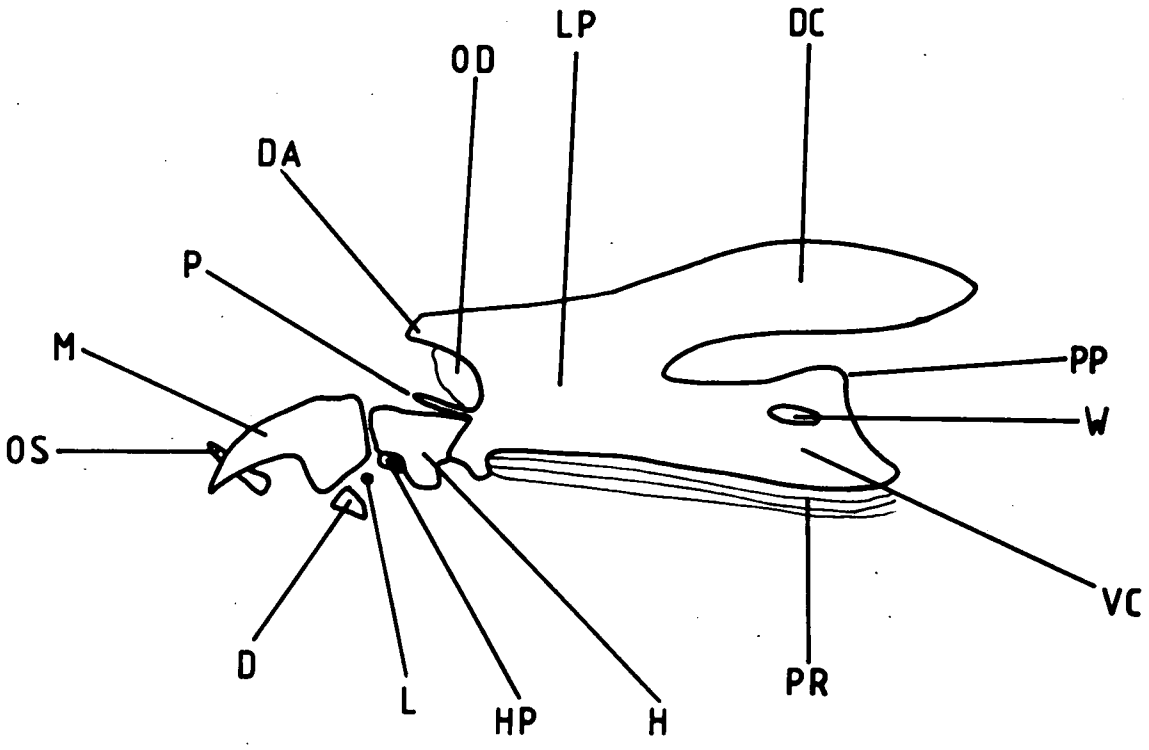
Figs. 217-218. Terminology of third instar cephalopharyngeal skeleton. (217) Lateral view, (218) Ventral view. OS = Oral sclerite, M = Mouth-hook, D = Dental sclerite, L = Liguloid arch, HP = Hypostomal plate, H = Hypostomal sclerite, P = Parastomal bar, DA = Dorsal arch, OD = Ocular depression, LP = Lateral plae, DC = Dorsal cornu, PP = Posterodorsal process, W = Window, VC = Ventral cornu, PR = Pharyngeal ridges.



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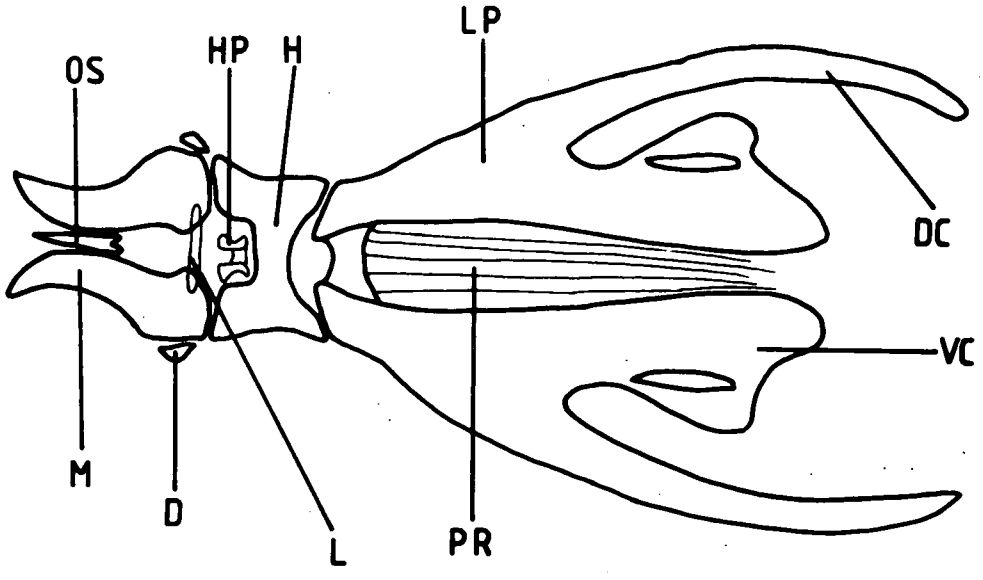

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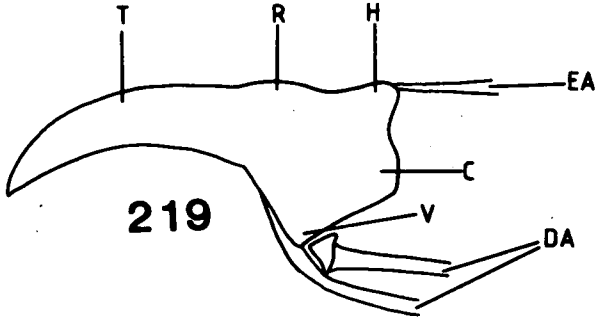
Figs. 219-223. (219) Mouth-hook anatomy (T = Tooth, R = Dorsal ridge, H = Dorsal horn, C = Condyle, V = Ventral angle, EA = Elevator apodeme, DA = Depressor apodemes), (220) Dental sclerite (1 = Left lateral view, 2 = Posterior view, A = Unit A, B = Unit B, P = Process), (221) Interstage I/II (S = Second instar element), (222) Interstage II/III (T = Third instar element), (223) Skeleton (M = Prothoracic membrane, O = Margin of ocular depression, P = Unpigmented phragmata).



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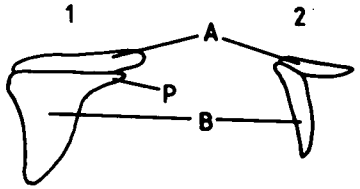

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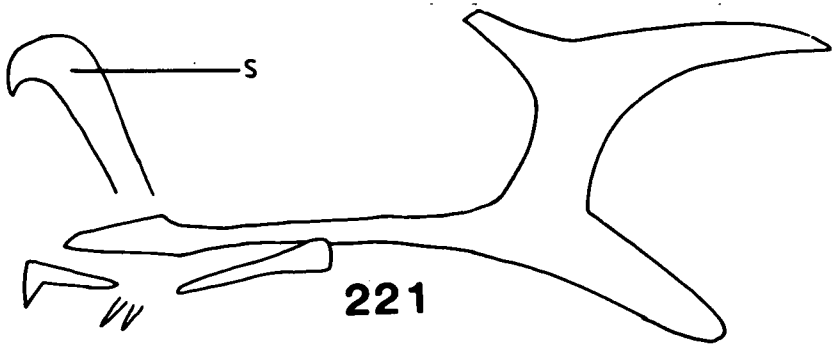

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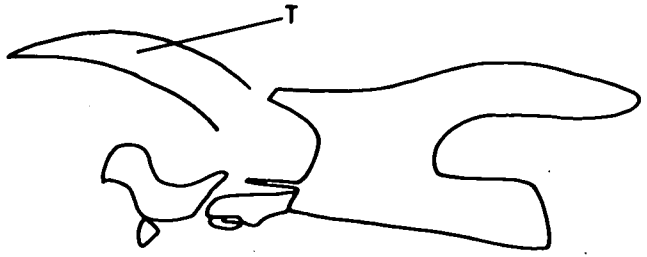

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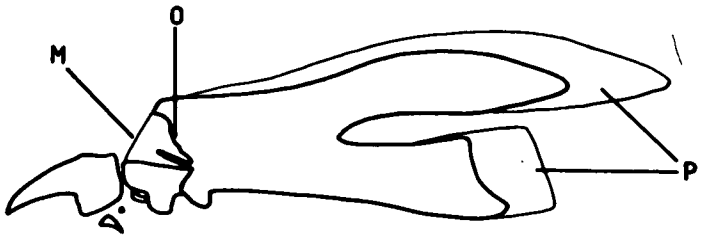

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Figs. 224-229. Third instar skeletons (x65). (224) Calliphora vicina, (225) Calliphora vomitoria, (226) Calliphora uralensis, (227) Calliphora alpina, (228) Calliphora subalpina, (229) Calliphora loewi.

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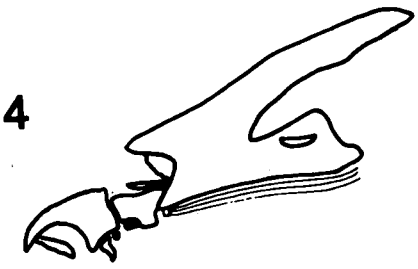

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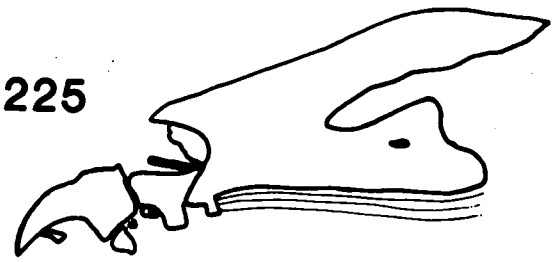

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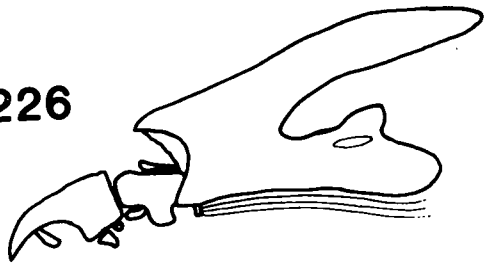

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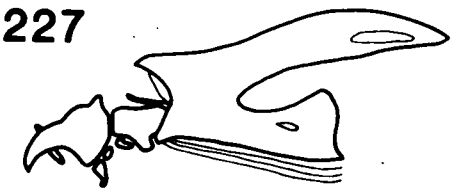

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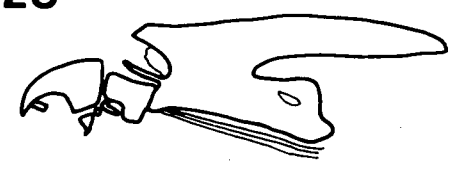

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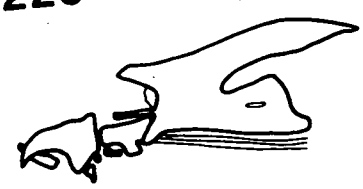

Figs. 230-235. Third instar skeletons (x60). (230) Calliphora stygia, (231) Calliphora lata, (232) Calliphora augur, (233) Calliphora quadrimaculata, (234) Calliphora croceipalpis, (235) Calliphora hortona.

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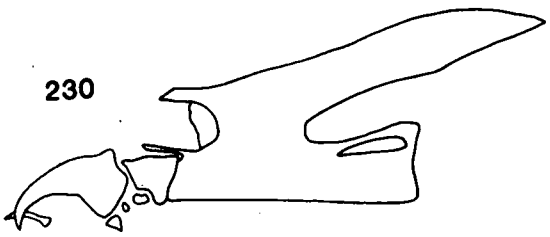

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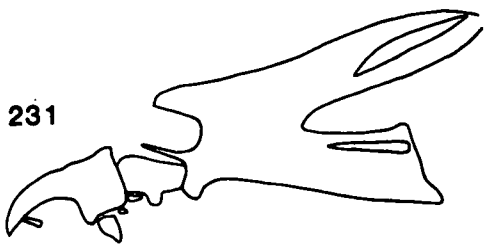

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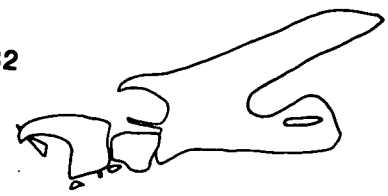

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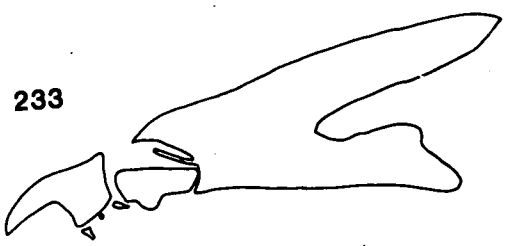

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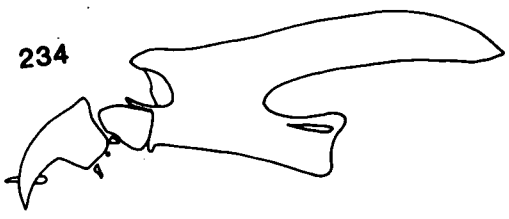

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Figs. 236-245. Second instar skeletons. (236) Calliphora vicina (x65), (237) Calliphora vomitoria (x65), (238) Calliphora uralensis (x65), (239) Calliphora alpina (x65), (240) Calliphora subalpina (x65), (241) Calliphora loewi (x65), (242) Calliphora croceipalpis (x45), (243) Calliphora terraenovae (x45), (244) Calliphora stygia (x45), (245) Calliphora hortona (x45).

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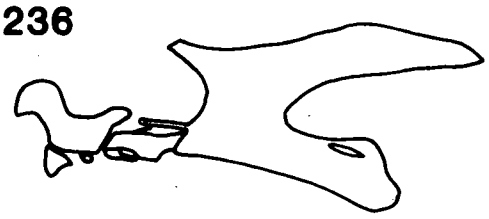

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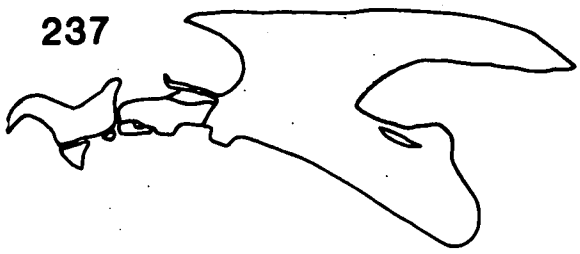

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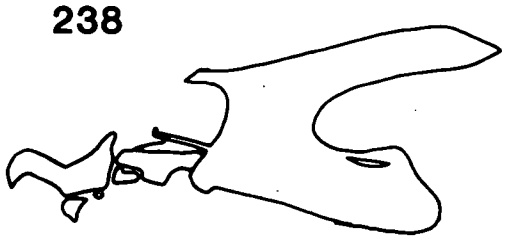

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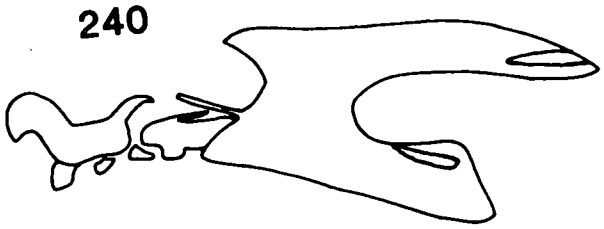

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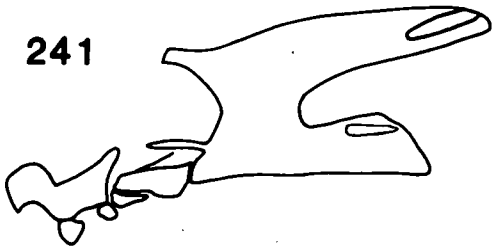

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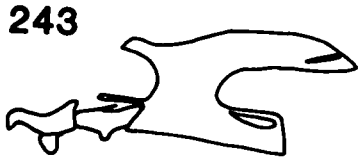

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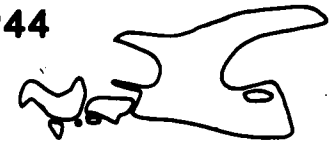

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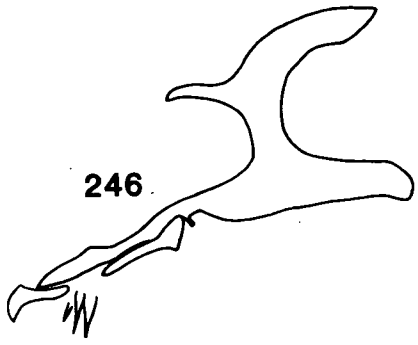
Figs. 246-253. First instar skeletons (x140), (246) Calliphora vicina, (247) Calliphora vomitoria, (248) Calliphora uralensis, (249) Calliphora alpina, (250) Calliphora subalpina, (251) Calliphora loewi, (252) Calliphora croceipalpis, (253) Calliphora hortona.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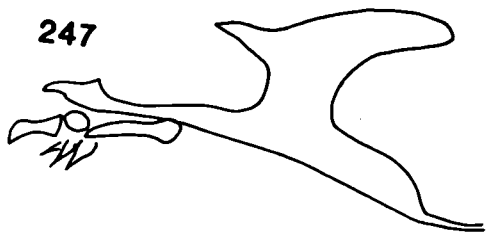
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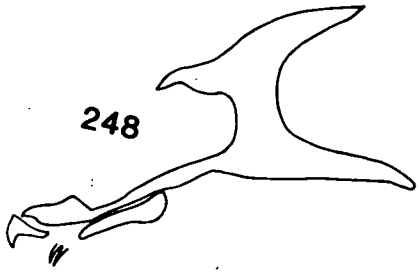
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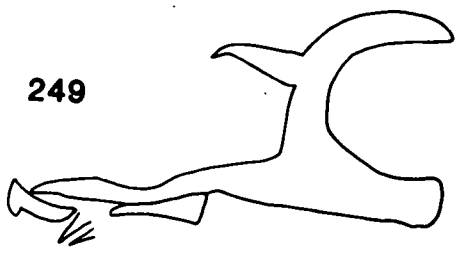
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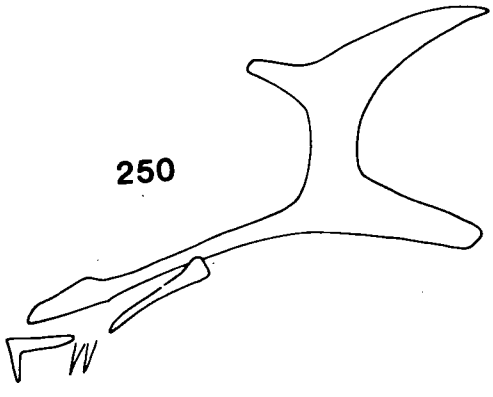
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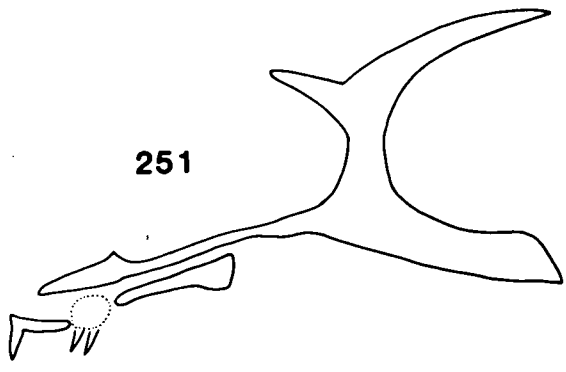
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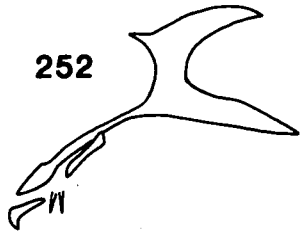
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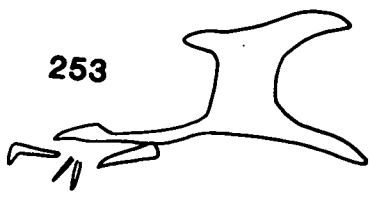
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Figs. 254-260. (254-257 First instar skeletons, x140; 258-260 Second instar skeletons, x65). (254) Lucilia sericata, (255) Lucilia cuprina, (256) Triceratopyga calliphoroides, (257) Cynomya mortuorum, (258) Lucilia sericata, (259) Cynomya mortuorum, (260) Lucilia cuprina.

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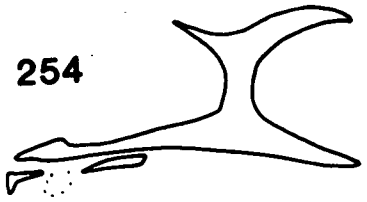

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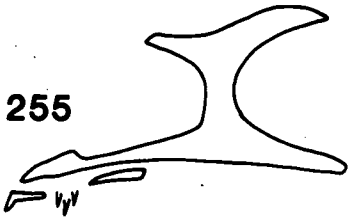

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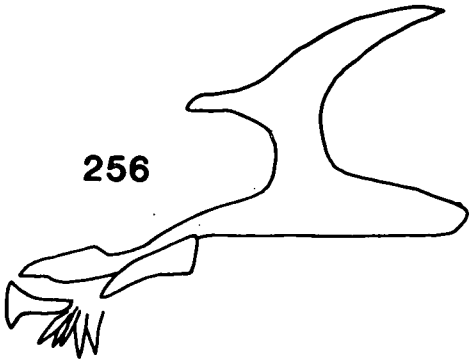

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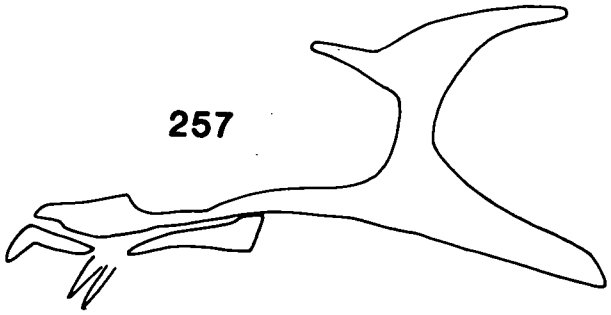

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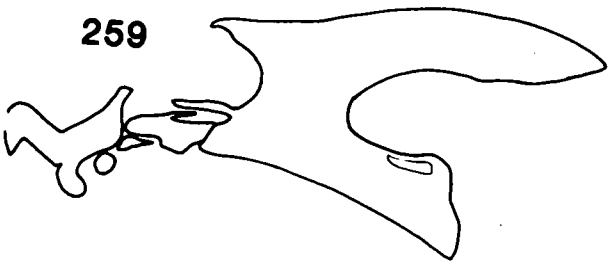

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Figs. 261-267. Third instar skeletons. (261) Triceratopyga calliphoroides (x65), (262) Cynomya mortuorum (x65), (263) Hemipyrellia fernandica (x65), (264) Lucilia ampullacea (x85), (265) Lucilia sericata, (266) Lucilia cuprina, (267) Lucilia bufonivora.


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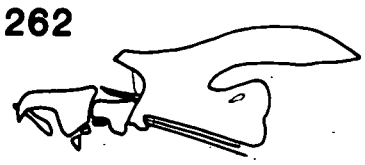
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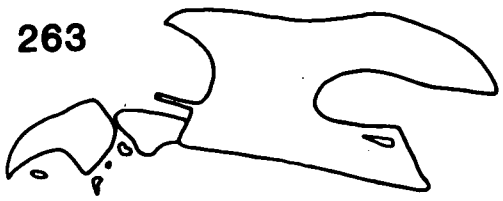
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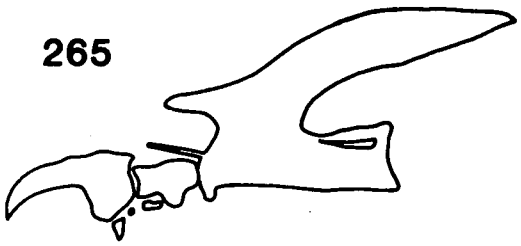
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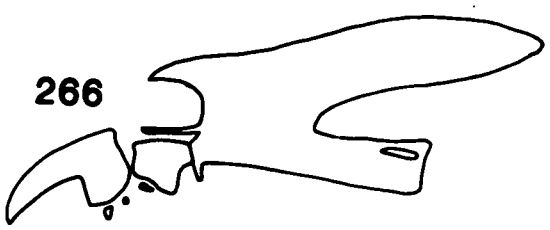
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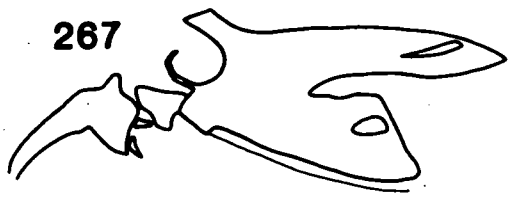
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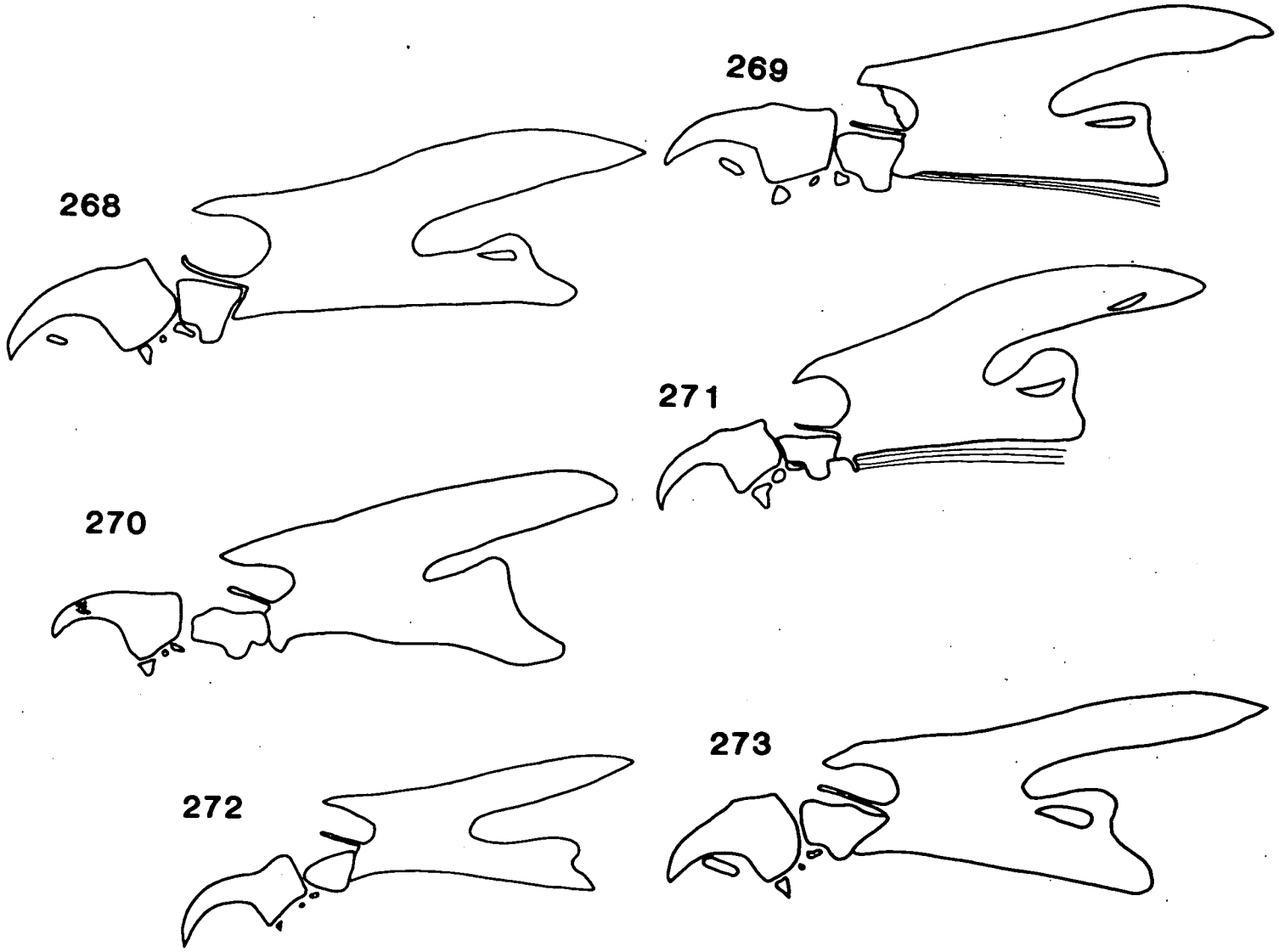
Figs. 268-273. Third instar skeletons (x75). (268) Chrysomya megacephala, (269) Chrysomya marginalis, (270) Chrysomya chloropyga, (271) Chrysomya putoria, (272) Chrysomya bezziana, (273) Chrysomya pinguis.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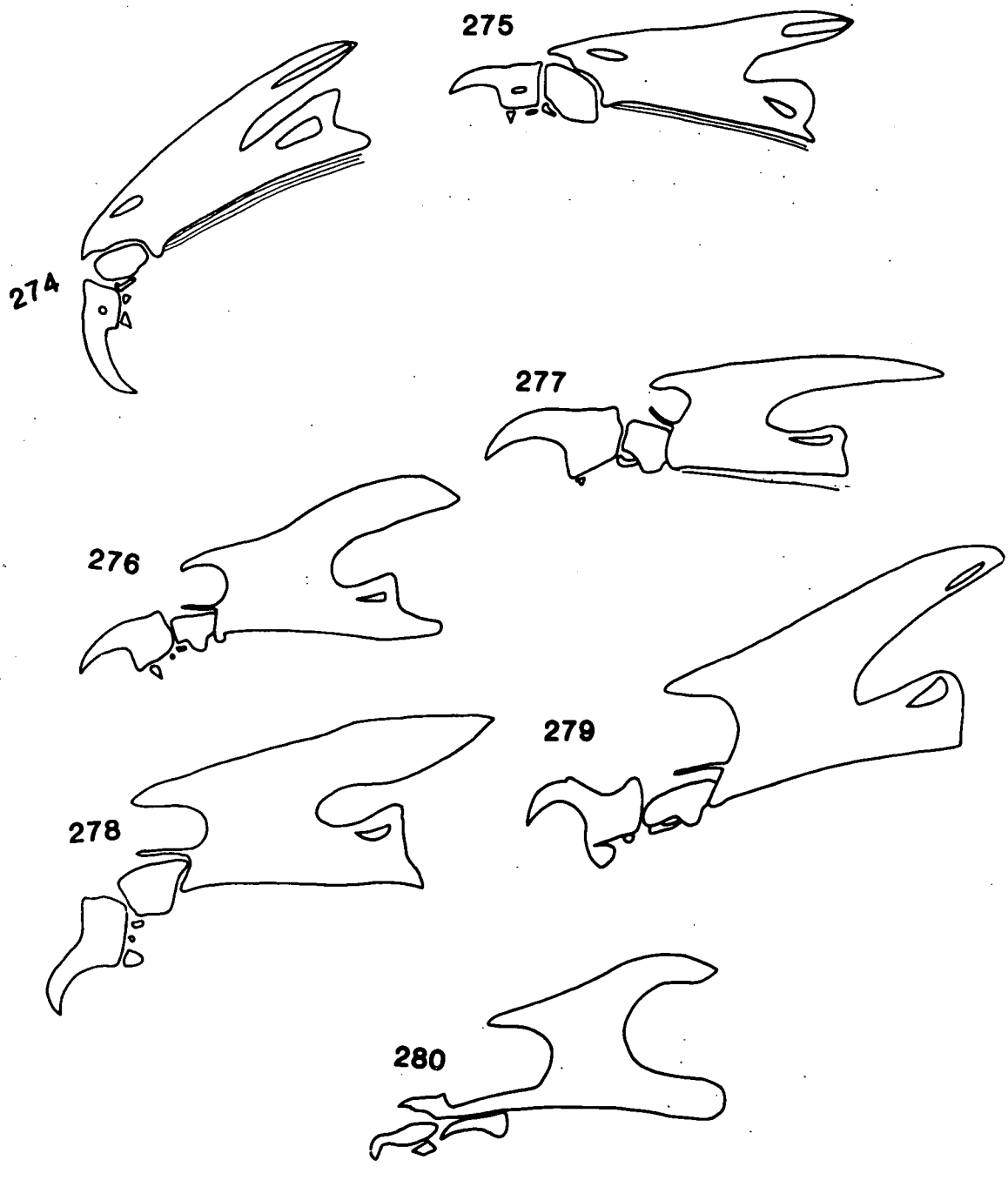
Figs. 274-280. Skeletons (x75). (274) Third instar Chrysomya albiceps, (275) Third instar Chrysomya rufifacies, (276) Third instar Cochliomyia macellaria, (277) Third instar Cochliomyia hominovorax, (278) Second instar Chrysomya albiceps, (279) Second instar Chrysomya putoria, (280) First instar Chrysomya putoria.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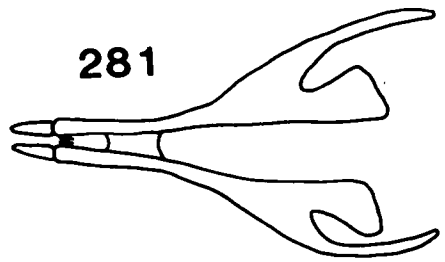
Figs. 281-289. Skeletons. (281) First instar Protocalliphora azurea (Ventral) (x75), (282) Same in lateral view, (283) Second instar Protocalliphora azurea (x75), (284) Third instar Protocalliphora azurea (x65), (285) Third instar Protocalliphora sialia (x65), (286) Third instar Boreellus atriceps (x65), (287) Second instar Phormia regina (x75), (288) Third instar Phormia regina (x65), (289) Third instar Phormia terraenovae (x65).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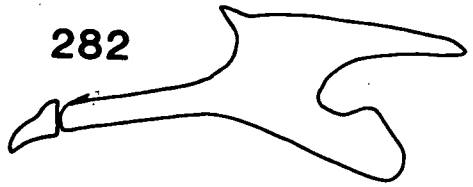
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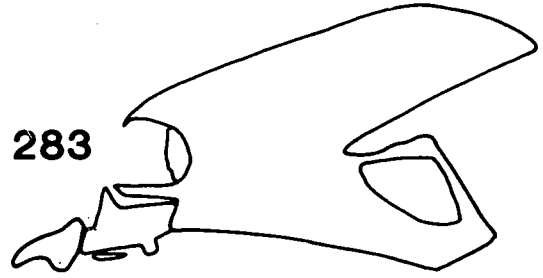
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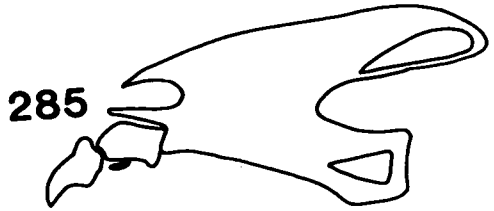
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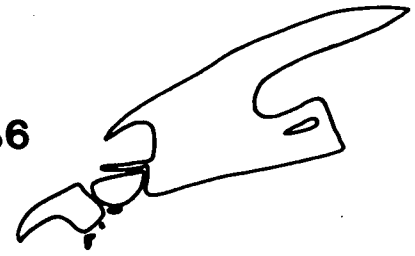
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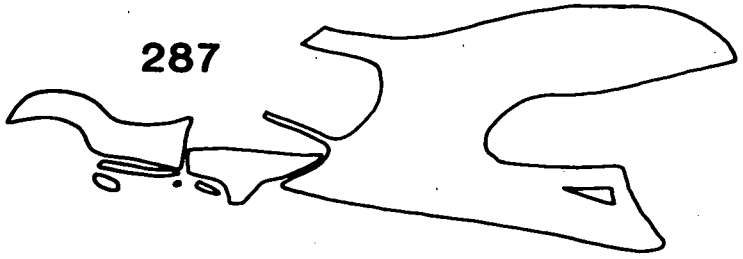
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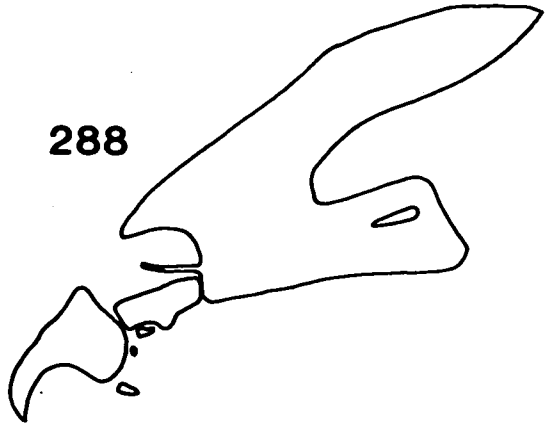
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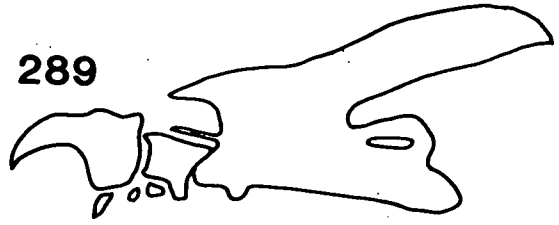
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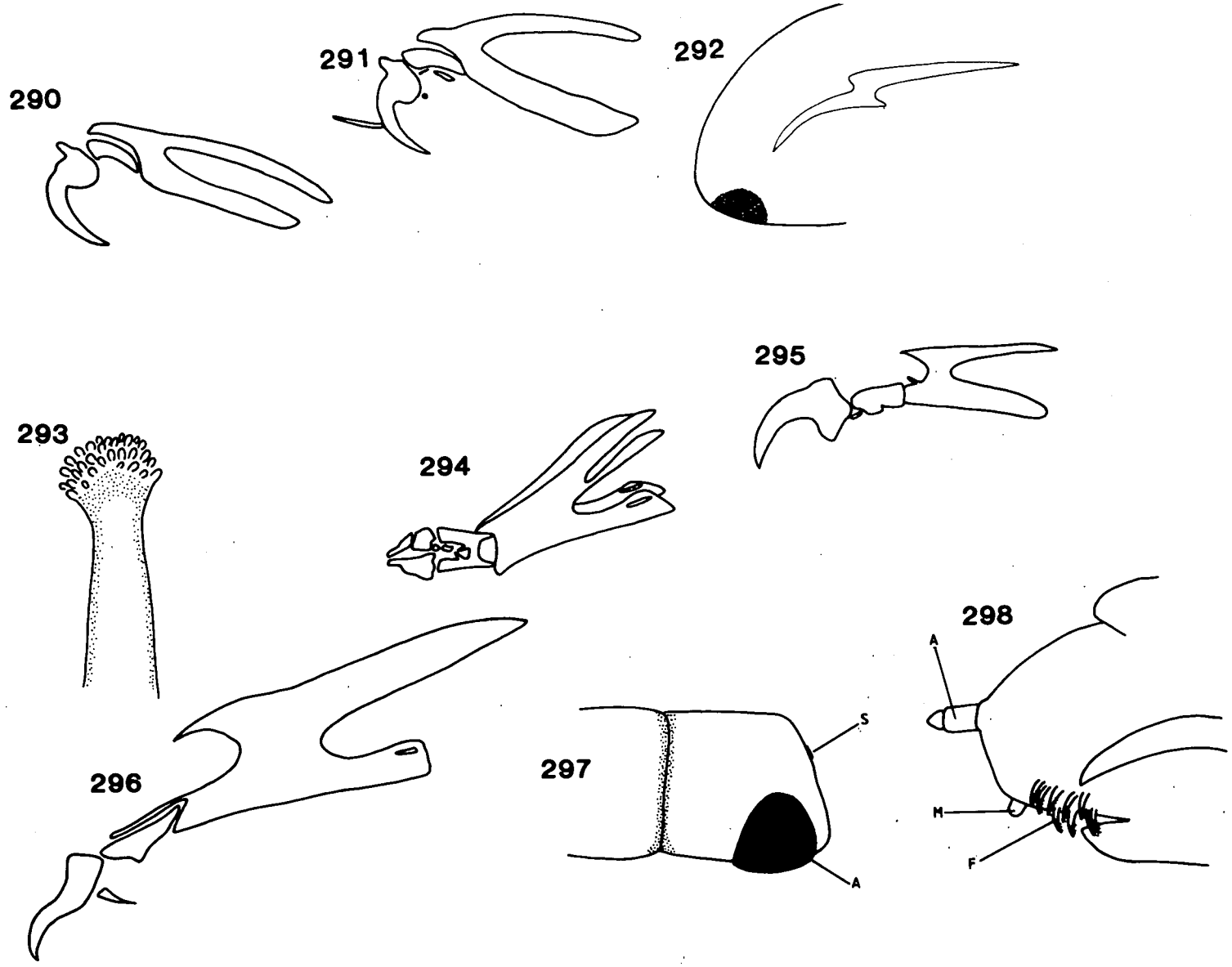
Figs. 290-298. (290) Second instar Amenia leonina (x75), (291) Second instar Amenia imperialis (x75), (292) First instar Amenia leonina (x70), (293) Amenia leonina anterior spiracle, (294) Stomorhina cribrata third instar (x60), (295) Pollenia rudis third instar (x60), (296) Tricyclea deemingi third instar (x75), (297) Tricyclea deemingi posterior end (S = Spiracle, A = Anal plate), (298) Tricyclea deemingi anterior end (A = Antenna, M = Maxillary Palp, F = Feathery processes).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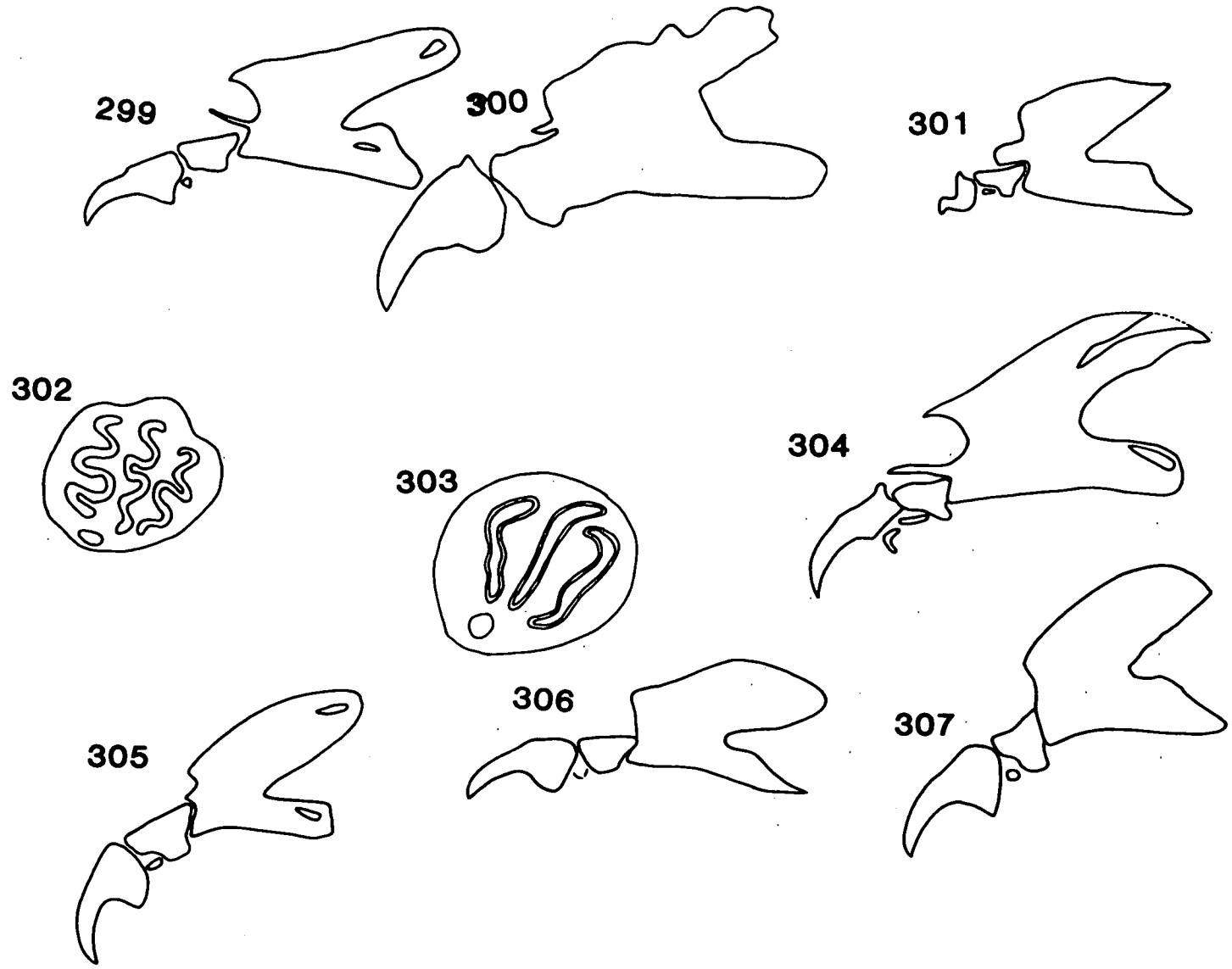
Figs. 299-307 (x70). (299) Third instar Cordylobia anthropophaga, (300) Third instar Cordylobia rodhaini, (301) Third instar Cordylobia ruandae, (302) Posterior spiracle, Cordylobia rodhaini, (303) Posterior spiracle, Cordylobia ruandae, (304) Third instar Auchmeromyia luteola, (305) Third instar Booponus intonsus, (306) Second instar Elephantoloemus indicus, (307) Third instar Elephantoloemus indicus.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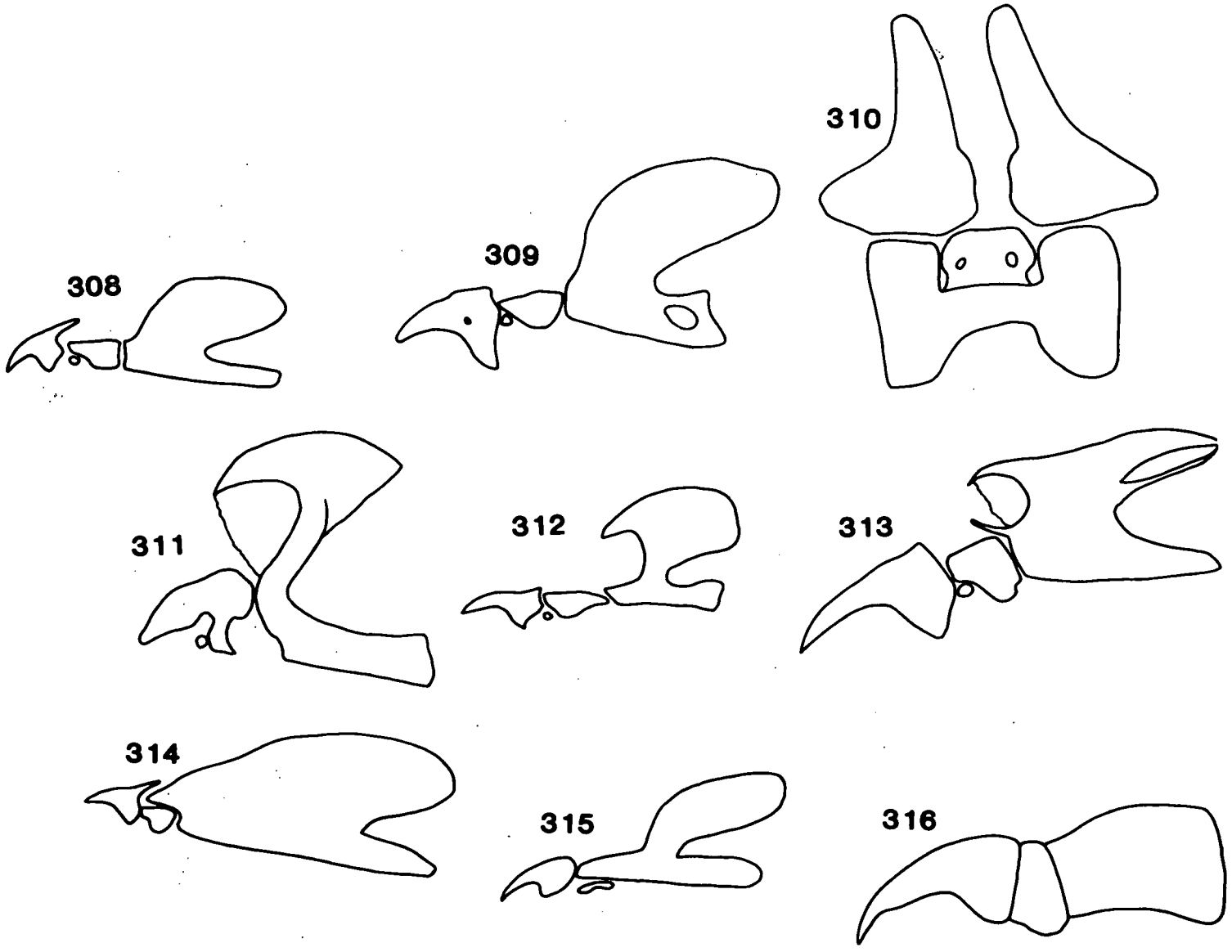
Figs. 308-316. Skeletons of Tachinidae (x75; except (310) = x130). (308) Argyrophylax aureiventris, (309) Zygobothria ciliata, (310) Z. ciliata ventral view of anterior end, (311) Schistocercophaga dampfi, (312) Medina egregla, (313) Therobia abdominalis, (314) Plesiocyptera sp., (315) Actia painei, (316) Phryxe vulgaris.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Figs. 317-323. Skeletons. (317) Sarcophaga argyrostoma (x70), (318) Helicophagella melanura (x120), (319) Physocephala sp. (x70), (320) Gyrostigma pavesii (x55), (321) G. pavesii (ventral) (x55), (322) Platycobboldia loxodonta (ventral) (x55), (323) Gasterophilus pecorum (x55).

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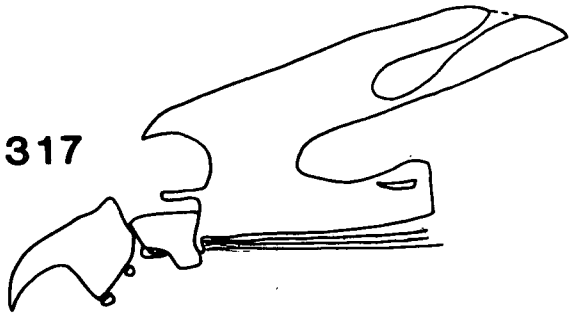

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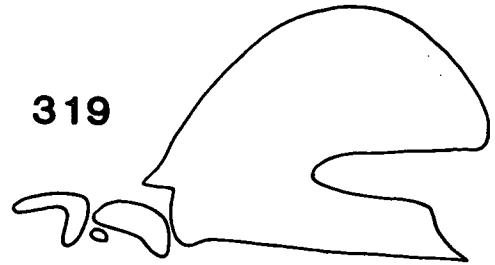

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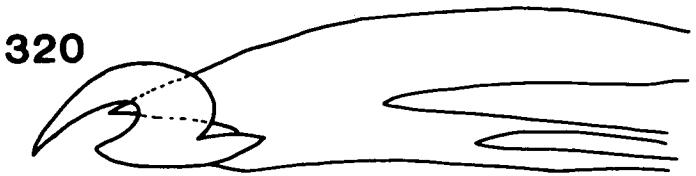

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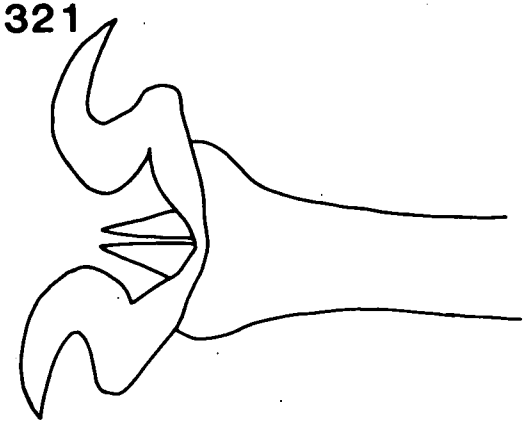

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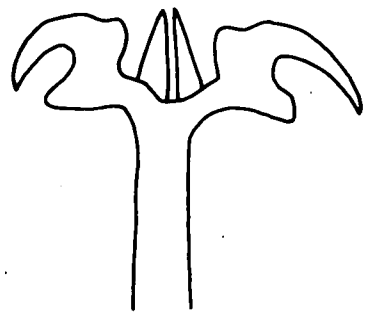

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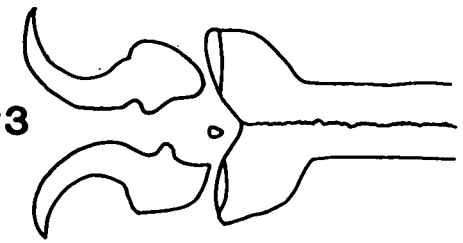
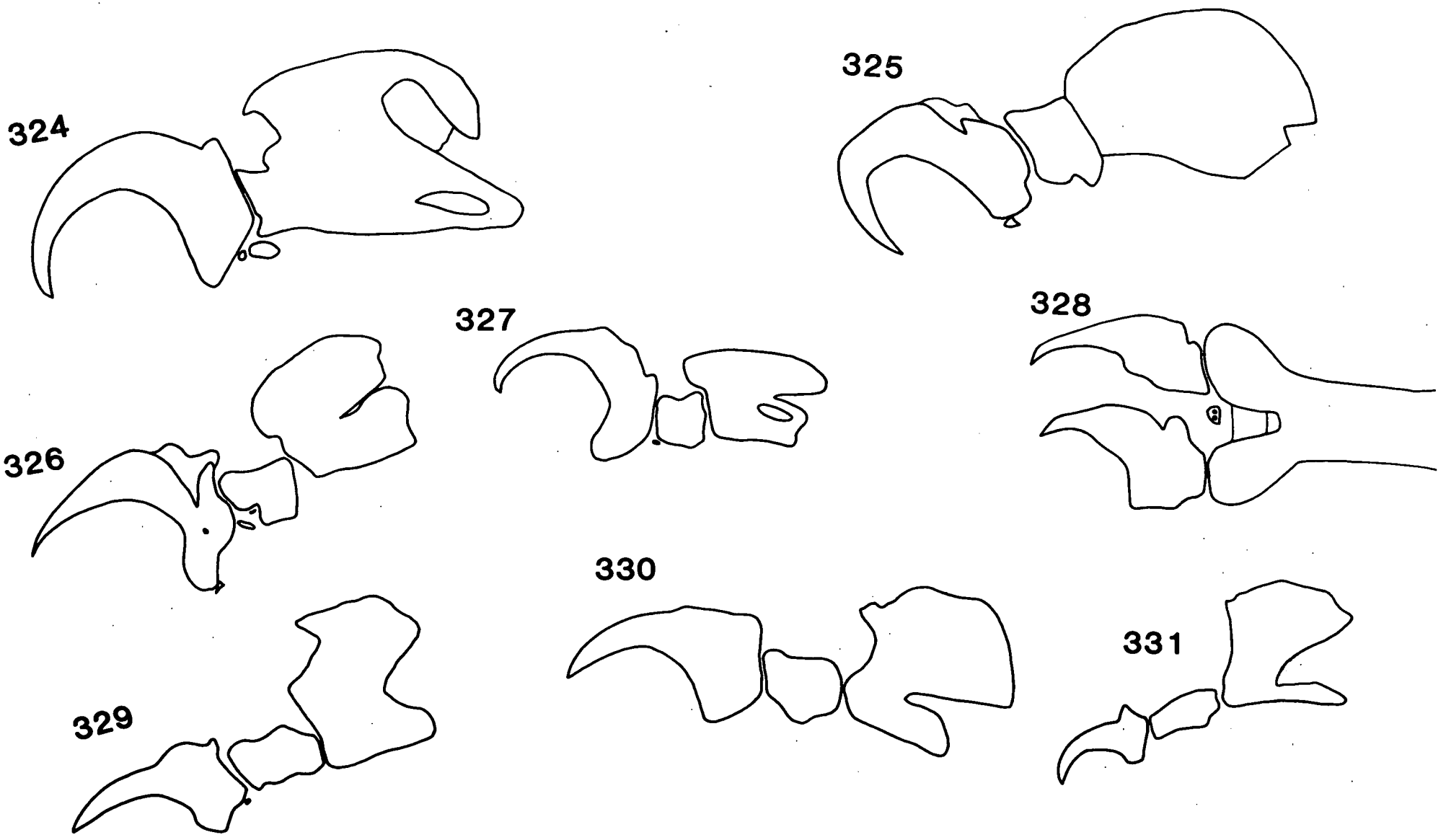


Figs. 324-331. Skeletons (x55). (324) Tracheomyia macropi, (325) Pharyngobolus africanus, (326) Oestrus ovis, (327) Rhinoestrus vanzyli, (328) Cephenomyia auribarbis, (329) Cuterebra sp., (330) Dermatobia hominis, (331) Alouattamyia baeri.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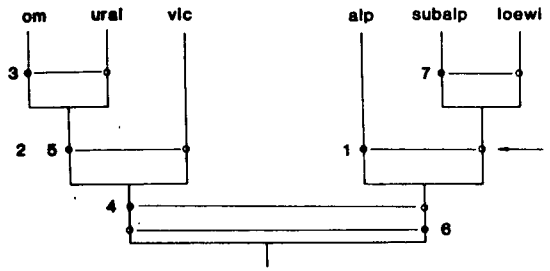
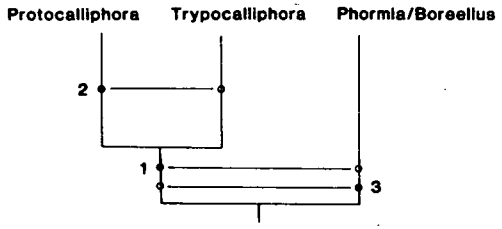
Figs. 332-336. Cladograms. (332) British Calliphora species (Characters: 1 = Cuticle structure, 2 = SDF, 3 = Spines, 4 = SDF, 5 = Anal spine pattern, 6 = Anterior spiracle, 7 = Ventral cornu), (333) Phormiinae genera (Characters: 1 = Spines, 2 = Oral hairs, 3 = Posterior papillae), (334) Chrysomya species groups (Characters: 1 = Body processes, 2 = Posterior spiracle, 3 = Oral sclerite, 4 = Spines, 5 = Posterior spiracle, 6 = Parastomal bars, 7 = Hypostomal plates), (335) Cordylobia species (Characters: 1 = Parastomal bars, 2 = Mouth-hook, 3 = Spines, 4 = Posterior spiracle), (336) Genetic and phylogenetic relationship not necessarily identical (C = Cow, L = Lungfish, S = Salmon).

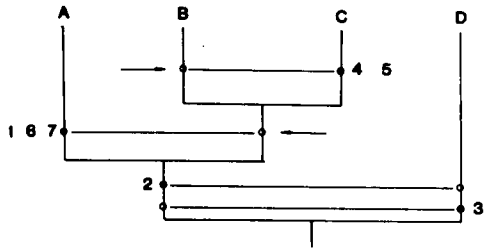
332 CALLIPHORA



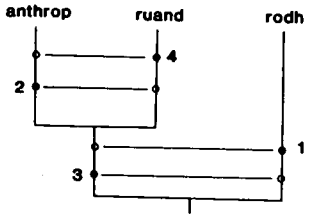
333 PHORMIINAE



334 CHRYSOMYA



335 CORDYLOBIA



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