CRETACEOUS DIPTERA FROM ORAPA, BOTSWANA

VOLUME ONE

SASKIA WATERS

A DISSERTATION SUBMITTED TO THE FACULTY OF SCIENCE, UNIVERSITY OF THE WITWATERSRAND, JOHANNESBURG, FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

JOHANNESBURG, 1990

ABSTRACT

An assemblage of Cretaceous Diptera, recovered from the sediments of the Orapa Diamond Mine, Botswana, is described.

The fossil Diptera are placed in the following families: Tipulidae, Empididae, Hybotidae, Bibionidae, and possibly the Mycetophilidae, Rhagionidae and Anisopodidae. A new pulid species, Helius botswanensis (Tipulidae, subfamily Limoniinae), is described; it is the oldest representative of the subfamily. Eleven other tipulids are described; these are not as distinctly preserved and can not be classified to lower than family level with confidence (eight probably belong to the subfamily Limoniinae). Two new species, Empis orapaensis sp. nov. (Empididae, subfamily Empidinae) and Pseudoacarterus orapaensis gen. et sp. nov. (Hybotidae, subfamily Hybotinae) are the earliest record of their respective subfamilies (they are the only Mesozoic members of these families from the southern hemisphere). Specimens which probably belong to the families Mycetophilidae and Rhagionidae and/or Tabanidae are described, together with the wing of a possible Rhagionid. Ten poorly preserved dipterans of unidentified families are also recorded and illustrated; some tentative identifications include the families Mycetophilidae and Anisopodidae. Four specimens of the family Bibionidae form the basis of a new genus and species, Cretobibionida anticus.

The fossils reveal details of the palaeoenvironment of the Orapa region. The fauna lived in a crater formed by the eruption of a Kimberlite pipe. The Diptera fed and bred near the crater lake, in a warm, humid, probably well-wooded or shrubbed habitat, with seasonal rainfall. The Diptera were early pollinators of angiosperms.

The concept of fossil species is discussed. Many of the dipterans show remarkable stasis.

DECLARATION

I declare that this dissertation is my own unaided work. It is being submitted for the degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

(Name of candidate)

------------ day of -------------1990

ACKNOWLEDGEMENTS

I would like to thank the Office of the President and the National Museum of Botswana, and the Debswana Mining Company for the invitation and permission to collect fossils. The latter also provided accommodation and financial support. Also, I acknowledge the financial support provided by the Council of Scientific and Industrial Research and the University of the Witwatersrand.

I am grateful for the help of the following people in the collection of fossils from Orapa: Prof. J. Kitching; Drs R.J. Rayner, J. Maguire, C. Gow, J. Masters; Mr. I.J. McKay, Mrs. M.K. Bamford, Mr. A. Potts, Mr. and Mrs. P. Forchammer, Miss G. Goelst, Mrs. A. Cadman, Mr. A. Cambell, Miss C. Kleinjan, Mr. P. Bender and Mr. B. Weissenbacher.

My grateful and special thanks to Dr. Richard Rayner for endless support and supervision, and, for helpful comments and discussion, I am indebted to my friends Ian McKay and Marion Bamford.

With appreciation, I wish to acknowledge the help of the following people for providing me with valuable information or access to their facilities: Dr. P.S. Cranston and Dr. R.I. Vane-Wright (British Museum, Natural History), Dr. W. Krzemiński (Polish academy of Sciences, Krakow) and various anonymous referees and Tipulid specialists for providing extensive comments on the tipulid described in Chapter 2 (and Appendix 1); Dr. K.G.V. Smith (British Museum, Natural

History) for checking the identification of the empid and the hybotid in Chapters 4 & 5, and, for reading and improving drafts of the manuscripts (Appendix 2 & 3); Dr Paul Selden (Manchester University, U.K.) and Dianne Edwards (Cardiff University), for criticism and help with the aphid (Appendix 4) and Hybotid papers (Chapter 5; Appendix 3); Drs I. Gauld and J. Cox (British Museum, Natural History) who edited the Empid paper; Dr. O.E. Heie (Institute of Biology, Royal Danish School of Educational Studies) for constructive criticism of the aphid (Chapters 1 & 8; Appendix 4); Dr. Judith Masters for constructive advice on Chapter 9; Dr. B. Levey (British Museum, Natural History) and D. Cullinane (Botanical Museum, Harvard University) for sending references which were unobtainable in South Africa; Dr. C. Feather of AARL for permission to use his company's microscope; Ian McKay and Desirée Pearce and especially Dick Rayner, and, my sister Sandra Schermacher and Brian Griffin (De Beers Marine, Cape Town) for help with the photography and loan of equipment and materials; the Graphics Department at the University of the Witwatersrand for photographing most drawings. Special thanks go to my husband Keith Waters for constructive criticism and printing of many drafts, plotting of fig. 39, and, especially for support and encouragement, and, Mr. A.D. Waters (Barlow Rand Computer Division, Johannesburg) for making his photocopier available to me.

CONTENTS

VOLUME I

CHAPTER ONE - INTRODUCTION

CHAPTER TWO - SUPERFAMILY TIPULOIDEA: TIPULIDAE

CHAPTER THREE - OTHER TIPULIDAE

CHAPTER FOUR - SUPERFAMILY EMPIDOIDEA: EMPIDIDAE

CHAPTER FIVE - SUPERFAMILY EMPIDOIDEA: HYBOTIDAE

CHAPTER SIX - SUPERFAMILY MYCETOPHILOIDEA:

MYCETOPHILIDAE AND TABANOIDEA: RHAGIONIDAE

CHAPTER SEVEN - UNIDENTIFIED DIPTERANS

CHAPTER EIGHT - SUPERFAMILY BIBIONOIDEA: BIBIONIDAE

CHAPTER NINE - DISCUSSION AND CONCLUSIONS

APPENDICES: PUBLICATIONS

1. Rayner, R.J. & Waters, S.B., 1990. A Cretaceous Crane Fly (Diptera: Tipulidae): 93 Million Years of Stasis. *Zoological Journal of the Linnaean Society of London*, in press.

2. Waters, S.B., 1989a. A Cretaceous Dance Fly (Diptera: Empididae) from Botswana. *Systematic Entomology*, 14: 233-241.

3. Waters, S.B., 1989b. A New Hybotine Fly from the Cretaceous of Botswana. *Palaeontology*, 32: 657-667.

4. Rayner, R.J. & Waters, S.B., 1989. A New Aphid from the Cretaceous of Botswana. *Palaeontology*, 32: 669-673.

VOLUME II: FIGURES:

LIST OF FIGURES:

CHAPTER ONE: INTRODUCTION:

CHAPTER TWO: TIPULIDAE:

SPECIMEN BP/2/26000a (part) and BP/2/26000b (counterpart).

CHAPTER THREE: OTHER TIPULIDAE:

CHAPTER FOUR: EMPIDIDAE:

37. *Empis orapaensis*: (BP/2/26943), whole specimen; insert, the hypopygium, enlarged.
38. *E. orapaensis*: (BP/2/26943), composite drawing of left and right wing.
39. Presumed phylogeny of the Empidoidea.
40. Hunting and mating of *Rhamphomyia nigrita* (subfamily Empidinae).
41. Distribution in southern Africa of *Empis* (subgenus *Coptophlebia*).

CHAPTER FIVE: HYBOTIDAE:

42. *Pseudoacarterus orapaensis* (BP/2/25224a – part), whole specimen.
43. *P. orapaensis* (BP/2/25224b – counterpart), whole specimen.
44. *P. orapaensis* (BP/2/25224a and b), composite drawing of the wings (left and right of part and counterpart).
45. Wing of *Trichinites cretaceus*.
46. Distribution in southern Africa of *Acarterus*, *Syndyas* and *Sabinios* (Hybotidae: Hybotinae).

CHAPTER SIX: MYCETOPHILIDAE:

47. SPECIMEN 1: (BP/2/22455), whole specimen. Inset, chaetotaxy on legs.
48. SPECIMEN 2: (BP/2/25896), wing.
49. SPECIMEN 3: (BP/2/18217), whole specimen.

CHAPTER SEVEN: UNIDENTIFIED DIPTERANS:

CHAPTER EIGHT: BIBIONIDAE:

CHAPTER NINE: DISCUSSION:

LIST OF PLATES:

CHAPTER ONE:

PLATE 1:

A. Rubble removal in the Orapa open-pit mine, Botswana

B. Access road into the interior of the "crater".

C. Sequential deepening of pit by "terracing" at 10m intervals.

D. One of the students collecting rock samples at various levels of one of the 10m high exposed rock faces.

E. Layered mudstones breaking up neatly along bedding planes, providing fairly easy access to the fossils compressed between these layers.

CHAPTER TWO:

PLATE 2:

SPECIMEN BP/2/26000a (part) and BP/2/26000b (counterpart), ♂.

A. Composite photograph of the specimen.

B. Details of the hairs on the specimen's leg.

C. Hairs on the leading edge of the wing.

D. Enlarged view of the specimen's compound eyes.

E. Hypopygium.

CHAPTER THREE:

PLATE 3:

A. SPECIMEN 1: (BP/2/27578a - part), whole specimen.

B. SPECIMEN 1: (BP/2/27578b - counterpart), whole specimen.

C. SPECIMEN 1: (BP/2/27578a - part), wing.

D. SPECIMEN 1: (BP/2/27578b - counterpart), w

PLATE 4:

A. SPECIMEN 2: (BP/2/25228), whole specimen.

B. SPECIMEN 3: (BP/2/25843), whole specimen (wing).

C. SPECIMEN 4: (BP/2/25939), whole specimen.

D. SPECIMEN 4: (BP/2/25939), details of left wing.

PLATE 5:

A. SPECIMEN 5: (BP/2/25948), whole specimen.

B. SPECIMEN 5: (BP/2/25948), details of head and thorax.

C. SPECIMEN 6: (BP/2/26717), whole specimen.

D. SPECIMEN 7: (BP/2/25871), whole specimen.

PLATE 6:

A. SPECIMEN 8: (BP/2/25919), whole specimen.

B. SPECIMEN 8: (BP/2/25919), details of head.

C. SPECIMEN 9: (BP/2/25269), whole specimen.

D. SPECIMEN 9: (BP/2/25269), details of head.

PLATE 7:

A. SPECIMEN 10: (BP/2/28228), whole specimen.

B. SPECIMEN 10: (BP/2/28228), details of head.

C. SPECIMEN 11: (BP/2/28229), whole specimen.

CHAPTER FOUR:

PLATE 8:

Empis orapaensis sp.n., holotype, BP/2/26953, ♂.

A. Whole specimen.

B. Left haltere.

C. Genital segments.

D. Tibia showing well-developed chaetotaxy.

E. Anterior margin of wing showing michrotrichia on blade and stout bristles on the costa.

F. Chaetotaxy of a section of the abdomen.

CHAPTER FIVE:

PLATE 9:

<u>Pseudoscarterus orapaensis</u> gen. et sp. nov.
(BP/2/25224a - part).

A. Whole specimen.

B. Haltere.

C. Tibia and tarsi with 2 pectinate claws.

<u>P. orapaensis</u> (BP/2/25224b - counterpart).

D. Whole specimen.

CHAPTER SIX:

PLATE 10:

A. SPECIMEN 1: (BP/2/22455), whole specimen.

B. SPECIMEN 1: (BP/2/22455), details of head.

C. SPECIMEN 2: (BP/2/25896), wing.

D. SPECIMEN 3: (BP/2/18217), whole specimen.

CHAPTER SEVEN:

PLATE 11:

A. SPECIMEN 1: (BP/2/26238), whole specimen.

B. SPECIMEN 2: (BP/2/fragment), whole specimen.

C. SPECIMEN 3: (BP/2/25974), whole specimen.

PLATE 12:

A. SPECIMEN 4: (BP/2/26852), whole specimen.

B. SPECIMEN 5: (BP/2/25248), whole specimen.

C. SPECIMEN 6: (BP/2/25911), whole specimen.

D. SPECIMEN 7: (BP/2/2585[illegible]), whole specimen.

PLATE 13:

A. SPECIMEN 8: (BP/2/22455), whole specimen.

B. SPECIMEN 8: (BP/2/22455), details of head.

C. SPECIMEN 9: (BP/2/26872), whole specimen.

D. SPECIMEN 10: (BP/2/26238), whole specimen.

PLATE 14:

A. SPECIMEN 2: (BP/2/22453), whole specimen.

B. SPECIMEN 3: (BP/2/22455), whole specimen.

C. SPECIMEN 1: (BP/2/22454), whole specimen.

D. SPECIMEN 4: (BP/2/22456), whole specimen.

CHAPTER ONE

INTRODUCTION

1.1. LOCALITY

The Orapa diamond mine (2125 A/K1) is located over a kimberlite pipe in the Central District of Botswana, approximately 220km west of Francistown at 21°17'S and 25°21'E (Fig. 1). The surrounding area has an average elevation of 960m above sea level, and the countryside is flat with a few low hills and ridges (Allen, 1981). The climate is semi-arid, with an average rainfall of approximately 500mm. Rainfall is sporadic and, when it occurs, sudden rainstorms are characteristic. Temperature varies from 42°C in summer to 0°C in winter. The surrounding vegetation consists of small mopane trees and grasslands (Allen, 1981).

1.2. GEOLOGY

The subsurface geology of the area is a typical Karoo sequence, with Stormberg-age (Lower Jurassic) basalts at the surface (Fig. 4). Underlying these are cave-sandstones (Lower Jurassic), and below this are the shales of the Ecca stage (Lower Permian). Overlying the Karoo sequence are wind-blown sands, calcretes, silts and silcretes of Kalahari age (Tertiary).

The diamondiferous orebody is a kimberlite pipe, overlain by kimberlitic sedimentary rocks contained within a crater approximately 80m deep and 1km in diameter (Plate 1: A-E). This is illustrated in Fig. 2 (a simple aerial plan) and Fig. 3 (a cross-section). Figure 4 represents a 3-dimensional reconstruction of the north-eastern sector of the volcano, and illustrates the crater, its surroundings and the interior at a time shortly after the eruption. Mass movement of material by gravity avalanching and wet viscous debris flows caused the collapse of parts of the volcanic cone and rim into the crater, placing the sediments in their present positions (that is before mining operations started removing them).

In the following section I intend to review briefly the types of sediment found in the crater, and what fossils they have yielded. In addition, data on the age of the eruption and burial of the fossils are presented. These subjects are dealt with in more detail in a manuscript (in preparation) of which I am co-author.

Four types of sediments have been distinguished (Dobbs, 1978).

(a) Coarse sediments, in the form of steeply dipping talus and shallow dipping debris flows, around the 5km circumference of the crater in 3 major fans.

(b) Granular mud flows within the borders of the above.

(c) A few fluvial sediments.

(d) Fine-grained sediments (the playa group) composed of

> shales. These sediments probably preceded and followed the granular mudflows with which they are interbedded. These fine-grained sediments were also probably deposited by the settling out from suspension in a crater lake, after subaqueous mudflows had occurred.

It is within these fine-grained shales and mudstones (Plate 1: D) that fossil insects and plants have been found (Figs 2 & 3). The coarser sediments, although far richer in diamonds, have yielded only a few, rather poorly preserved fossils.

Several kimberlite pipes (including Orapa), located within the Transvaal Craton, have given radiometric ages ranging between 95.4 and 81.7 million years (Myr) (Davis, 1977). Orapa has been so dated at 93.1 Myr, or around the Cenomanian/Turonian boundary in the Upper Cretaceous. The dates are based on estimates of the accumulation of lead isotopes (the decay products of uranium) within zircon crystals in the kimberlite. Additional results from fission track dating of the Orapa zircons have given results of 87.4 ± 5.7 Myr, and 92.4 ± 6.1 Myr (Haggerty et al., 1983). A palynological study has been carried out on the sediments which also indicates an early Upper Cretaceous age (Scholtz, pers. comm.).

The radiometric dates represent the time of eruption of the kimberlite, or, more correctly, the time of the lowering of the temperature of the zircons below 1 200°C (McKay & Rayner, 1986). However, it seems likely from the nature of the erupted kimberlite, the sediments, and the basin, that the crater would have taken little time to fill, perhaps less than 0.5 Myr (McKay & Rayner, 1986), or even as little as 200 000 yrs in the case of a similar pipe (Smith, 1986). The age difference between the kimberlite and the sediments may, therefore, not be significant. In addition, the recent study of the sediments shows that much of the fine material represents turbidite deposition. This is also consistent with a rapid sedimentation rate.

McKay (1987) stated that inferences from the insect fossil fauna of Orapa, particularly the carabid beetle _Palaeoaxinidium_, support the radiometric and palynological dates of Upper Cretaceous for the deposition of the sediments.

1.3. FOSSIL FAUNA AND FLORA OF ORAPA

The sediments of the Orapa Diamond Mine have already yielded a large number of fossil insects and plants (Dobbs, 1978; McKay & Rayner, 1986; Rayner & McKay, 1986; Rayner, 1987; McKay, 1987; Waters, 1989a & b; Rayner & Waters, 1989; Bamford, 1989; Rayner & Waters, 1990). The assemblage is entirely of a terrestrial nature, with the exception of two tentative identifications: one of a gyrinid, the other an Odonata. Indeed, there are neither aquatic organisms nor trace fossils (burrows and tracks of, for example, insect larvae) that would indicate the presence of animals living within the lake or its sediments.

Some of the fossils, the insects particularly, are so exquisitely preserved that specimens have been placed not only into extant families, but subfamilies, tribes and even in recent genera, or subgenera (McKay, 1987; Waters, 1989a & b; Rayner & Waters, 1989; Rayner & Waters, 1990). In addition, some extinct forms have been found (McKay, 1987; Water 989b; Bamford, 1989). Almost 6 000 specimens have been recovered from the mine, from 15 sites. In this collection 44% are plants, 51% are insects and 5% are unidentified fragments (McKay, 1987).

The flora of Orapa (Bamford, 1989) has been grouped into five categories.

(a) Pteridophyte (fern) fragments (9%).
(b) Angiosperm flowers (14%).
(c) Leaves (45%), belonging to the Lauraceae, Cunoninaceae, Hamamelidaceae, palmate Dilleniidae, Saxifragales.
(d) Stems (15%).
(e) Seeds (17%).

Small amounts of charcoal, indicating the possible presence of natural fires, were also collected.

Amongst the insects, most modern orders are represented, however, 46.67% of the total cannot be identified. The remaining 53.33% comprises the following taxa (as listed by

McKay, 1987) (with a few additions which are referenced).

(a) Blattodea (cockroaches) (10.83%).

(b) Dermaptera (earwigs) (0.8%).

(c) Orthoptera (grasshoppers, locusts and crickets) (1.31%).

(d) Hemiptera (bugs) (3.08%) - A member of the Aphidoidae (Genus Siphonophoroides) has been found (Rayner & Waters, 1989).

(e) Coleoptera (beetles) (35%) - Five families have been identified.

i. Carabidae (ground beetles), with the following four subfamilies as Cretaceous representatives: Promecognathinae, Scaratinae, Harpalinae, Anchomeninae;

ii. Staphilinidae (rove beetles);

iii. Scarabaeidae (dung, rose and rhinoceros beetles);

iv. Elateroidea (click beetles);

v. Curculionoidea (weevils).

(f) Diptera (flies) (4.05%) - Approximately five definite and three possible families are represented in the collection; Fig. 68 is a diagramatic representation of their relative percentages.

i. Tipulidae (crane flies) with representatives of the subfamilies Limoniinae (Rayner & Waters, 1990) and Tipulinae; Figs 11-36 illustrate 12 Tipulidae.

ii. Bibionidae (march flies) - subfamily Bibioniinae. (Rayner, 1987); 4 specimens are illustrated in Figs 64-67.

iii. Empididae (dance flies) - subfamily Empidinae (Waters, 1989a); Figs 37 & 38.

iv. Hybotidae - subfamily Hybotinae (Waters, 1989b); Figs 42-44.

v. Mycetophilidae - Figs 47 & 50.

vi. ?Rhagionidae - Figs 48 & 49.

vii. ?Anisopodidae - Figs 53 & 54.

(g) Hymenoptera (wasps only, no bees or ants have been collected) (3.96%). The families (i) Ichneumonidae and (ii) Braconidae (both parasitic wasps of the suborder Apocrita) are represented, as is the superfamily (iii) *Proctotrupoidea*.

In addition, two other arthropods have been identified in the assemblage belonging to the order Arachnida.

In contrast, there have been no other animal remains reported or collected from the mine sediments (Dobbs, 1978). McKay and Rayner (1986) and McKay (1987) indicated possible reasons for their absence. They concluded that the most likely reason was that the lake waters were poisoned by excess salinity or volcanic residues and that most plants and insects preserved in the sediments came from outside the lake.

The plants were more abundant in the higher levels of the succession, whereas the insects in the lower parts, suggesting an increase in floral diversity and abundance only at later stages of the infill of the crater.

1.4. METHODS AND MATERIALS

Material was collected from 15 different sites in the Orapa Mine during several trips to the mine from 1983 to 1988. Large blocks of rock were removed from the various rock faces exposed by mining activities, a relatively easy task since, after blasting, blocks break away along clean, neat and more or less horizontal bedding planes (Plate 1: D & E). Pieces bearing fossils were easily identified. These were immediately wrapped in newspaper to prevent cracking due to rapid heating and drying of blocks in the sun. Cracks were treated with Glyptal (a lacquer cement produced by <u>General Electric</u>) to avoid further fracturing of the pieces. Care was taken that Glyptal was not painted onto the fossils since this causes excessive glare when viewed under the microscope.

Specimens are currently housed at the Herbarium of the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa. In due course, many of these will be lodged in the National Museum in Gaborone, Botswana.

Specimens were not prepared in any way before observing them under a microscope as the shales and mudstones are extremely brittle. Cleaning a specimen with a fine paint brush, or with an inseot mounting needle caused unwanted flaking of fine delicate layers. Before observation, the specimen was lightly dusted with a blower brush.

Specimens were observed and photographed using a Zeiss SV8 microscope (some were photographed with a Zeiss Pyramid photomicroscope) using Ilford Pan F film. Specimens were illuminated with the aid of fibre-optic lights with polarising filters; fine details of the fossiliferous material were enhanced in this manner. A <u>camera-lucida</u> and photograph-projector were used for the detailed drawings. In these, dense or sparse dotting/shading indicates the amount of organic matter remaining. To make the thesis more convenient to use, plates and figures are in a separate volume from the text.

Classification and terminology (Figs 5,6,7 & 8) follow that of McAlpine (1981), except in Chapters 4 & 5 which concern the superfamily Empidoidea; here, a more recent classification system is employed (i.e. after Chvála, 1983).

Mode of fossil preservation at Orapa: all fossil dipterans are coalified compressions; only the rhagionid/?tabanid (Chapter 6) displays some relief.

1.5. DIPTERANS AS A RESEARCH TOPIC

Of the insect orders, I chose to study the Diptera for the following reasons.

(a) Sediments deposited in the crater are relatively rich in fossil dipterans. The quality of preservation is generally good, and in some cases excellent. Study material was therefore readily available.

(b) Very little is known about Cretaceous dipterans; much more information is available on dipterans of the periods preceeding and following the Cretaceous era (Rohdendorf, 1974; Hennig, 1981). The Cretaceous is, however, of great significance, as it is then that we see the sudden appearance of angiosperm dominated floras. It was also a period of many other major geological and climatic changes, and a time of faunal extinctions and origins.

(c) The taxonomy, biogeography and ecology of extant Diptera are relatively well understood. This is necessary for comparison of fossil specimens to modern species. It is also essential for interpreting the environment, climate and geography of the area at the time the fossil lived, and it is a prerequisite for interpretations of the biology of the fossil. Thus, study of Cretaceous Diptera enables conclusions to be drawn with regard to the palaeoenvironment of the Orapa region. Knowledge of the modern species is also necessary to gauge the implications of the fossil in evolutionary patterns.

(d) The fossils may provide details of the phylogeny of the Diptera. Data on Cretaceous Diptera are lacking. It should be noted, however, that the phylogeny of the diptera (and all other animal and plant groups for that matter), can only partially be described with the aid of fossils. Temporal and spacial deficiencies of fossil material are real, and fossil material, when available, is often incomplete. Also, the material only allows for the morphology of the organism to be studied, all other aspects need to be deduced. Deductions are necessary as phylogeny is not defined on morphological characters alone but also on the behaviour, preferences and relationships of a fossil (when still living) compared to its contemporaries, members of a modern, extant order, family or sometimes even genus.

1.6. INTRODUCTION TO THE DIPTERA

The Diptera constitutes one of the largest orders of insects, with more than 150 000 described and undescribed species in the world fauna (Colless & McAlpine, 1970). There are 16 318 valid species in the Afrotropical Region (Crosskey et al., 1980) and these are distributed in 2 009 genera; an average of 8.12 species per genus. This is consistent with averages calculated for the other major zoogeographical regions studied (the Nearctic and Oriental Regions). The Diptera is an extremely successful and highly diverse order; however, the factors responsible for this are still not clearly understood (Hennig, 1973 & 1981).

The order comprises many common and familiar forms, a number of which are of economic importance. Mosquitoes, black flies, horse flies, stable flies and others are bloodsucking and are serious pests of humans and animals, and many are vectors of disease. This is particularly a problem in tropical Africa. Others, by virtue of their parasitic or predatory habits, are beneficial, playing an important role in regulating the populations of numerous plants and animals that adversely affect human welfare. Even the most primitive Diptera are known to be predators on other insects (Downes, 1958). Their role in the pollination of plants is also of vital importance. There are also, unfortunately, a great many forms which, due to the fact that they are neither advantageous or a nuisance to humans, are inadequately known.

Among Mesozoic insect fossils, the Diptera are better represented than any other group (Remm, 1976; Hennig, 1981), and, as a palaeontologist, this stimulated my interest in the group as a whole. As a result of this relatively good fossil record, the phylogeny of the Diptera has already been the subject of a number of studies (Hardy, G.H., 1951a . & 1951b; Rohdendorf, 1974; Hennig, 1954, 1973 & 1981).

1.6.1 DIAGNOSTIC CHARACTERS OF THE DIPTERA

Of primary importance in this study has been an understanding of the means of identification between various groups of insects and, more specifically, recognition of the Diptera. A knowledge of the groundplan characteristics of the order was therefore essential. This was even more important, since much of the fossil material is fragmentary.

Hennig (1973) listed the known derived groundplan characters of the body parts of the Diptera in general. In two other papers (Hennig, 1954 & 1981), he discussed in more detail what he considered to be the fundamental features of the typical groundplan wing.

In adult Diptera, as with many other insects, wing venation is the main feature used for identification of recent as well as fossil specimens. The ground-plan venation of a typical dipteran wing is illustrated in Figs 8 & 9. The two illustrations show the same basic wing venation; however, the terminology in Fig. 8 (McAlpine et al., 1981) is more up to date and a pterostigma and anal lobe are included, in contrast with Hennig's original illustration (Fig. 9). The wings are the only parts normally preserved in detail in the Orapa fossils, therefore I list the main characteristics below.

(a) With a few exceptions, most Diptera can be readily distinguished from other insects by the possession of a single pair of wings, the fore wings. The hind wings are reduced to small club like organs called halteres; these serve as structures of equilibrium, and their presence is usually sufficient to identify adult status. (Dipteran larvae are not as readily distinguished from larvae of other insect orders: the former are mainly characterised by the absence of thoracic legs and spiracles that cannot close). The halteres also distinguish the

Diptera from its closely-allied sister group, the Mecoptera.

(b) The base of the front wings is narrow.

(c) The costa (C) is present around the entire wing edge.

(d) The hind branch of the subcosta (Sc_2) is partially merged with R_1.

(e) The radial sector is dichotomously forked, and four free branches reach the wing margin. MA^+ is fused with the last branch R_5. (This, however, is not confined to the Diptera, but is characteristic of most Neoptera).

(f) MP^- is the only representative of the media in the Diptera (as in most Neoptera), and it is also dichotomously forked into four branches. However, the fourth branch (M_4) is not free but is fused with the anterior branch of CuA_1.

(g) The cubitus has only one free branch (CuA_2).

(h) The posterior vein of the cubitus (CuP) is reduced and only slightly sclerotised; its basal part, developed as a vein, is closely pulled towards CuA, and, the distal part is only visible as a fold.

(i) Two anal veins are present (A_1 and A_2).

(j) There are very few crossveins in the Diptera:

-there is no crossvein between the two anal veins (A_1 and A_2) which are part of the groundplan of the Diptera.

-the costal and subcostal fields are almost entirely without crossveins. In the costal field, only the humeral (h) crossvein has been retained.

- there is a connection between the posterior branch of the radial sector (R_{4+5}) and the anterior branch of the media (M_{1+2}) and this has been called the anterior crossvein (ta). It is not considered to be a true crossvein.
- the so-called posterior crossvein (tp) between M_2 (or M_1+M_2) and M_3 is a true crossvein.
- a connection resembling a crossvein (earlier called tp, now sometimes m-m) also exists between the posterior edge of the discal cell and CuA_2. In the groundplan of the Diptera, this consists of two sections, probably corresponding to the basal sections of CuA_1 and M_4.

1.6.2. PHYLOGENY AND GENEALOGY OF THE DIPTERA

The Diptera, together with its sister group the Mecoptera, probably represent a monophyletic group of higher order, the Mecopteroidea (Neoptera: Holometabola) (Hennig, 1981). Dipteran wings may be differentiated from those of the Mecoptera by the possession of halteres, the Sc_2 vein which is partially merged with R_1, the CuP vein which is reduced, and the presence of two anal veins; there are however numerous other characters not related to the wings (Hennig, 1954, 1973 & 1981). There are also numerous similarities between the sister groups [see Hennig (1981) for a review and complete list].

The Upper Permian group, the Paratrichoptera (otherwise known as the Protodiptera), seems to be the most likely ancestor (or stem group) of the Diptera (Hennig, 1973). This, however, has not yet been confirmed directly by any specific fossil find. Several species, Laurentiptera gallica Willmann, Permotipula patricia Hennig and Pseudopolycentropus latipennis Hennig have previously (and individually) been considered as possible members of the stem group by various authors, but these are now regarded as controversial (Hennig, 1981).

The probable existence of the Mecoptera (Nannochoristidae) in the Upper Permian provides the best, although indirect, evidence that the Diptera were in existence in the Palaeozoic. It is as yet, however, impossible to trace any of the subgroups of the Diptera back to this time (Hennig, 1981). A controversial fossil, Permotipula patricia, from the Upper Permian of Warner's Bay (New South Wales), described by Tillyard (1929 & 1937), was initially thought to be the earliest dipteran. Its wing venation resembles that of the typical dipteran ground plan venation in nearly all aspects. It was, however, later excluded from the order on the basis of the presence of a pair of hind wings (Hennig, 1954).

The oldest fossils that can be reliably assigned to the Diptera (sensu stricto) are from the Mesozoic; they are known from wing impressions of the Upper Triassic of Middle Asia (Hennig, 1973). Indeed, various subgroups are distinguishable as early as the Upper Triassic: i.e. *Architipula radiata* (Tipulomorpha), *Architendipes tshernovskyi*, *Palaeotendipes alexii* (Chironomidea), and about 30 fossils with partly derived venation that probably belong to a variety of subgroups of the Bibionomorpha (Hennig, 1973).

The Jurassic has so far been the richest source of dipteran fossils, the Upper Triassic less so and the Cretaceous rather poor. This makes the position of monophyletic groups within orders difficult to establish. Also, the more subordinate the group, the more difficult it is to detect the morphological details required for phylogenetic classification (Hennig, 1981).

Two suborders are usually recognised within the Diptera, the Nematocera and Brachycera. Representatives of the Nematocera are known from the Upper Triassic, and members of the various subgroups of the Brachycera are first seen in the Lower Jurassic (e.g. *Protobrachyceron*) (Hennig, 1973). Details of the derived groundplan characteristics of the Nematocera and Brachycera and the various subgroups below are listed in detail in Hennig (1973). The genealogy of the Diptera outlined below follows that of Hennig (1981) unless otherwise stated. Hennig (1954) provided a detailed account of what procedures he followed to form the dipteran groupings and trace their lines of descent, and how it was possible to deduce whether similarities of a character or characters between two or more groups indicated symplesiomorphy, synapomorphy or convergence. He tabulated and summarised his findings on the basis of a list of 34 morphological characteristics (all of which were based on the groundplan characters). He also explained the use and importance of fossils in the deduction of descent lines and systematics of the Diptera, and provided a phylogenetic tree including various dipteran fossils. A more recent version from Hennig (1981) is illustrated in Fig. 10.

The Nematocera is possibly a paraphyletic group (Hardy, G.H., 1951b; Hennig, 1954 & 1981; Rohdendorf, 1974), with the Brachycera considered as a sister group of only part of it (Hennig, 1954).

The infraorders Tipulomorpha, Psychodomorpha, Culicomorpha and the Bibionomorpha (all part of the Nematocera) and the Brachycera are well founded monophyletic groups. McAlpine et al. (1981) included three additional infraorders as part of the Nematocera: Blephariceromorpha, Ptychopteromorpha and Axymyiomorpha. Further classification according to McAlpine is found at the end of section 1.6.2. No definite relationships have been established amongst Hennig's five groups, but analyses have predicted the phylogenetic scheme depicted in Fig. 10.

Hennig (1981) suggested a sister group relationship between the Tipulomorpha ('Polyneura') and the rest of the Diptera ('Oligoneura'). In the Oligoneura there may be a sister group relationship between the Psychodomorpha and the Culicomorpha + Bibionomorpha + Brachycera. As a monophyletic group the Psychodomorpha [= Blephariceridae + Deuterophlebiidae (Blephariceroidea)· Nymphomyiidae; Tanyderidae + Ptychopteridae (=Ptychopteroidea); Psychodidae] is not as well founded as the Tipulomorpha. They have few constitutive characters; none of which are in the wing venation.

The Tanyderidae (Tipulomorpha) have the most primitive (plesiomorphic) wing venation of all of the recent Diptera (i.e. the wings have the greatest number of longitudinal veins seen in dipterans and are similar to those of the ground plan of the Pterygota (Hennig, 1954).

It is possible that the Culicomorpha, Bibionomorpha and Brachycera also form a single monophyletic group. (The synapomorphic characters of these three groups may be the development of true lobe-like pulvilli and the allula, though this may only be weakly distinct). Hennig further suggested that there could be a sister group relationship between the Culicomorpha and the Bibionomorpha + Brachycera.

The Culicomorpha [= Dixidae + Chaoboridae + Culicidae (=Culicoidea); Thaumaleidae + Simuliidae + Ceratopogonidae + Chironomidae (= Chironomoidea)] are undoubtedly a monophyletic group. Reductions in their venation are evident. As in the Tipulomorpha and Psychodomorpha, the discal cell is absent, the result of reduction of the posterior crossvein. Both media and radial sectors have only three free branches. The Culicomorpha probably contain two sister groups, the Culicoidea and Chironomoidea, which have followed separate paths in their mode of life and larval morphology. The Culicoidea comprises the sister groups Dixidae and Culicidae. The relationships among the various groups of the Chironomoidea remain unresolved.

The Bibionomorpha is definitely a monophyletic group as are the Bibioniformia and Mycetophiliformia. Representatives of the Bibioniformia are first seen in the Upper Triassic; those of the Mycetophiliformia, in the lower Cretaceous (Hennig, 1973). The position of several of the families (Pachyneuridae; Perissommatidae; Axymyiidae; Anisopodidae and Cramptonomyiidae) however, remains uncertain. The Bibionomorpha show convergence in venation. The Anisopodidae and Cramptonomyiidae have the most primitive venation. They have retained a closed discal cell and a media with the complete number of branches.

It is still not known whether the Bibionomorpha and Brachycera are a monophyletic group of higher rank.

The Brachycera (of Lower Jurassic origin) are undoubtedly a monophyletic group. All the groups that could be considered as the possible sister group of the Brachycera have been recorded from the Upper Triassic, and from this it may be inferred that the Brachycera must have been in existence at that time.

The division of the Brachycera into monophyletic subgroups is not definite. For example the families of the Homoeodactyla (= Tabaniformia) possibly form a monophyletic group. The Brachycera excluding the Homoeodactyla, that is the Heterodactyla, is also possibly a monophyletic group. Among the subgroups of the Brachycera are the Empidiformia (Empidoidea + Dolichopodidae), its sister group the Cyclorrhapha and the Asiliformia. The Cyclorrhapha is a monophyletic group.

McAlpine et al. (1981), on the other hand, grouped the taxa discussed above in a different manner. The arrangement follows fairly closely that proposed by Hennig (1973) (Hennig (1981) was not yet available) but it incorporates some modifications suggested by Griffiths (1972) and Steyskal (1974). It also reflects their own views on evolutionary relationships of various dipteran groups.

Suborder Nematocera:

Tipulomorpha (Tanyderidae + Tipuloidea);
Blephariceromorpha (Blephariceroidea + Deuterophlebioidea + Nymphomyioidea);
Axymyiomorpha (Axymyioidea);
Bibionomorpha (Pachyneuroidea + Bibionoidea + Sciaroidea);
Psychodomorpha (Psychodoidea + Trichoceroidea + Anisopodoidea + Scatopsoidea);
Ptychopteromorpha (Ptychopteroidea);
Culicomorpha (Culicoidea + Chironomoidea).

Suborder Brachycera:

Tabanomorpha (Tabanoidea + Stratiomyoidea);
Asilomorpha (Asiloidea + Bombylioidea + Empidoidea);
Muscomorpha.

1.7. INTRODUCTION TO THE MESOZOIC INSECTS

The general appearance of the Mesozoic insect fauna is relatively modern in character from the Triassic onwards (Hennig, 1981). It seems that the main reason for this is that only a few of the groups that can be recognised as side branches of the stem groups of recent orders survived beyond the end of the Permian (Hennig, 1981). The transition from the Palaeozoic to the Mesozoic seems to have been a critical period in terms of insect survival. This conforms with what is known about changes in other animal and plant communities at the time.

Most Mesozoic insects are closely related to the recent species of the orders to which they belong, and some of those from the early Mesozoic can be assigned to more restricted subgroups within their particular orders. Of the late Mesozoic Diptera from Orapa, some have been assigned to modern genera or even subgenera.

1.8. OUTLINE OF CONTENTS OF CHAPTERS

Chapter 2. A fossil belonging to the family Tipulidae is described. This crane fly, of the extant genus Helius, shows how well preserved the fossil material can be. It has been assigned to a new species Helius botswanensis.

Chapter 3. Eleven crane flies (family Tipulidae) are described. They are not well enough preserved for further definite identification, but I have tried to place some of them into subfamilies.

Chapter 4. A dance fly (family Empididae) is described. It belongs to the genus Empis (sensu stricto). Excellent preservation has permitted the erection of a new species, E. (s.s.) orapaensis.

Chapter 5. A member of the Family Hybotidae is described. It has been given a new generic and specific status Pseudoacarterus orapaensis. Its phylogenetic position in the subfamily Hybotinae is discussed.

Chapter 6. This chapter describes three specimens which have been tentatively placed in the superfamilies Mycetophiloidea and Tabanoidea. The first may belong to the family Mycetophilidae (Mycetophiloidea), the second, a single fossil wing, possibly belongs to the Rhagionidae (Tabanoidea), and, the third which lacks wings, is not as distinctive but is similar to extant representatives of the two families Rhagionidae or Tabanidae (Tabanoidea).

Chapter 7. Ten dipterans, not assignable to family level are illustrated and described.

Chapter 8. Four bibionids (Bibionidae) are described. They are exquisitely preserved and are all assigned to the same species, Cretobibionida anticus gen. et sp. nov.

Chapter 9. This chapter comprises a discussion on the palaeoenvironment of Orapa. In addition, implications of these Diptera for evolutionary theory and pollination of angiosperms are discussed.

CHAPTER TWO

Helius botswanensis gen. et sp. nov.

2.1. INTRODUCTION

A new fossil species of Crane-Fly, Helius botswanensis (Diptera: Tipulidae) is described. It is extremely well-preserved, has a distinctive morphology, and is placed with confidence in the extant genus Helius. The single specimen puts the origin of the subfamily Limoniinae, and the genus back into the Cretaceous, and provides data on the southern African Cretaceous palaeoenvironment. I present evidence to show that the tipulid had an association with primitive angiosperms. The conservative nature of a dipteran of such antiquity, assignable to an extant genus which has an association with flowers, has implications for evolutionary theory.

There are two commonly used systems of classification of the family, i.e. that of Savtchenko (1983) and Alexander (Hutson, 1980a; Alexander & Byers, 1981). Here I propose to follow the latter system as it is more generally available, more commonly used, and thus more familiar to me. The main difference between the two systems is that, in the former, Tipulidae is considered as a separate family from the 'Limoniidae', and in the latter (Alexander's) system, the Tipulidae comprises the 'Limoniinae' as a subfamily.

2.2. SYSTEMATIC DESCRIPTION AND DIAGNOSIS

Family: Tipulidae

Subfamily: Limoniinae

Tribe: Limoniini

Genus: _Helius_ LePeletier & Serville 1828

Species: _H. botswanensis_ sp. nov.

Type specimen

The dipteran is preserved on the surface of two blocks as part and counterpart (BP/2/26000a & BP/2/26000b respectively, ♂) of a compression fossil (_sensu_ Schopf, 1975), in a red mudstone. The more complete specimen is illustrated in Plate 2A (this is a composite photograph), and in Fig. 12 (a _camera lucida_ drawing).

Derivation of specific epithet

Latin form of "Botswana".

Diagnosis

Slender body, 7mm long, with long slender legs and narrow wings; rostrum relatively broad, c.1/3 body length, divided into two segmented palps anteriorly; of the 5 palpal segments, the proximal small and inconspicuous, terminal segment as long as previous two combined; antennae half the length of rostrum; flagellomeres short and crowded; large compound eyes, glabrous, nearly joining at (?)dorsal midline; abdomen of 11 segments; hypopygium with two large gonocoxites, each with two gonostyli at the tips; inner gonostyli small, turned inwards, larger than outer gonostyli;

tibia lacking tibia spurs; wings: span 11.7mm; well developed anal lobes; C thickened up to R_{4+5}; Sc_1 complete, does not exceed fork of Rs, ends in C beyond midlength of Rs; Sc_2 at tip of Sc_1, at midlength of Rs; Rs leaves R_1 near distal end of Sc_1; basal section of Rs short and curved, not in alignment with R_3; tip of R_1 present, oval stigmata occupy this region; R_2 lacking; three branches of R reach wing margin, Rs with only two branches, R_3 and R_{4+5}; origins of R_3, R_{4+5} and M_{1+2} close together, R_{4+5} and M_{1+2} 1/3 total wing length; r-m short; R_3 curves anteriorly, all veins behind it posteriorly; r_3 expands towards margin; r_1 and r_3 divergent; dm large, rectangular, emits three veins M_{1+2}, M_3, M_4, just less than M_4 in length; all veins from R_3 to A_2 reach margin, all simple; m-cu emerges 1/6 dm's length behind fork of M; Cu_1 straight, not constricted at m-cu; A_1 and A_2 present; haltere rounded.

Description

The body and both wings are complete; the left wing, however, is slightly folded. The body is 7mm in length. Only the three legs on the left side (Fig. 12) of the abdomen and one antenna, also on the left, are preserved.

The rostrum, a very distinctive feature, is elongate and comprises approximately one-third of the total body length (Plate 2A & Fig. 13); it extends almost 2mm from the eye, and apparently a further 1mm beneath it. Towards the anterior, the rostrum divides into two segmented palps. Of the five palpal segments characteristic of the genus, the distal four are easily distinguishable in the fossil (Fig. 13), a valuable bonus for identification purposes. The first palpal segment, however, is indistinct, but this fortunately does not affect identification adversely. Different parts of the terminal palpal segment are preserved on the left and right palps, i.e. the distal part on the right, the proximal part on the left (Fig. 13). The terminal segment of these maxillary palps is fairly long, approximately as long as the two preceding segments combined. This character is present on extant members of the genus, and it indicates that the character had evolved by the middle of the Cretaceous and was stabilised over the succeeding period.

The antennae appear to be relatively short and curved; they are approximately half the length of the rostrum (Fig. 13). The more distinct one is shown on the left side of the rostrum in Plate 2A & Fig. 13. The antennae arise directly from the anterior dorsal side of the head between the compound eyes, and it is likely that no part of them is hidden beneath the head. If this is so, the first segment is the scape and the second the pedicel, and they are of about equal length, 0.18mm and 0.17mm respectively. The terminal portions, representing the flagellum divided into flagellomeres, are indistinct, but individual flagellomeres are probably short and crowded and the last few may be missing.

The compound eyes are round to oval and 0.6mm wide. They are glabrous, and, on the part (?ventral view), the rostrum continues over the area of the eyes, and divides them. The counterpart (?dorsal view) superficially suggests an holoptic condition. Close inspection of the latter (Plate 2 & Fig. 13), however, reveals a slightly curved black line running vertically in the photograph dividing the two eyes. So well-preserved are the eyes that individual facets show up under high magnification. There is even an indication of the facets from the underside of the structure as the eyes collapsed under compression associated with burial.

The abdomen is narrow and elongated, and appears to consist of 11 segments. At the posterior end, the structure of the genitalia indicates that the specimen is an adult male; some fine detail of the male hypopygium can be discerned (Plate 2E & Fig. 14). It is impossible to even attempt clearing the structure in oxidising acids and alkali, therefore details of gross morphology are all that are available. The gonocoxites are fairly conspicuous, and of approximately the average size commonly seen in the genus. The gonostyli are visible, and both the inner ones are particularly distinct. They are turned inwards and lie on the gonocoxites (Fig. 14). The outer gonostyli are indistinct, but they appear to be small.

Only portions of three of the legs have been preserved. The most complete leg is the hind left in Fig. 12. This absence of legs is predictable with crane-flies, where the legs often break, making the collection of complete specimens extremely difficult. Nevertheless, the longest is 16mm in length (Fig. 12), and the portions of these legs that remain are particularly well-preserved, there is even evidence of numerous fine hairs on their surfaces (Plate 2B). However, the tops of the tibia are not preserved and there is no evidence of tibial spurs.

The two wings have slightly different lengths (Plate 2A); evidently the body has twisted after burial towards the right wing. The total wing span is 11.7mm. The posterior of one wing is slightly folded over itself, but most of the details of the venation are revealed on the other, despite the fact that the veins are less distinct proximally. This is surprising, since other parts of the wing are in an excellent state of preservation. Indeed, there are a large number of fine hairs preserved on the leading edge of both of the wings (Plate 2C). As often occurs with fossils, neither part nor counterpart is complete. The details of venation have, therefore, been compiled from a study of both, and the sketch (Fig. 11) shows the result of combining camera lucida drawings of both specimens.

The anal lobes are well-developed. The costa (C) is thickened up to the tip of R_{4+5}. The axillary vein (Sc_1) is complete; it does not exceed the fork of Rs, but ends in the costa just beyond the midlength of Rs. Sc_2 is situated at the tip of Sc_1, midway between the origin and the fork of Rs. Rs leaves R_1 nearer the distal end of Sc_1 than the proximal end, at an approximate ratio of 5:1. The basal section of Rs is short and curved and is not in alignment with R_3. The tip of R_1 is present and there is a trace of oval stigmata in this region. R_2 is lacking. Three branches of R reach the wing margin and Rs has only two branches namely R_3 and R_{4+5} (R_4 and R_5 are fused up to the margin). The origins of R_3, R_{4+5} and M_{1+2} are close to one another, the latter two are a third of the total wing length. Crossvein r-m is short. R_3 curves towards the anterior, and all veins posterior to it curve in the opposite direction; cell r_3 is, therefore, widened particularly near the wing margin. Cells r_1 and r_3 are divergent. Cell dm is large and rectangular and has three veins issuing from its distal side (M_{1+2}, M_3 and M_4), and it is just less than M_4 in length. All veins from R_3 to the A_2 reach the wing margin, and all are simple. The crossvein m-cu emerges at a point 1/6 of the dm cell's length behind the fork of M. Cu_1 is straight and not constricted at m-cu. Two anal veins A_1 and A_2 are present and both reach the wing margin.

There is some indication of a rounded structure lying adjacent to the right side of the abdomen, at the level of the anal lobe (Plate 2A & Fig. 12). This I interpret as being a haltere. Further details are not available.

2.3. DISCUSSION

Helius

The Tipulidae is the largest family of Diptera, with a total of approximately 13 000 known species (Hutson, 1980). However, there are approximately 1 300 described species in the Afrotropical (Hutson, 1980a), making it the fourth largest family (Barraclough & Londt, 1985). There are very few genera unique to the Afrotropical region, but there are also several major groups that are notably absent (e.g. the tribe Pediciini) (Hutson, 1980a). They are mosquito-like flies, with very long deciduous legs, hence their common name, "daddy-long-legs".

The genus *Helius* LePeletier & Serville 1828 (Latreille *et al.*, 1828), comprising about 200 extant species, is widespread throughout the world; most species live in South and South-East Asia (Krzeminski, 1985). In the Afrotropical region, the genus *Helius* comprises 29 species in four subgenera, 23 of these are in the subgenus *Helius* LePeletier & Serville 1828. Six species of the genus *Helius* are recognised in South Africa, five in the subgenus *Helius*, and one in the subgenus *Prohelius* Alexander 1975. They are *Helius* (*Helius*) *brevisector* Alexander 1956, *H.* (*H.*) *capensis* Alexander 1917, *H.* (*H.*) *flavitarsus* Alexander 1920, *H.* (*H.*) *lunigerus* Riedel 1914, *H.* (*H.*) *pararorosus* Alexander 1949 and *H.* (*Prohelius*) *dugaldi* Alexander 1945. The absence of relevant information on the fossil makes identification below the genus level impossible. For example, colour is important in distinguishing and describing species, and this information is lacking despite the indication of some pigment on the wings. Also, the body length to wing length ratio of the Orapa fossil is not consistent with any of the six Helius species. However, the short antennae with compressed flagellomeres are similar to those of H. (P.) dugaldi (Alexander, 1945).

Biology

Adult members of the genus are usually associated with water, and the larvae live either in water or moist soil, feeding mostly on decaying plant matter. Curiously, the adults have not frequently been seen feeding, but some of those occasions have been at flowers (Hutson, 1980a). This may indicate that the adults require little food, but the peculiar mouth parts of this species, and indeed the genus, invite a functional explanation: they are probably adapted for sucking. This dipteran may therefore have visited flowers and indeed may have had an intimate association with the flowering angiosperms. Both sexes of tipulids are often attracted to light, and the males of some species gather in dancing swarms (Hutson, 1980a) in woodlands, forests or near water. As far as I have observed, adults are diurnal and Knizeski et al. (1984) demonstrated their seasonality. The presence of deciduous leaves in the fossil flora, and the varved nature of the sediments imply that seasonal conditions prevailed (Rayner, 1987). Indeed, tipulid activity is very susceptible to rain and wind (Pritchard, 1980).

The six South African species have been recorded from forested or densely vegetated and wet habitats, often near streams, in grass, in saturated earth, on mossy rocks and darkened places (Alexander, 1945, 1949 & 1964). The larvae of the genus Helius are also habitat specific; they are found in marsh borders, in decomposing aquatic vegetation or in marshy areas in woods (Alexander & Byers, 1981). The larvae of the members of the subfamily as a whole, however, occupy a large diversity of habitats ranging from the intertidal zone to running fresh water, and from the leaves of terrestrial plants to dry soils (Pritchard, 1983).

Origins of the Tipulidae

Tipulidae, and other families of the superfamily Tipuloidea belong to the natural group of lower Nematocera, which was considered, by Savtshenko (1966), to be monophyletic. Like all other dipterans, the members of the Tipuloidea have their origin in the Mesozoic Panorpoidae and Savtshenko (1966) indicated that the original characteristics of the Tipuloidea were derived from this group. These characters include dichoptic eyes, many jointed antennae, fairly complex wing venation, sporadic appearance of macrotrichia in the wing cells, and a v-shaped transverse suture on the mesonotum. The Tipuloidea, in turn, gave rise to the Architipuloidea from which the Tipulidae was derived.

As early as 1937, Hendel (in Rohdendorf, 1974) reviewed the Diptera, and concluded that, at the beginning of the

Jurassic, or still earlier, the superfamily Tipulcidea was already in existence. Rohdendorf (1974) believed the origin of this superfamily (the most diverse and ancient dipterans) to be even earlier; i.e. from Upper Triassic-Jurassic times. According to him, the family Tipulidae branched off from the Architipulidae during the mid-Jurassic [either directly or through an unknown intermediate (Rohdendorf, 1974; Savtshenko, 1966; Alexander & Byers, 1981)]. This conclusion was based on the fact that Triassic fossils of the superfamily Tipulidea were all representatives of the Mesozo family Architipulidae (Rohdendorf, 1974; Savtshenko, 1966).

As fossil evidence of members of the Tipulidae (as with most insects) is extremely rare, the evolution of the family has been inferred from studies on extant members of the group. Savtshenko (1966), for example, reviewed plesiomorphic and apomorphic characters of eggs, larvae, pupae, imagos, and general biology to postulate a phylogeny of the Tipulidae and some of its subfamilies. In another study, Downes (1968) looked at the organs and processes of sperm-transfer of the lower Diptera and inferred details of their evolutionary history. Rohdendorf (1974), on the other hand, studied both extant and extinct lower dipterans, and concentrated mainly on wing venation, with particular reference to its functional significance. It is clear that changes in the wing structure in flies, together with the morphological alterations of the thorax, have been very important in the evolution of faster, more manoeuvrable and more precise flight (Ennos, 1989).

The oldest fossil tipulids found to date are from the Cretaceous. A few crane flies from the ea. / Cretaceous Wealden beds of southern England (119-144 million years), including a specimen of the Limoniinae, were observed by Jarzembowski (1984). Jell and Duncan (1986) described a larva, pupae and adults from the Lower Cretaceous Koonwarra fossil bed (South Gippsland, Victoria); the latter included a member of the Limoniinae. Jell and Duncan's specimens are the only southern Hemisphere fossils other than those from the Orapa deposits. From late Cretaceous amber of central Canada (about 70 million years) one tipulid was described by Carpenter (1937). These Cretaceous fossils and particularly the Orapa tipulids (see also chapter three) clearly demonstrate that the family (including two of its subfamilies, Tipulinae and Limoniinae) was well established by the early to middle Cretaceous (or even earlier in the Jurassic), having largely undergone most of its major evolutionary developments by that time. As pre-Mesozoic forms were very different to Mesozoic Tipuloidea, most tipulid evolution must have occurred swiftly with much diversification in a period lasting about 70 to 90 million years, i.e. from the beginning of the Triassic to the middle stages of the Jurassic.

Fossil Tipulidae from post Cretaceous times are more numerous; they include specimens from the Eocene, Oligocene and Miocene (Tertiary). From the Eocene (Redbank Plains Series) a tipulid was described and assigned to the subfamily Limoniinae (Tribe Hexatomini) (Riek, 1954). Spahr

(1985) listed several tipulid species (mainly Eocene) from various ambers and copals. Alexander (1931) and Theobald (1937, in Hennig, 1973) described fossil members of the family Tipulidae from the Eocene-Oligocene boundary (40-50 Myrs), at which time the family was well-established and some extant subfamilies (limoniinae and Tipulinae) and genera could be recognised (e.g. <u>Tipula</u> from the Palaeoarctic and <u>Megistocera</u> and <u>Brachypremna</u> from the tropics). Alexander and Byers (1981) noted the presence of a few more genera (especially of the Tipulinae) of equivalent age from the Isle of Wight. Krzemiński (1985) described five new species from Baltic Amber (Eocene-Oligocene), and assigned them to the subfamily Limoniinae; a new species of <u>Helius</u>, <u>H. abditus</u> was among them. The Florissant shales, Colorado (30 Myrs: Upper Oligocene-lower Miocene) have yielded genera of the Limoniinae, Tipulinae and Cylindrotominae (Scudder, 1894). An additional two new species of the Limoniinae were described by Gentilini (1984) from the Upper Miocene of Italy.

<u>Stasis</u>

The conservative nature of the family and its genera is apparent. Rohdendorf (1974) indicated that the Triassic-Jurassic representatives of the superfamily Tipuloidea closely resembled those of today. Savtshenko (1966) described the modern-day distribution of the family Tipulidae, and emphasised the presence of many genera in Australia (e.g. <u>Dolichopeza</u>), which broke away from the rest of Gondwana in the early Cretaceous, as support for the Mesozoic origin of the group. This was later backed by fossil evidence (see above). The Orapa tipulid, being a member of the subfamily Limoniinae (and the extant genus <u>Helius</u>), indicates that the subfamily probably appeared shortly after the Architipulidae. The suggestion by Wighton (1980) that the two sister groups, Tipulinae and Limoniinae (<u>sensu</u> Hennig, 1950), diverged in the mid-late Palaeocene, was obviously grossly underestimated. The Orapa specimens from Cenomanian deposits clearly show that, if the Limoniinae and Tipulinae are indeed sister groups, as the morphological evidence suggests, the two subfamilies were established considerably earlier than this, at the very least during the Lower Cretaceous.

The stable nature of the genus <u>Helius</u> is obvious and in keeping with the group as a whole. Although other animals and plants of such antiquity have been confidently assigned to living families, few of them can be included in modern genera. Within the genus, a number of characters are shown by the fossil to have been remarkably stable. For example, the overall wing venation, particularly the manner in which cell r_3 widens distally and the character and detail of the distinctive mouth parts (size of rostrum, size of terminal palpal segment). Stasis of this duration is not easy to explain, particularly in the context of the number and type of evolutionary changes which have occurred since the early Upper Cretaceous in most animal and plant groups.

The genus apparently had as wide a distribution in the past as it enjoys today; it has been found in the South Africa from the Cretaceous to the present and in the northern Hemisphere from the Eocene-Oligocene to the present. Its persistence in South Africa may be attributed to the position of the continent in Cenomanian times; it lay approximately 15° to the south of its present position, in other words, Orapa was about where Cape Town is today. The fact that the genus is so tightly connected with its preferred habitat makes it more likely for the group to have shifted its geographical range as the climate changed, than passively undergo speciation or suffer extinction. Looked at in this way, the presence of members of a 93 million year old fossil taxon, identical to those living today is not so surprising, and may even be predictable.

<u>SMRS and implications for evolutionary theory</u>

The numerous coloured spots which are common on extant species (and there is an indication of some of them on this specimen) may also have a bearing on the existence of stasis. It has been suggested previously that they serve as structural thickenings or camouflage (Gentilini, 1984). A more complete explanation, however, may concern their function as recognition signals (<u>sensu</u> Paterson, 1981) between members of the species. The most important adaptations are those which facilitate mating and syngamy. Characters which function in courtship and recognition, therefore, are fundamental for the identification of a genetic species. Tipulids communicate through visual signals (the structure of the eye, their diurnal nature and their swarming behaviour all indicate this), and their morphology therefore controls communication. Overall morphology, particularly the colour and pattern of their wings, would therefore come under intense stabilising selection, for any variation would result in the individual not being recognised as a potential mate by conspecifics.

CHAPTER THREE

FAMILY TIPULIDAE

3.1. INTRODUCTION

In the following section I describe 11 members of the family Tipulidae. Many of the fossils are incompletely preserved, but I have nevertheless been able to place them in the Tipulidae with varying degrees of confidence. They are included to give a complete picture of the Orapa dipteran fauna. A significant part of the Orapa fauna consists of tipulids. This is consistent with other data which show that the oldest sediments containing recognisably "modern forms" of insects nearly always include tipulids (e.g. Carpenter, 1937; Jarzembowski, 1984; Jell & Duncan, 1986). In addition the family Tipulidae is the largest today, and is among the most ancient. It is perhaps predictable that tipulids would be present in the Orapa sediments in significant numbers.

For each of the 11 specimens described in this chapter, a description and a short discussion is given. I have attempted to key out each specimen as far as possible, even though evidence is sometimes vague. Keying-out specimens below family level is based mainly on gross morphology, i.e. the structure of the head, antennae, and, where possible, wing venation. This unfortunately does not take into account adequately the broad spectrum of diagnostic features required. but the data available are fragmentary. As the family was discussed in detail in the previous chapter, a general discussion is omitted here and the information below comprises systematic descriptions.

3.2. DESCRIPTIONS AND DISCUSSIONS

Suborder: Nematocera
Infraorder: Tipulomorpha
Superfamily: Tipuloidea
Family: Tipulidae

3.2.1. SPECIMEN 1

The specimen is preserved as part, BP/2/27578a (Plate 3A & C; Figs 15 & 17) and counterpart, BP/2/27578b (Plate 3B & D; Figs 16 & 18), as a compression on grey mudstone.

Description

The specimen is well-preserved, particularly the part, which forms the main basis of the description. The head (with antenna), thorax (with all six legs and both fore wings) and the abdomen are preserved. The head, thorax and abdomen combined are 5.5mm long (excluding the antenna). The most complete wing (the right wing of the part) is long and narrow measuring 4.85mm by 1.43mm.

HEAD. The antennae are made up of approximately 11 segments (poor preservation prevents me being absolutely certain), and measure about one and a half times the length of the head. The segments are marginally longer than broad, and very hairy. The length of the hairs is twice the width of the segments (Fig. 16). The rostrum is short, and the eyes appear to be dichoptic.

THORAX. Individual sclerites of the thorax are indistinguishable.

Legs: all six legs are preserved although five are incomplete. The left hind leg is complete; the right hind leg and left middle leg only lack details of their tips. Of the left front leg and right middle leg, only the femur and tibia are present; an unconnected set of tarsal segments may belong to either of these. The femur of the right front leg is all that remains of this limb. Femora, tibiae and tarsal segments are long and slender. The leg is approximately twice the length of the body, the longest (LHL) measuring 10.82mm. The coxae are large and elongated, and the femora are slightly widened at their distal ends. The middle tibia of the left leg of the counterpart (Plate 3B; Fig. 16) has a single tibial spur. The tarsal segments are all approximately of equal length (0.44mm), the distal ones being only fractionally shorter; none is swollen.

Wings: (Plate 3C & D; Figs 17 & 18). The wing venation is indistinct, and it is not pigmented, but transparent throughout. It is long and narrow. The costa (C) extends up to vein R_3. Sc_1 is complete, long, but does not exceed the fork of Rs. The tip of Sc_2 is possibly present (Fig. 17), and, if so, it is nearly transversely orientated and distal to Rs. R_{1+2} and R_3 are slightly divergent at their tips only. The origin of Rs is rectangular and is positioned proximally one third along the length of the wing. Branches of R_3 and R_4 are gently divergent, and those of R_4 and R_5 are convergent at their tip, and are parallel for the rest of their lengths. Cell r_3 is two thirds of the length of r_4. Cell dm is rectangular. Crossvein m-cu is situated just proximal to the fork of M (Fig. 18). Three veins issue from dm, all are simple and reach the wing margin. The middle vein M_3 is two and a half times the length of the dm cell. CuA is straight; there is no constriction at branching of CuA_1 and CuA_2. CuA_1, CuA_2, A_1 and A_2 are all approximately straight, the latter three curving fractionally proximally where they reach the wing margin. Halteres are missing.

ABDOMEN. The abdomen comprising approximately 10 segments, is long and narrow (3.67mm by 1.15mm at its broadest point). The abdomen is broadest at segments two and three, and tapers to a point at the posterior end. A pair of cerci is visible and these are as long as the last two segments combined. They indicate that the specimen is a female. All segments (excluding the genitalia) are broader than they are long.

Discussion

The gross morphology, particularly the size ratios, indicates that the specimen undoubtedly belongs to the Tipulidae. Several features of the wing venation exclude the fossil from the subfamily Tipulinae, and place it either with the Limoniinae or Cylindrotominae. These are that: Sc_1 is complete; CuA is straight, and there is no constriction at branching of CuA_1 and CuA_2. Further, the presence of the tip of R_{1+2} indicates that the specimen is probably a member of the Limoniinae, rather than the Cylindromiinae. However, the antennae of approximately 11 segments is a common characteristic of the Tipulinae, and is only rarely found in the Limoniinae and Cylindromiinae. If this fossil is a member of the Tipulinae, it may be allocated to the tribe Hexatomini, as tibial spurs are present.

3.2.2. SPECIMEN 2

The part, BP/2/25228 (Plate 4A; Fig. 19) is a poorly preserved compression on reddish-grey mudstone; the counterpart is missing. The head and its appendages are missing, as are all of the legs, and both halteres. The thorax is distorted, and has partially broken away from the abdomen. Both wings are present but one has folded over itself obscuring the venation; the venation in the left wing is incomplete. Together, the thorax and abdomen measure 6.5mm in length. The wings are nearly as long as the body and measure 4.5mm and 5.1mm (left and right respectively). The basal portion of the left wing is missing.

Description

THORAX. Individual segments are not discernible.

Wings: no pigmentation is present. They are long (at least 5mm) and relatively narrow (1.4mm) (left wing). Approximately nine or ten veins reach the wing margin.

The basal cells are over two thirds of the wing length. The costa (C) is incomplete and the presence, absence or positions of Sc_1 and Sc_2 are impossible to determine with confidence. R probably branches twice giving rise to $R_{1(?+2)}$, R_3 and R_{4+5}. The origin of Rs is almost rectangular. Branching of Rs, M and CuA occur in an almost linear transverse line; in the distinctive region near the apical third of the wing (the 'cord'). Crossvein m-cu lies just proximal to cell dm, which is small; three simple veins (M_{1+2}, M_3 and CuA_1) issue from its distal side with the middle vein M_3 being nearly two and a half times the cell's length. Two complete anal veins and an anal lobe are present.

ABDOMEN. This is narrow, elongated, and composed of eight or nine segments. Abdominal segments are approximately as broad as long and nearly all of equal width, and the abdomen therefore does not taper distally. The first segment is the shortest in length, the second the longest, and each progressive segment is a fraction shorter than the preceding one. The hypopygium is barely visible; it has two swollen appendages which possibly represent the gonostyli.

Discussion

Although the overall morphology of the specimen is very similar to that of members of the families Tipulidae, Pachyneuridae and Trichoceridae, the [illegible] several features which exclude this specimen from the other two. In the

Pachyneuridae there is a pigment spot on the wing and the 'cord' lies at the centre of the wing. In the Trichoceridae, the wings are hairier, and m-cu lies just beyond the dm cell. Other general features which indicate that the specimen belongs to the family Tipulidae, are the large number of veins reaching the wing margin (nine or ten) and the presence of two anal veins. Considering the Tipulidae alone, the swollen gonostyli and the m-cu cross vein positioned just a fraction proximally to the dm cell, remind me superficially of the genus Limonia. I discuss this genus in more detail later.

3.2.3. SPECIMEN 3

Part, BP/2/25843 (Plate 4B; Fig. 20). The fossil is an excellently preserved wing, and is compressed on a block of grey mudstone. Venation is distinct, but the base of the wing is missing and the basal-posterior region is folded over itself. Venation in this region is, however, not entirely obscured.

Description

The single wing (up to the missing proximal region) is moderately long (3.4mm) and narrow (1.3mm), and the blade is densely covered with fine hairs. The hairs on the veins are stouter, particularly those on the costa. The wing is more or less clear throughout, but very slightly darkened (?pigmented) between Sc_1 and R, at the tip of R_{1+2}, at the origins of Rs, R_3, R_{4+5}, M_{1+2} and at the proximal side of cell dm. The costal vein (C) ends at the tip of the third longitudinal vein (R_{4+5}). Sc_1 is complete, ending in the costa; it is long, terminating just prior to the fork of Rs. The free tip of Sc_2 is lacking, with Sc_2 ending in R_{1+2} directly opposite to tip of Sc_1. R branches twice and, therefore, has three branches R_{1+2}, R_3 and R_{4+5}. Rs is gently arcuated. R_{1+2} ends in the costa at equal distances from Sc_1 and R_3. All longitudinal veins are simple, and all reach the wing margin, with the possible exception of the anal veins. The discal cell (dm) has three veins arising from it (M_{1+2}, M_3, and M_4). Cell dm is blunt and shorter than the middle vein issuing from it. The postical cell (cu) is long, half the length of the wing. There appears to be an abberation in the venation in that there is an extra crossvein between R_{4+5} and M_{1+2} just beyond dm. All veins beyond R_{1+2} are curved gently towards the posterior, they are more or less parallel along their lengths and they diverge slightly distally.

Discussion

The wing venation indicates the dipteran belongs to the family Tipulidae, subfamily Limoniinae, tribe Hexatomini or Limoniini. In the Hexatomini, a distinguishing feature is the lack of the free tip of Sc_2, as in the fossil. In the Limoniini however, the free tip of Sc_2 is present. In the Limoniini, R_4 and R_5 are fused to the margin and there are only two branches of Rs (R_3 and R_{4+5}), this is also the case in the fossil. In the Hexatomini, however, R_4 and R_5 are separate, R_4 is usually captured by R_{2+3} to form a distinct element R_{2+3+4} and usually three branches of Rs are present [some exceptions exist, e.g. Atarba (Fig. 21)]. The wing of this latter genus does display a few similarities with that of the fossil. However, the wing of the genus Limonia (Dicranomyia Stephens) marleyi (Fig. 22) shows a remarkable resemblance to that of the fossil, but the pigmentation of the fossil is considerably less distinct. 'Wing spots' or 'pigmentation' on fossils however may not always be a direct reflection of their presence or absence in the living specimen. In some instances, colouration may be completely lost during fossilisation, or, alternatively, staining of the wings may be added during this process. In some of the exquisitely preserved Orapa specimens, distinct stigmata are preserved (Chapters 2 & 8); one might therefore expect pigment to be preserved if it were present on the original. Although this may not be conclusive evidence, I regard the darkened patches on specimen 3 to be pigment, which was present on the living specimen.

The Hexatomini is a major tribe within the family, and includes 12 genera (260 species) in the Afrotropical Region, of which seven occur in South Africa (Hutson, 1980a). The genus Atarba is a relatively large genus, with representatives in all major regions of the world, and a great concentration in the Neotropics (Alexander, 1964). In the Afrotropical region this genus has only ten species in two genera of which four species occur in South Africa. One of these, the species Atarba capensis, is very similar to the fossil, i.e. the shape of the wing and lay-out of the veins are nearly identical. However, a number of differences are obvious: the wing of A. capensis is not pigmented (Fig. 21), R_2 does not join R_3 from R_{1+2}, R_3 curves anteriorly and Sc is short ending a long distance before the fork of Rs which is nearly opposite the origin of Rs. Today in South Africa, A. capensis is restricted in distribution to the Cape, and immature individuals are known to live in sodden decaying wood (Alexander, 1964).

The tribe Limoniini is very large indeed. In the Afrotropical region this tribe is represented by eight genera with about 300 species, and, in South Africa, there are 52 species in six genera. Limonia (Dicranomyia) marleyi whose general wing shape appears to be more elongated than that of the fossil, has very similar venation and pigmentation (Fig. 22).

The pigmentation of L. marleyi was described by Alexander (1917) as follows.

(a) Large stigma spot which is rounded.

(b) Paler markings along seams as follows:

- tip of Sc
- base of Rs
- tip of R_{1+2}
- outer ends of cell dm
- proximal end of cell dm
- m-cu

(c) The veins are dark.

A differing venational feature is the square origin of Rs.

Limonia (Dicranomyia) is reported to occur at the intertidal zones or in brackish water on the Atlantic (Alexander & Byers, 1981).

Cape environmental conditions (as preferred by Atarba) are likely in Cretaceous Orapa as are brackish or saline environments (see Chapters 1 & 9). Most of the other dipterans found in the sediments have affinities with a more Cape-like climate.

3.2.4. SPECIMEN 4

The specimen, BP/2/25939 (Plate 4C & D; Figs 23 & 24) is a compression on grey mudstone. The head, thorax and abdomen have been relatively well-preserved, whereas portions of only three legs remain, and these are poorly preserved (of the three, the left fore leg is the most complete). The left wing is present and, although the venation is unclear in places, description and identification are based almost entirely on this wing. The right wing is present only in parts and these are very badly crumpled and useless for identification purposes. The left wing is relatively long (4.45mm), elongated and narrow (1.0mm). It exceeds the length of the head (with rostrum, but without palps), thorax and abdomen (with cerci) combined, which measure 0.6mm, 0.7mm and 2.9mm respectively (4.2mm combined).

Description

HEAD. The rostrum is conspicuously extended (Fig. 23). The mouthparts (?left and right palps) are long, i.e. one and a half times the length of the rostrum itself. Individual segments cannot be delimited. The antennae are filiform, of moderate size and they are equal in length to the rostrum. Individual flagellomeres are not distinguishable. The compound eyes are large, but widely separated displaying the broad posterior vertex. This is the dichoptic condition.

THORAX. The pronotum, prescutum and scutum are large and can be identified (Fig. 24).

Legs: long and slender (4.6mm) measuring about one and a half times the length of the body. No part of the legs appears to be thickened, i.e. each segment is of equal width throughout. No tibial spurs are visible, but this may be due to poor preservation. Indeed, only one leg (with tibia) was available for study. The right ?front coxa is present; it is conspicuously large and elongate. Tarsal claws cannot be observed.

Wing: the wing is entirely covered in microtrichia. It is completely transluscent, and has no trace of pigmentation. Venation (Fig. 24): although venation is indistinct certain characters were determined by careful observation. Eleven veins reach the wing margin. The costa (C) ends nearly at the tip of the wing, at the end of R_4. Sc_1 is long, ending beyond the fork of Rs, in line with the branching of Rs into R_{3+4} and R_5. The origin of Rs is at the boundary of the proximal third of the wing. The position of Sc_2 is unknown; it does not appear to end in the costa. R_{1+2}, although indistinct, appears to end in the costa halfway between Sc_1 and R_3. R_3, R_4 and R_5 are separate, i.e. Rs has three branches reaching the wing margin. Two branches of M (M_{1+2} and M_3) reach wing margin. Cell dm is not distinguishable. CuA_1 is straight for most of its length, but distally it curves distinctly towards the posterior so that it ends just a little in front of CuA_2. M_3 and the two anal veins also curve towards the posterior edge of the wing. All veins anterior to M_3 curve anteriorly. Crossvein r-m originates in R_5, and it is unclear whether m-cu is present. Basal cells br and bm are approximately two thirds of the wing's length long. There are two complete anal veins.

ABDOMEN. The abdomen is relatively long and slender, and approximately equal in width to the thorax at its widest. The abdomen tapers sharply from segment four onwards ending as a pointed tip at the posterior end. It consists of approximately ten segments (the segmental divisions, particularly towards the posterior end, are indistinct). I suggest the terminalia at the posterior of the abdomen are cerci, and the specimen is therefore an adult female. These cerci are lengthened, equal to segments two and three combined. They were possibly curved upwards in the living specimen as the one cercus is curved towards the right side of the fossil.

Discussion

The gross general morphology (including the lengthened rostrum), and the distinctive wing venation (especially the 11 veins reaching the margin and the presence of two anal veins) are typical of members of the family Tipulidae. The rostrum, the long complete Sc_1 vein which exceeds the fork of Rs and the specimen's moderate overall size, is similar to members of the subfamily Limoniinae, and particularly the tribe Pediciini.

3.2.5. SPECIMEN 5

The specimen, BP/2/25948 (Plate 5A & B; Figs 25 & 26), is preserved as a compression on grey mudstone. Both wings, the abdomen, thorax and head, one complete leg, and portions of at least three other legs have been preserved. The mouthparts and antennae are also present, as is a portion of the genital segments, and possibly a halter; all are comparatively indistinct. Together the head, thorax and abdomen (without cerci) measure 5.2mm. The wings are narrow and elongated. They exceed the length of the abdomen, measuring 5.6mm and 4.8mm for the left and right wings respectively. It is impossible to map out the wing venation, since they have both folded over themselves (Fig. 25).

Description

HEAD. Figure 26 shows two large compound eyes, separated by a broad posterior vertex. Individual hexagonal facets of the right eye are clearly preserved. No ocelli are present. The rostrum is extented and there are palps visible which are as long as the rostrum. Antennae are filiform, long, and consist of 13 segments (see left antenna, which appears to be complete). The scape and pedicel of the left antenna are clear; they are large and approximately twice as broad as the succeeding segments. The right antenna is missing the scape, pedicel and the first couple of flagellomeres, thereby consisting of only eight segments. The point of origin of the antennae and mouthparts on the head is unclear.

THORAX. The thorax has been compressed laterally (rotating towards the left during fossilisation) exposing details of the right side (Fig. 26). Individual sclerites are discernible, but some of the delimitations are vague. The pronotum, prescutum and scutum are obvious and very robust. Eight other segments (i.e. katepisternum, anepisternum, anepimeron, meron, scutellum, mediotergite, anatergite and katatergite) may also be identified, but with less certainty.

Legs: long and slender, approximately two and a half times the length of the abdomen, and just short of twice the length of the head, thorax and abdomen combined. The three right-hand coxae, and the left-hand hind coxa are preserved; they are elongated as are the trochanters. No tibial spurs or tarsal claws can be seen. From coxa to tip, the back right leg, the only complete one, measures 8.3mm. The distal ends of the femur and tibia (RHL) are very slightly broadened.

Wings: both are crumpled, and no details are preserved, except their long and narrow outline. A structure, which possibly represents the knob of a halter, lies on the right side of the specimen in line with the 1st abdominal segment at the base of the right wing. The base and stem of this halter are not preserved. The knob is elongated and split in half distally (probably due to compression). If the halter was still attached at the time of death or burial and is lying in the correct position, the stem was fairly long and probably narrow (approximately 0.5mm in length), and attached between the meron and the scutellum of the thorax.

ABDOMEN. The abdomen is long and comparatively slender, consisting of about ten segments. The second and third segments are the widest, being two and a half times as wide as long. The first three segments are the longest, segments four to seven are shorter (all of which are approximately equal in length), and between segments eight, nine and ten the segment boundaries are not clearly defined. The abdomen tapers from the third segment onwards, and ends bluntly at the end of the tenth segment. The last segment bears the left cercus and indicates that the specimen is an adult female. The cercus is as long as segments five and six combined. It is preserved curving gently to the left, and, as in the previous specimen, this may suggest that it was curved gently upwards when the tipulid was alive.

Discussion

The general features indicate that the specimen belongs to the family Tipulidae. The small extented rostrum and antennae, consisting of 13 flagellomeres, indicate its possible affinity to the subfamily Limoniinae.

3.2.6. SPECIMEN 6

The fossil, BP/2/26717 (Plate 5C; Fig. 27) is compressed laterally on grey mudstone, with its left side uppermost. The abdomen, thorax, head, both wings, portions of two legs, and the mouthparts are preserved. Both halteres and antennae however are missing. The quality of preservation overall is poor. From head to abdominal tip, the specimen measures 4.4mm. The wings are elongated and narrow, the left measuring 3.8mm by 1.2mm, and the right 3.7mm (width unknown, as the wing is folded over itself).

Description

HEAD. The head is hypognathous as the palps point downwards. The lateral compression shows clearly the hexagonal facets of the left compound eye. The eye is very large, but does not reach the mid-dorsal line, and a portion of the posterior vertex can be seen. The specimen is therefore dichoptic. The lengthened rostrum is visible, as is the distinctly forward projecting nasus. Palps are also distinguishable; they are long and thin, but individual segments are not discernible. The labellum is also present (Fig. 27).

THORAX. The thorax is not clearly preserved. Some sclerites can be readily identified, while others less so. The pronotum, prescutum and scutum are large. I can identify the mediotergite, anatergite, anapimeron, anepisternum and katepisternum.

Legs: very long and slender, but their total length is unknown as none is complete; the femora alone are at least 80% of the length of the abdomen. The middle and hind coxae on the left-hand side are preserved; they are very long and narrow. Two femora (?left hind and middle leg) and a tibia (?left middle leg) are also preserved, they are long and slender and are not dilated at any point along their length. No tibial spurs or tarsal claws are preserved (and probably not present in the living specimen).

Wings: blades are transparent throughout, without trace of pigment. Venation in both the left and right wings is indistinct, but particularly so in the latter. In the left wing an important region (in terms of identification) has flaked away; this is the section containing (if present) the dm cell. The right wing also obscures these venational details. The description below is therefore based on careful observation of the left wing. Approximately nine to ten veins appear to reach the wing margin. Sc_1 is moderately long, ending in the costa midway between the origin of Rs and the fork of Rs. The origin of Rs is at the end of the first third of the wing. ?Sc_1/R_{1+2} ends midway between Sc_1 and R_3. R_4 and R_5 are fused along their entire lengths, therefore Rs has only two branches reaching the wing margin: R_3 and R_{4+5}. Cell r_3 is two thirds of the length of r_{1+2}. Two branches of M reach the wing margin: M_{1+2} and M_3. Cross vein r-m is just proximal to the middle of the wing's length. Cross vein m-cu is possibly present, placed two thirds of the way along the wing's length, more or less in line with the points of origin of M_{1+2} and M_3 on the fossil. Cu is present but its distal portions, CuA_1 and CuA_2, are not distinguishable. The basal cells, br and bm, extend to over half the length of the wing. Two anal veins, A_1 and A_2, are present, and both appear complete.

ABDOMEN: The abdomen is 2.6mm long, it is slender, and composed of approximately nine to ten segments. It tapers distally from segment seven downwards. Tergites and sternites are clearly visible; between them is a darkly pigmented strip (? secondary segmentation). Parts of the terminalia are preserved; these are two swollen bulbous structures at the tip of the abdomen on the dorsal side. Although there is not enough detail to identify them, the specimen is believed to be an adult male, the structures possibly representing two large outer gonocoxites.

Discussion

The overall morphology and wing venation places this specimen in the family Tipulidae. The enlarged rostrum, the complete Sc_1 vein which is of moderate length and does not exceed the fork of Rs, the fact that R_4 and R_5 are fused to the wing margin, and, the specimen's overall moderate size suggests it is a member of the subfamily Limoniinae, and more specifically of the genus Limonia.

3.2.7. SPECIMEN 7

The fossil, BP/2/25871 (Plate 5D; Fig. 28) is a lateral compression on a reddish coarse matrix, with its left side exposed. This slender-bodied 'dipteran is 5.5mm long. The head, thorax and abdomen are preserved, but parts there of, only poorly so. One antenna, one wing and the mouthparts are present.

Description

HEAD. The head is approximately three-quarters of the length of the thorax. A rostrum is present which is noticeably extended distally (= ?nasus), but the compound eyes are indistinct. No ocelli are visible. The antenna is moderately long, as long as the length of the head and rostrum combined, and it is filiform. Individual flagellomeres are narrow and elongated; at least nine are distinguishable, but it is not clear whether this is the complete antenna. Although the mouthparts are visible, fine details are impossible to distinguish.

THORAX. There are three sclerites present, the pronotum, prescutum and the scutum; all are large and well developed. The possible positions of the scutellum, mediotergite, laterotergite, anepimeron, anepisternum and katepisternum are illustrated in Fig. 28. Possible positions of two coxae (left fore and hind) are also indicated on the figure. They are elongated and oval in shape.

Wings: the ?left wing is preserved. It is narrow and elongated, 4.1mm in length, and does not exceed the abdomen in length. The anterior end has folded over itself, and no venation is preserved. Halteres are missing.

ABDOMEN. The abdomen is slender, composed of approximately ten segments. It has rotated towards its right; this is particularly noticeable towards the posterior. It thereby exposes the sternites clearly, but shows only little of the tergites, particularly posteriorly. Segments two, three and four are the longest and broadest, the last four the shortest and slightly narrower. The abdomen ends bluntly and three projections are visible at the distal end. What they represent is unknown, but the blunt end of the abdomen may indicate that this specimen is a male.

Discussion

This specimen is a member of the Tipulidae. The general morphology confirms this, particularly its elongated rostrum (with its extended end - ?nasus). The complete absence of all six legs may be an indication of their frailty (a well-known phenomenon in the Tipulidae) and may be another pointer to their affinity to members of this family. The length of the wing with respect to body length, is similar to that of the Cylindrotominae and Limoniinae; however, the nasus-like tip of the rostrum is similar to some members of the Tipulinae. The fossil is not preserved well enough for a more positive identification.

3.2.8. SPECIMEN 8

The fossil, BP/2/25919 (Plate 6A; Figs 29 & 30) is compressed on a coarser red mudstone, and fine details are obscured by particles of matrix. However, the head (particularly the compound eyes with facets), the thorax and abdomen are preserved, and together are 5.5mm in length. Only a faint impression of a wing is visible from which no details were obtainable, and halteres are missing completely. None of the legs is preserved. The specimen is lying on its left side; the head however is twisted to the right revealing its dorsal surface.

Description

HEAD. The head is small (0.8mm) and rounded and is situated anteriorly on the thorax, thereby projecting directly forwards. Large compound eyes are present, joined for a short distance along the dorsal midline of the head [i.e. partially holoptic (Fig. 30)]. The dorsal facets are extremely large, but the ventral ones are not visible. The antennae and mouthparts are indistinct. The antennae may be short, but it appears as if the distal ends are missing. Analysis of the mouthparts needs to be treated with equal caution; I have identified the labium, labrum and hypopharynx, and I interpret these segments in Fig. 30.

THORAX. Large and rounded (1.8mm), two and a half times the length of the head (without appendages). Only the pronotum, prescutum, scutum and scutellum can be distinguished with certainty (Figs 29 & 30). The positions and presence of the cervical sclerites (Figs 29 & 30), the mediotergite and the fore, middle and hind coxae (cx1, cx2 and cx3 respectively) (Fig. 29), are also indicated; no other segments are distinguishable.

Legs: only a tiny remnant of the proximal part of the right middle femur remains. Its base indicates that it is slender.

Wings: only the proximal part of one wing is preserved; it is very indistinct, and is only preserved as a faint impression. It is relatively broad (1.8mm) with a narrow base and large anal lobe (Fig. 29). The halteres are absent.

ABDOMEN. The abdomen is long (2.9mm) and relatively narrow, comprising approximately ten segments, and it ends rather bluntly in rounded genitalia of which fine details are missing; however, the specimen appears to be a male. The fifth segment is the longest and broadest, the others preceding and following this one decrease steadily in size.

Discussion

I tentatively consider this specimen to be a tipulid according to its overall gross morphology (e.g. small head projected anteriorly from a larger and rounder thorax; the placement of the thoracic segments; the long narrow abdomen, and, the length, shape and position of the coxae). The absence of important characters such as the legs (length and breadth) and wings (venation), provides little further substantial evidence for this diagnosis and it may indeed be incorrect. However, the absence of legs, as in the previous specimen, may offer some indirect support for its assignment to the Tipulidae. The possibility that it has a broad wing and short antennae argues against this identification, as do the mouthparts which look more like those of other Diptera (e.g. some Muscidae) than Tipulidae.

3.2.9. SPECIMEN 9

This specimen, BP/2/25269 (Plate 6C, D; Figs 31 & 32) is compressed on grey mudstone. Preservation is good, but unfortunately the wings are folded over the abdomen, obscuring the all-important wing venation. As in the previous specimen, this one is lying on its left side, with the head twisted so as to expose its dorsal side.

Description

The head (excluding the antennae), thorax and abdomen combined measure 6.1mm and compared to extant Tipulidae, this would be considered only moderately long. The wings are at least 3.8mm in length (the basal region is not preserved). If the base had been present, I estimate that the wing may have been as long as 5.0mm.

HEAD. This is small and somewhat elongated, situated antero-ventrally with respect to the thorax. There are two large compound eyes on either side of the head, which are not connected at the dorsal-midline of the head (i.e. dichoptic). Individual eye facets are not preserved. The head is distorted dorso-ventrally and laterally, and the eyes are therefore contorted. The antennae are of medium length (approximately two to three times the length of the head). They are elongated and comprise approximately 11 to 13 flagellomeres (according to the right antenna; half of the left one is missing). Thirteen antennal divisions are numbered on Fig. 32, but it appears as though some whole segments may actually have broken up into one or two smaller portions. For example, flagellomeres seven and eight may actually represent a single segment, or segments six, seven and eight may correspond to one whole, as may the portions nine and ten. The scape and pedicel can both be distinguished and they arise directly from the anterior side of the head. These and flagellomeres one - four are subrounded and approximately as long as wide. From flagellomere five onwards they are distinctly more elongated, nearly two to three times as long as broad. The rostrum is either absent or very small indeed. The nasus is absent. The palpus comprises four segments; the first three segments are all of approximately the same size (just slightly longer than broad). The last palpal segment, on the other hand, is approximately two to three times as long as broad. The labellum is distinct and indicated on Fig. 32.

THORAX. This is large and rounded in comparison to the head. Some of the dorsal and ventral thoracic segments are distinguishable (Fig. 31) and these include the pronotum, prescutum, scutum and possibly the scutellum; the katepisternum, meron and the right fore, middle and hind coxae (cx1, cx2, and cx3 respectively). Figure 32, in addition, shows the prosternum, propleuron and cervical sclerites.

Legs: portions of five legs are preserved; only the ?middle left leg is missing. The right middle leg is the most complete (6.7mm). The legs are slender and longer than the abdomen, thorax and head combined. They are not swollen, only marginally thickened at the bases of the femora.

Wings: venation is indistinct. Approximately nine longitudinal veins reach the wing margin. However, as the wings overlap, some of the veins may belong to the (left) wing which lies beneath the right one. The only vein preserved in any detail is the costa, and possibly Sc_1 (Fig. 31). If Sc_1 is identified correctly, it appears to be complete.

ABDOMEN. This comprises approximately ten segments of which the first six are broad and the last four narrower, terminating in a blunt end. The genitalia are indistinct.

Discussion

Gross morphology indicates this fossil belongs to the family Tipulidae, as are the number of wing veins reaching the wing margin (approximately nine). If this is correct, the relatively small size of its body and wings, the absence of the nasus and the large number of flagellomeres indicate that it belongs to the Limoniinae or Cylindrotominae and not the Tipulinae. However, definitive detailed wing venation is not preserved. If the subcostal vein (Sc_1) is complete, this would help to validate this identification, but the somewhat longer terminal palpal segment contradicts it. The Limoniinae and Cylindrotominae are the groups known to display the former character, the Tipulinae display the latter.

3.2.10. SPECIMEN 10

This specimen, BP/2/28228 (Plate 7A & B; Figs 33 & 34) is a lateral compression on grey mudstone. Its head is twisted at 180° in relation to the thorax and abdomen, and hence, the dorsal side of the head lies upwards whereas the dorsal side of the body is directed downwards; the specimen's right side is in view. Overall preservation however is fairly poor.

Description

The fossil is of moderate length, the slender specimen measures 5.0mm and has wings at least 3.6mm long (the basal region is obscured).

HEAD. This is small and rounded, with two large compound eyes, which do not meet at the dorsal midline (i.e. the dichoptic condition). No ocelli are distinguishable. An elongated, medium length, rostrum (subequal to the remainder of head), bearing an elongated palpus at its tip, is present. Individual palpal segments are only preserved faintly , segments one to four decrease in length sequentially. The palpus is equal in length to the head including the rostrum. The presence of the labellum is indicated in Fig. 34, but it is indistinct.

THORAX. This is relatively robust and rounded in comparison to the head. Individual thoracic segments are indistinct, except for the cervical sclerites.

Legs: Three legs are preserved (right and left front legs and left back leg). They are long and slender (the incomplete front legs measuring approximately 6.7-7.1mm) and somewhat thickened at the distal ends of the femora. No tibial spurs are present and only one tarsal segment is visible at the end of the ?right front tibia; this segment is also long and slender. Coxae (cx1, Fig. 33) are fairly robust. Dense hairs cover the legs, but in particular the tibiae where the hairs are at least as long as the width of the tibiae, or up to twice this length. The femora are also covered with fine hairs, but to a lesser extent. Some additional structures (of unknown identity) are preserved near the front legs (Fig. 33).

Wings: only one wing is preserved which is twisted so as to obscure its venation. Eight longitudinal veins are distinguishable however, but their identity is not known. The wing is long (as long as the thorax and one and a half times the abdomen combined) and appears to be fairly narrow. A structure, which I consider to be a halter, is present on the dorsal side of the thorax (i.e. lower side, Fig. 33). The stalk is long and is attached to the narrow end of a pear-shaped knob. Together, the stalk and knob measure 0.7mm.

ABDOMEN. The abdomen is long (3.0mm) and narrow (0.5mm) and ends bluntly. The number of segments is unclear as divisions are not distinct; there are approximately nine or ten. No further details are available.

Discussion

General morphology (long slim body with slender legs and wings and the head with an elongated rostrum) marks the specimen as a member of the Tipulidae. The absence of details of wing venation prevents further investigation. The small to moderate size of the specimen, and particularly the wing (<10mm) would, today, distinguish it as belonging to the Cylindrotominae or Limoniinae. The Tipulinae usually have wings over 10mm long. However, no tipulids as large as this have thus far been found in the Orapa deposits. Size differences in the family may have existed between the Mesozoic and the present.

The relatively long rostrum reminds me of the extant genus Limonia. Its presence in the Cretaceous could be quite possible. Firstly, this genus has the largest number of species of all the Tipulidae (Alexander, 1964) - approximately 2 000 of the 12 000 species (or 16.6%) belong to the genus Limonia (Theowald, 1977; Hutson, 1980a). Secondly, in an interesting study on faunas of three groups of islands (Madeira, Canaries and Azores), Theowald (1977) noted that the closer the island was to the mainland, the more species of Limonia were present, and the proportion of these species relative to others increased dramatically with distance from the mainland. Further, he divided the extant Tipulidae into three groups on the basis of age (i.e. young, older and the oldest), and found that the third group had by far the greatest proportion of Limonia species in it (86%). From these data, he concluded that Limonia is the oldest genus of the family. Although I have now found that Helius is among the oldest genera, they are both members of the Limoniinae, and the subfamily as a whole was therefore among the earliest to have evolved. This would also explain why as many as three other Orapa tipulids (Specimens 2, 3 and 6) in addition to this one, resemble members of the genus Limonia.

3.2.11. SPECIMEN 11

The fossil, BP/2/28229 (Plate 7C; Figs 35, 36a & b) is a compression on red mudstone. The specimen is fairly well-preserved; it is long and slender measuring 5.2mm in length (not including the antennae). Head, thorax and abdomen are distinguishable, including some of their appendages such as portions of all six legs, both fore wings (although venation is absent in parts), and both antennae.

Description

HEAD. This is small and rounded, approximately a third of the length of the thorax (0.5mm - without antennae)(the antennae measure another 0.5mm), but fine details are not clear. The compound eyes are only faintly preserved; they are widely separated displaying the broad posterior vertex. The rostrum is small and inconspicuous, and no palps can be identified. The antennae are of moderate length (this observation is based on the left one since most of the right antenna is missing); it is approximately one and a half times the length of the head. The number of flagellomeres is unclear.

THORAX. Relatively slender and elongated, possibly somewhat distorted. Individual segments are not distinguishable.
Legs: the legs are long and slender, most of them incomplete with the exception of the left hind leg; this leg is 8.2mm long. The coxae are well-developed (see right hind leg). The slender tibiae are probably without tibial spurs. Four elongated tarsal segments are present with an empodium; the tarsal claws are not distinguishable.
Wings: (Figs 36 a & b). The wings are of moderate length and elongated, the right and left measuring 3.4mm x 1.3mm and 3.8mm x 1.1mm respectively. They are transparent throughout, without a trace of pigmentation. Venation: approximately ten veins appear to reach the wing margin (Sc_1, R_{1+2}, R_3, R_4, R_5, M_{1+2}, $?M_3$, CuA_1, A_1 and A_2). The costal vein (C), extents up to R_5. Sc_1 is complete, reaching wing margin just beyond the half way mark of the wing length, near the cord; Sc_1 is short and does not exceed the fork of Rs. Sc_2 is not distinguishable. R_{1+2} is straight, curving only slightly towards the anterior edge of the wing at its distal end; it is parallel with Sc_1 for the entire length of SC_1. Rs divides into three branches, i.e., R_4 and R_5 are separate; R_4 is captured by R_{2+3} to form a distinct element R_{2+3+4}. All curve gently, in a

posterior direction, and meet the wing margin in this manner. The distal two thirds of R_4 is parallel with R_5. These longitudinal veins are all fairly long as the distinctive cord-region lies only just beyond the middle of the wing; the basal cells are thus long, longer than half the wing length. M possibly has two or three branches; M_{1+2} may in fact branch into M_1 and M_2 at its extremity, and, the vein lying posterior to this may either be M_3 or CuA_1 (see Fig. 36b). The presence or absence of cell dm is uncertain. Crossvein m-cu lies distal to m-m (Fig. 36b). It does not appear as though CuA is constricted at its branching point. Two anal veins are present, A_1 and A_2. No halteres are preserved.

ABDOMEN. The abdomen is long and slender with nine segments. The third and fourth are the broadest, with the succeeding ones narrowing progressively to a blunt end. The terminal segment (ninth) is the genital segment whose features indicate clearly that this specimen is a male (Fig. 35). The structures are tentatively identified as follows; large inner and outer gonostyli (of equal length and size) and a smaller gonocoxite at their base. A possible paramere and the position of the aedegus is also indicated in the figure.

Discussion

The following diagnostic characters indicate that this dipteran is a member of the family Tipulidae: the long, slender body with long, narrow legs and wings; wings with two anal veins and with more than nine veins reaching the wing margin; basal cells at least half the length of the wing, and, the presence of the distinctive region near the apical third of the wing, the cord.

The specimen's identity can be narrowed down to the subfamily Limoniinae by a process of elimination of other groups, rather than the presence of characters typical of the Limoniinae: small inconspicuous rostrum, nasus absent (therefore not Tipulinae); Sc_1 complete (therefore not Tipulinae); CuA not constricted at branching point (therefore not Tipulinae); tip of R_{1+2} present, R_1 not appearing to converge with R_3 (therefore not Cylindrotominae).

To identify the specimen to the level of tribe proved impossible. The only certainty is that it does not belong to the tribe Pediciini as Sc_1 is short and does not exceed the fork of Rs.

The non preservation of Sc_2 renders further identification impossible. If Sc_2 is actually lacking, the tribe Limoniinae may be eliminated. Supporting this elimination would be the fact that Rs has three branches with R_4 and R_5 separate and R_4 emerging from R_{2+3+4}; this would place it in the Hexatomini or Eriopterini. Eriopterini has no tibial spurs as is the case in the fossil. As missing characters may indicate non-preservation, they cannot be considered diagnostic, and must be regarded with caution.

CHAPTER FOUR

Empis orapaensis sp. nov.

4.1. INTRODUCTION

This is the first description of a fossil Dance fly, from Africa. Indeed, this specimen, of the superfamily Empidoidea, is the first fossil member of the Empididae from the Southern Hemisphere; it is also the oldest member of the subfamily Empidinae and family Empididae. The fossil has a more plesiomorphic wing venational pattern than the extant species of Empis; I regard it as unique and I have therefore chosen to erect a new species, Empis orapaensis. I provide a full diagnosis and a summary of the apomorphic and plesiomorphic characteristics. The specimen modifies earlier ideas on the phylogeny of the Empidoidea, and provides us with more conclusive evidence on the environment of Cretaceous southern Africa. I believe E. orapaensis had a similar life-style to extant members of the group and, therefore, visited and pollinated flowers.

I have chosen to follow the new system of classification of Chvála (1983) which I regard as the most accurate.

4.2. SYSTEMATIC DESCRIPTION AND DIAGNOSIS

Superfamily: Empidoidea
Family: Empididae
Subfamily: Empidinae

Tribe: Empidini

Genus: *Empis* Linnaeus

Subgenus: *empis sensu stricto* Linnaeus

Species: *Empis empis orapaensis* sp. nov.

Type specimen

The specimen is preserved on the bedding surface of a block of grey mudstone as a compression. *Empis orapaensis*, BP/2/26953 ♂, is illustrated in Plate 8A-F, Figs 37 & 38, and Appendix 2.

Derivation of specific epithet

Latin form of Orapa.

Diagnosis

Stout thorax; tapering abdomen, upturned at eighth segment; legs slender with well-developed chaetotaxy; wings with large, distinct, rectangular axillary lobes; acute axillary excision; subcosta ends in costa; C extends to R_5; R with four branches; Rs short, with "narrow" or "closed" fork, and with three branches reaching wing margin; cells br and bm moderately long; cell dm present; M three-branched, all branches complete; CuA_2 strongly recurrent; A_1 distinct; A_2 present but reduced; four cross-veins present: h, r-m m-m and m-cu; a secondary cross-vein r-m (?aberrant vein) present; cells br and bm long; cu short, shorter than bm.

Description

The dipteran is well-preserved with both wings, abdomen and thorax present. Portions of three of its legs remain, but the others, and the head, are missing. Both halteres (Plate 8B; Fig. 37) are clearly preserved. The thorax and abdomen combined are 3.9mm long. The wings (Plate 8A; Figs 37 & 38), of which the basal parts are missing, are large and measure 3.3mm and 3.1mm for the left and right wing respectively.

The body is relatively short (2.67mm) and broad (0.78mm proximally - 0.39mm distally) (Plate 8A; Fig. 37). The abdomen consists of eight pregenital and approximately two genital segments; these individual segments are clearly preserved as vertical bands. Each segment bears numerous long hairs which may be more than half the width of these segments (Plate 8F). Hairs on the tergites are somewhat shorter than those on the sternites; also, hairs on the genital segments are shorter than the hairs on the pregenital segments, and hairs at the centre of the sclerites are shorter than those at the edges.

The genital segments (Plate 8C; Fig. 37) at the posterior end are visible, but indistinct. In the living specimen the genitalia seem to have been tilted upwards and have consequently been compressed sideways during fossilisation (Plate 8A). This tilt is also observable in the orientation of the sclerites of the abdominal segments. The abdomen turns upwards at the eighth segment, as the eighth tergite is reduced to a short narrow band dorsally, and ventrally the sternite is much longer. The structure and modifications of the hind segments indicate that this specimen is a male. Individual structures of the hypopygium (Plate 8C) are not distinguishable, excepting for the paired rounded bulbous structures at the tip of the abdomen. These possibly represent the cerci and/or surstyli. There is a long spine (of similar dimensions to abdominal hairs) emerging from the middle of one of the above-mentioned structures. It is possibly a stray hair that broke off from another part of the body before fossilisation, or, it may be the aedeagus which often protrudes beyond the genital lamellae in Empidinae. The abdomen tapers to a blunt, rounded and broad end.

The abdominal segments are all similar in shape: slightly wider than long, each tergite a little shorter than the preceding one, as the abdomen narrows distally. The first abdominal segment (0.07mm) however, is much shorter than the other pregenital segments, being one-fifth of the length of the second segment. Segment 2 is the longest (0.33mm). The first segment is commonly firmly fused to the metathorax, in the fossil there is a clean break between them.

Apart from a few short stout hairs near the point of origin of the wing, the thorax is virtually hairless. Individual thoracic sclerites are not distinguishable. Just above the thorax, on the right hand side, a structure is preserved which, unfortunately, is not identifiable.

Parts of three legs are preserved (Plate 8A & D; Fig. 37); two of them are nearly entirely obscured beneath the wings. The legs are long (approximately 3.25mm; proximal parts are obscured) and slender. The tibia of the exposed leg on the left hand side of the thorax (Plate 8D), bears many moderately long (as long as the tibia is wide) stout bristles. At the distal end of the right wing, the three last basitarsi of one leg are visible. They are all very small (0.07mm in length) and slender. A faint imprint of a femur lies below this same wing and it is twice to three times as broad as the other leg segments.

The two wings are almost completely preserved, both having clear, identifiable venation and pigmentation (Plate 8A; Figs 37 & 38). The wing membrane is entirely covered with microtichia, and the veins are bare except for the costal vein, which has distinct bristles (Plate 8E). The costal vein (C) ends at the tip of the third longitudinal vein (at R_5). The auxillary vein (Sc) ends in the costa (complete) but is very weakly developed distally. The first longitudinal vein (R_1) ends in the costa between Sc and R_{2+3} at an approximate ratio of 1:2. The third longitudinal vein (R_{4+5}) is forked. The fourth longitudinal vein (M_1) is simple. The sixth longitudinal vein (A_1) possibly reaches the hind margin of the wing, but its distal end is indistinct. The discal cell (dm) has three veins issuing from its end (M_1, M_2, M_3). All three join the wing margin and are simple. The dm cell is rather blunt and is shorter than the middle vein issuing from its end. The anal cell (cup) is short, the vein closing it (CuA_2), is strongly recurrent, and the anal lobe is large. An unusual feature of the venation is the extra, ?aberrant, crossvein running between the fourth longitudinal vein (M_1) and the third (R_{4+5}) on both wings. This vein (2nd r-m) is located just prior to the fork of M_1 and M_2 and is as far beyond the crossvein r-m as cell br is long. The wings are transparent with a narrow and dark pterostigma (pt) which extends between Sc and R_{2+3}.

The body has been rotated slightly over to the right partially covering the right haltere, but clearly exposing the left one (Plate 8A & B; Fig. 37). Halteres are moderately long (the knob is 0.29mm long, the stalk 0.33mm). The knob is oval, its anterior surface is covered with very fine short hairs, but the posterior side appears hairless. The stem is broad at the base and narrow where it joins onto the knob. Both halteres have broken away from their points of attachment.

4.3. DISCUSSION

Morphology

A typical feature of many living members of the family Empididae, and of this fossil, is that the terminalia are directed more or less vertically upwards (Plate 8A; Fig. 37). The specimen also displays typical reduced Brachycerous wing venation as is known in the family Empididae, subfamily Empidinae (i.e. the costa is not continued around the wing margin; the discal cell, dm, is present and has three branches; the anal cell is present, with the axillary lobe well-developed; the lower branch of the fifth vein, which closes the anal cell, is strongly recurrent) (Fig. 38). A critical character separating the two tribes in Smith's (1969) key is the presence (Empidini) or absence (Hilarini) of metapleural hairs. This character is unfortunately obscured in this fossil. According to Smith's key and (later) personal communication, however, the fossil specimen is assignable to the genus Empis, since the third longitudinal vein is forked (R_4 and R_5), and to the subgenus Empis empis s.s. since all branches of vein M issuing from cell dm are complete and reach the wing margin (Fig. 38). The well-developed chaetotaxy of the legs (Plate 8D) is an additional distinguishing feature of the subfamily. Observations of the gross morphology, and proportions of the body and its various appendages are consistent with this identification.

Primitive and advanced features of the wing venation

The wings of Empis orapaensis (Fig. 38) display both plesiomorphic and apomorphic characteristics. The wings have large, distinct rectangular (plesiomorphic) axillary lobes; this is a feature shared with the primitive form Protempis antennata as well as with a number of extant forms. P. antennata was probably an ancestor of the superfamily Empidoidea (Chvála, 1983). A well developed axillary lobe undoubtedly features in the groundplan of this superfamily (Chvála, 1983), and is present in the Oreogetoninae and most Empidinae, in the Atelestidae, and in the primitive Hybotidae. In these forms the axillary excision is very acute or almost right angled. The absence, or only very slight development of this lobe is an apomorphic condition.

Another plesiomorphic character is that the subcosta ends in the costa. Chvála (1983) studied a great number of extant Empidinae, and in all of them the subcosta ends before the costa, setting the Orapa specimen apart as an older, more primitive empid, and also as a new species. The radial vein (R) has four branches, Rs has three as R_{4+5} is forked. In many living Empis species the more "open" radial fork of R_4 and R_5 is an apomorphous state (Chvála, 1983), but the Orapa specimen does not have such a wide fork. Other primitive features are: Rs is short, and the medial vein M is three-branched; cells br and bm are rather long; A_1 and possibly A_2 are present, although the latter appears considerably reduced; not including the extra crossvein mentioned in the description, there are four crossveins: h, r-m, m-m, m-cu.

The following apomorphies are present: the short anal cell, cup (it is shorter than cell bm); vein CuA2 is recurrent and meets the anal vein at an angle of less than 90° ; the costa does not extend around the whole wing but extends only to R_5. An apomorphic feature, not relat the wing, is the presence of the reduced eighth abdominal sternite (where the abdomen is upturned).

<u>Biology</u>

The Empididae is a very large family of Diptera, comprising six subfamilies (Chvála, 1983): Oreogetoninae, Empidinae, Hemerodromiinae, Ceratomerinae, Brachystomatinae and Clinocerinae, totalling approximately 2 000 species world-wide. However, only approximately 250 species are known from the Afrotropical Region. Of the world fauna, the Empidinae is the most species-rich with about 1 450 species in 21 genera which are separated into two tribes, the Empidini and Hilarini (Chvála, 1981). In the Afrotropical Region the two tribes comprise 111 species (81 in South Africa) divided between six genera. The Empidini are represented mainly by the two large genera <u>Empis</u> and <u>Rhamphomyia</u>, which, with the exception of the Australian region, have a world-wide distribution (Chvála, 1981) and they are particularly common in the Holarctic region. In South Africa, the subfamilies Empidinae and Hemerodromiinae are most common (Smith, 1969 & 1980). <u>Empis</u> (Empidini), particularly the subgenus <u>Coptophlebia</u>, and <u>Hilarempis</u> (Hilarini) are the most common genera of Empidinae in South Africa today.

The members of the family Empididae are commonly found in moist places among undergrowth and in shady woods, bush, grassland and moist vegetation near water. They have also been observed on flowers, tree trunks and even on the surface of water (Smith, 1969). The genus Empis s.s. is found in South Africa today, in those habitats (Smith, 1969).

Members of the superfamily Empidoidea are of moderate to minute size measuring 1.5-12mm (Steyskal & Knutson, 1981). They have stout thoraces and tapering abdomens. They are recognised mainly by their brachycerous type of wing venation and their general predatory appearance (Colless & McAlpine, 1970). The legs are slender, but in some species, for example Empis sp. the front basitarsus of the male is swollen. (Unfortunately this segment lies obscured below the wing in the Orapa specimen). This condition has been associated with the production of silk for enmeshing prey for use in courtship (Eltringham, 1928), but this view is not held universally (Kessel, 1955 & 1959). Swollen basitarsi are not visible in the Orapa specimen. In most genera the proboscis is elongate to some extent and is adapted for piercing. The eyes are large. In some members of the family both male and female are holoptic, although usually this condition is restricted to the male. Large eyes, often with enlarged upper ommatidia, are associated with swarming and aerial mating (Chvála, 1976). In the virtually non-flying species (e.g. Rhamphomyia ursinella) such an adaptation is not found as it is non-essential (Downes, 1970). Terminalia of the male are large, sometimes turned upwards or forwards over previous abdominal segments. The tip of the female abdomen is flattened with an inconspicuous, normally withdrawn ovipositor.

Most adults are predominantly predacious on smaller arthropods (Colless & McAlpine, 1970), usually on other Diptera (Barraclough & Londt, 1985). Kessel (1955) even mentioned their cannibalistic tendencies associated with mating. Downes (1970), however, stated that no such observations have ever been recorded. Prey items are not generally specific and a variety of prey may be taken. Prey are usually swarming or emerging individuals but dead ones are also of interest (Downes & Smith, 1969). Living Empididae are not exclusively predacious, since many visit flowers, and both sexes of various species are known to feed on nectar (Laurence, 1955; Downes & Smith, 1969; Downes, 1970; Steyskal & Knutson, 1981).

The immature stages appear to be predacious. Smith (1969) listed reasons for this assumption. Larvae, including those of <u>Empis</u> (Steyskal & Knutson, 1981) live in terrestrial habitats such as soil, leaf-litter, rotting wood or dung. A few species live in intermediate situations (for example, surfaces covered by a thin film of flowing water), and some are aquatic.

<u>Courtship</u>

Some genera of the Empididae have evolved an elaborate courtship display in which the prey is used as an essential stimulus in initiating courtship (Smith, 1980). Some species form dancing swarms, for example <u>Empis</u> over dry land and <u>Hilara</u> over water, hence their common name: Dance flies. Such swarms are usually connected with mating behaviour (Smith, 1980).

In the Empididae swarming has undoubtedly reached the highest degree of development (Chvála, 1976), where swarms consist largely of males (Fig. 40). In some species of Empis the male captures an item of prey and offers it uneaten to the female at the moment of coupling. Further, the female has not been observed hunting and her only source of animal protein is that given to her by the male during repeated matings (to complete one ovarian cycle), demonstrating sexual differentiation in hunting and feeding habits. This type of sexual differentiation is restricted to the Empis-Hilara-Rhamphomyia (Empidinae) group (Downes & Smith, 1969). The prey, as a stimulus for copulation, probably transends its significance as food. Examples of this are demonstrated by some species of Hilara and Empis where prey transfer has been ritualised and the object transferred is no longer insect prey enclosed, as in some species, in a light-reflecting silken or frothy coccoon, but in a conspicuous balloon-like wrapping, empty or with at best an inedible fragment inside (Downes & Smith, 1969). Kessel (1955 & 1959) wrote detailed accounts of types and examples of ritualised mating sequences in empid species which clearly demonstrated prey/balloon-type or height of swarms is species-specific and response of a conspecific mate (female) is dependent on acceptance of the visual stimulus if the process of mating is to continue. The type of flight, general swarming style, choice of swarm marker and prey/display object type, daily and seasonal swarming times are also specific for each species (Chvála, 1976) and visual recognition of these factors is important for specific mating.

Distribution

The family Empididae is best represented in the northern temperate and montane regions but is also well represented in the Afrotropical Region, particularly southern Africa (Smith, 1980) (Fig. 41).

The members of the Empidinae from Orapa confirm previous finds (McKay & Rayner, 1986; Rayner, 1987; McKay, 1987 & 1990), that c.93 Mya the Orapa region represented a wooded or well vegetated area with abundant water. Rohdendorf (1974) indirectly supported this view by noting that the "Empididae" are abundantly represented in Baltic Amber, which is definitely connected with the characteristic ecology of this family: an inhabitant of forests and moist habitats. Extant members of the Empididae in southern Africa are mainly found in coastal regions of the Cape Province, or in regions with a similar climate (Fig. 41). It seems likely that Orapa had a similar climate in the middle Cretaceous. Some genera have however, on occasions, had representatives with a distribution reaching as far up as Zimbabwe, Smith (1969), for example, showed that Empis s.s. has been found in the S.W. Cape, E. Cape, Lesotho, Natal, Zimbabwe and north of southern Africa), but their absence in the drier open regions, including the Limpopo coastal region is significant.

Fossil Empididae

The earliest known fossil Empididae are from the Mesozoic period. For example, fossil remains of the subfamily Tachydromiinae; Archiplatypalpus (Kovalev, 1974) and Cretoplatypalpus archaeus (Kovalev, 1978) of the late Cretaceous deposits of Taymyr (Northern Siberia) have been recovered. From the subfamily Microphorinae are Cretomicrophorus rohdendorfi and Archichrysotus hennigi and A. minor (Negrobov, 1978). Negrobov (1978) mentions Jurassic representatives of the Karatau discovered by Ussatchov in 1968. The largest number of Empididae however are from Tertiary Baltic Amber (Melander, 1928), and other ambers and copals (Spahr, 1985). A few are from Tertiary (now believed to perhaps be Cretaceous) Burmite (Cockerell, 1917, in Spahr, 1985).

Evolution of hunting, feeding and courtship habits

The most primitive form of feeding is the entirely predatory nature of some empids, and, nectar feeders appeared only secondarily (Chvála, 1976). I suggest that, at some time during the phylogeny of the Empis-Hilara-Rhamphomyia complex, predatory behaviour was modified and incorporated into courtship and mating. This would have happened early, in a common ancestor to these three genera. The findings of a fully differentiated Empis member in the Cenomanian sediments of Orapa implies that these changes must have arisen long before this period, perhaps pre-Cretaceous.

The evolution of courtship behaviour of the Empididae was discussed by Kessel (1955) and Chvála (1976). Kessel believed in an evolutionary sequence of courtship patterns, based on prey (presence or absence of) and, if present, presentation of prey, which he categorised into eight stages. For example, ranging from the simplest category where no prey is involved, to more complex where an item of prey is included to more advanced with prey wrapped in a silken balloon, to the final stage, a cocoon containing no prey at all. This is a simplistic model, based on [illegible] more than a belief in increasing complexity through[illegible] fossil record. I see no reason why Cretaceous [illegible] should be less complex than extant ones. Indeed, the presence of this middle Cretaceous empid suggests an "advanced" state fairly early on in the history of the Empididae.

Chvála (1976) believed that primitive courtship behaviour of the Empididae was to both meet and mate in the air. The derived courtship involves meeting in the air but mating on the ground. Mating on the ground involves direct contact or pheromonal recognition. I suggest that the common ancestor of these hunting empids recognised each other in the air by the means of visual signals other than silk balloons or a protein "gift". At that stage both sexes were predatory and copulation took place in the air unencumbered by a prey item. The courtship display at that time must not only have involved recognition, but safe recognition - i.e. to ensure copulation rather than eradication. This recognition system came under intense stress during a speciation event and changed. The result was that the female became non-predatory, she thus required animal protein to complete her reproductive cycle. This was effected by the "gift" from the male.

Since modern (and presumably fossil) females visit flowers for nutrition, this speciation event was co-incident with the existence of the angiosperms. Extant females are carnivorous, and still require animal protein for their oocyte formation. This provides a mechanism for the strong stabilization of such exotic mating behaviour. If this hypothesis is correct, the speciation event of the common ancestor of this complex took place early in the Cretaceous in a closely related species to E. orapaensis.

This association between Angiosperms and Empidinae is known. I suggest, therefore, that the Empidoidea served as early pollinators of flowering plants.

Phylogeny of the Empidoidea

The phylogeny of the Empidoidea has been researched extensively by Chvála (1981 & 1983). Examination of some 14 000 specimens from all over the world comprising extant and fossil species, in addition to cladistic analyses, led Chvála to produce the phylogenetic tree illustrated here in Fig. 39. The reliably dated, and well-preserved fossil Empid supports some of his predictions, but it suggests that the subfamily Empidinae was well-established as early as the middle Cretaceous. The discovery of a fossil Hybotid (Empidoidea: Hybotidae), in Orapa further supports the earlier origin of Empidoidea families, in this case the Hybotidae. These finds, a fully differentiated fossil Empid and Hybotid, imply that the groups were well-established at a much earlier date than that predicted (Lower-Middle Palaeogene) and consequently, these observations have been added to Chvála's phylogenetic scheme (hatched areas in the figure). The width of the black areas in Fig. 39 reflect e relative numbers of extant species. The labels A - J represent important fossil finds in support of the predicted phylogeny. The basic phylogenetic pattern however, remains unaltered.

CHAPTER FIVE

Pseudoacarterus orapaensis gen. et sp. nov.

5.1. INTRODUCTION

In this chapter I describe Pseudoacarterus orapaensis gen. et sp. nov., the only Mesozoic record of the subfamily Hybotinae, and the first fossil assignable to the family Hybotidae from the southern hemisphere. P. orapaensis indicates that the Hybotidae originated and diversified at least 40 million years before the previously accepted date. P. orapaensis may be ancestral to the extant genera Sabinios and Syndyas, but not Acarterus. The fossil supports the predictions of a moist, well-vegetated and seasonal environment in Cretaceous Orapa. Diversification of the Hybotinae appears closely allied with that of the angiosperms.

5.2. SYSTEMATIC DESCRIPTION AND DIAGNOSIS

Superfamily: Empidoidea (sensu Chvāla, 1983)
Family: Hybotidae Chvála 1983
Subfamily: Hybotinae (sensu Chvála, 1983)
Genus: Pseudoacarterus gen. nov.
Species: P. orapaensis sp. nov.

Type and only known species

Pseudoacarterus orapaensis gen. et sp. nov., compressed as part, BP/2/25224a (Plate 9A, B, & C; Fig. 42) and counterpart, BP/2/25224b (Plate 9D; Fig. 43), in grey mudstone.

Derivation of generic and specific name

Greek: Pseudes, false, and Acarterus, the extant genus most closely resembling the fossil; and orapaensis, after the site of discovery: Orapa.

Diagnosis

Legs slender with well-developed chaetotaxy; one pair, presumably the hind pair, with thickened femora; halter with long, elongated stalk and large pear-shaped knob, both with well-developed chaetotaxy; characteristic Hybotidae and Hybotinae wing morphology and venation; wing length, >2.47mm, breadth, 0.99mm, clear with stigma from just in front of R_1 to R_{2+3}; blade uniformly covered in microtrichia, costal vein with stouter hairs, other veins bare; well-developed axillary lobe; C ends at tip of M_1; Sc is closely associated with R_1 distally and joins it far beyond radial bifurcation; all longitudinal veins simple; R_{4+5} and M_1 parallel; radial sector a little shorter than length of basal cells br and bm; br and bm long, a third of wing length, vein separating them weakly developed; A_1 reduced; dm large, elongated, lies near distal end of wing and has two veins issuing from it, both veins simple and complete; cup present, equal in length to br and bm.

Description.

The abdomen, head and thorax of Pseudoacarterus are crushed, and obscure a third of the right wing and a quarter of the left wing; most of the venation is visible in the left wing of the part (Plate 9A; Figs 42 & 44). Bristles have been observed on some areas of the body (Plate 9B). Whether these are on the thorax and/or on the abdomen is uncertain, as individual segments are not easily discernible. These non-differentiated hairs may be as long as the knob of the halter. The halter is found just above the right wing of the part [Plate 9A & B; Fig. 42 (arrowed)] and is 0.41mm in length. The body is approximately 2.50mm long (although this measurement is misleading because the dipteran lies over another insect; (a non-dipteran, as a small hind-wing is detectable) and the bodies of these two insects are not easily distinguishable from one another). The wing span is 5.42mm. The most complete wing of the hybotid (the left wing of the part) measures 2.47mm in length and 0.99mm in breadth (at the widest point).

THORAX. Thoracic details were indistinct.

Legs: fragments of five legs are preserved. The legs are elongated, the longest, presumably the hind leg, is 2.36mm long and has a thickened femur. Femora, tibia and tarsi are bristled. The complete femur of the counterpart (Plate 9D; Fig. 43) bears long, fine hairs (longer than width of segment) on the one side, presumably the ventral side, only. The tibia and tarsi however, which are all long and equally slender (Plate 9C), are uniformly covered with much shorter hairs (a third of the width of the segments). At the end of the last tarsal segment two pectinate claws are present (Plate 9C); the basitarsi are small and not swollen; no further details of the tarsi are distinguishable. No tibial gland is visible.

Wings: they are large and narrowly elliptical (Plate 9A & D; Figs 42, 43 & 44). The membrane is entirely and uniformly covered with microtrichia. The costal vein bears slightly longer and stouter hairs. All other veins are bare. By combining the drawings of both the left and right wings of the part and counterpart, a composite drawing has been made which illustrates venational details (Fig. 44). The wings are clear with a somewhat darker, narrow and elongate stigma. The stigma extends from just prior to the R_1 vein to the R_{2+3} vein. The axillary lobe is presumably well developed (the blade, at a quarter of the distance from the wings' point of origin, is approximately as wide as the rest of the blade, i.e. the wing-margin has not turned towards the anterior of the wing yet, suggesting a large lobe). The costal vein (C) ends at the tip of the fourth longitudinal vein M_1. The auxillary vein (Sc) is closely associated with R_1 distally; Sc joins R_1 far beyond the radial bifurcation. The longitudinal veins: R_{2+3}, R_{4+5} and M_1 are simple. R_{4+5} and M_1 are parallel. The radial sector is long, not much shorter than the basal section of M which separates the basal cells br and bm. The discal vein M between the basal cells br and bm is indistinct. The discal cell (dm) is large and elongated and lies relatively near the wings' edge. It has two veins issuing from its distal end and it is approximately as long as the anterior vein. Both veins M_1 and CuA_1 join the wing-margin. The anal cell (cup) is present and is about as long as the basal cells; the vein closing it, CuA_2, reaches the anal vein at right angles. The basal cells br, bm and cup are long, being greater than a third of the length of the wing. The sixth longitudinal vein A_1 is weakly developed, it is not certain whether it reaches the hind-margin of the wing.

The halter (Plate 9B) consists of a narrow elongate stalk with a large pear-shaped knob; the narrow end of the "pear" is attached to the stalk. The knob is eight times as wide as the stalk. Both sections of the halter are covered with especially fine short hairs, each about as long as the width of the stalk.

5.3. DISCUSSION

Biology

The family Hybotidae includes about 1 300 extant species in the world fauna (Chvála, 1983). In the Afrotropical Region, eight genera are known, represented by 52 species, and in South Africa, seven genera are present comprising 24 species (Smith, 1980).

Hybotids are small to medium in size with an average measurement of 6mm. Like the Empididae (Chapter 4), they are recognised mainly by the Brachycerous-type wing venation and their general predatory appearance (Colless & McAlpine, 1970). For example, one of the three pairs of legs are raptorial; these have thickened femora probably accommodating strong muscles and armed with spines or bristles (as can be seen in P. orapaensis) for catching prey (Smith, 1969). Indeed, Tuomikoski (1952) observed the genus Syndyas catching prey in flight by using its strong hind legs. Also in predatory species, the proboscis is adapted for piercing, and the eyes are large, often with enlarged upper ommatidia. Unfortunately, these characters were not available for observation in Pseudoacarterus.

Adult Hybotidae (usually both sexes) are predominantly predacious (Poulton, 1907 & 1913); they have, however, also been seen feeding on nectar. A predacious habit involving both sexes is a primitive habit which is exhibited in most of the other Empidoidea. The complex ritualised mating seen in extant Empididae, particularly Empidinae, is unknown in Hybotidae. Indeed, in the fossil specimen, no swollen basitarsi are present, a characteristic thought by some to be associated with species which enmesh their prey in silken balloons (functioning specifically as mate attractants). As in the Empididae, adult Hybotidae are mostly found among undergrowth and in shady woods, bush, grassland and moist vegetation near water. They have also been observed on tree trunks and on the surface of water. Larvae of most Hybotidae (Tuomikoski, 1966) live in terrestrial habitats such as soil, leaf-litter, rotting wood or dung; a few species live in intermediate situations (e.g. surfaces covered by a thin film of water) and some are aquatic.

Morphology

Wings. The family Hybotidae, comprising the three subfamilies Tachydrominae, Hybotinae and Ocydromiinae, is characterised by several autapomorphies. Of these, the only ones recognizable in the Orapa specimen are related to wing venation (i.e. the [illegible] sector has only two branches, and the vein R_{4+5} is not forked).

Characteristics typical of extant members of the subfamily Hybotinae are listed below; most are shared with the Cretaceous specimen, but I indicate where this does not occur.

(a) Wings often have an apparent costal stigma.

(b) Wings have a more or less developed axillary lobe and no alula (the latter is not distinguishable in *P. orapaensis*).

(c) The discal cell is present, emitting two veins (M_2 absent) to the wing margin.

(d) The anal cell (cup) is large, at least as long as or longer than basal cells (in *Pseudoacarterus* the anal cell is as long as the basal cells).

(e) Radial sector rather short, somewhat longer in *Syneches*, *Stenoproctus*, *Acarterus*, *Afrohybos* and *Parahybos* (in *Pseudoacarterus* the radial sector is of intermediate length).

The only two plesiomorphic features of the wing of the Orapa specimen are the long basal cells and the large anal cell. All other characters are apomorphic. The wings of *P. orapaensis* resemble those of the extant genera *Sabinios*, *Syndyas* and *Acarterus*, but are most similar to those of *Acarterus*.

Legs. The hind femora of members of the Hybotinae are usually more or less swollen and bristled as is the case in the genera *Sabinios*, *Syndyas* and the fossil *Pseudoacarterus*. This is not so in *Acarterus*.

Another distinguishing feature of the family Hybotidae is the gland on the fore-tibiae. This is not observable in the fossil, because only a few segments of the six legs are preserved, the front segments not being among these. Overall, the Hybotid displays a greater number of apomorphic than plesiomorphic morphological characteristics.

Classification and Phylogeny

The phylogeny of the Superfamily Empidoidea has been extensively researched by Hennig (1981) and Chvála (1981 & 1983). Morphologically, *Pseudoacarterus orapaensis* undoubtedly belongs to this group.

The placement of this new genus *Pseudoacarterus* into higher taxa follows the recent system of Chvála (1983), who studied all available type-material, including 14 000 specimens from many parts of the world, but mainly Europe, and in particular Scandinavia. Workers have supported this arrangement indirectly (Colless, 1963; Tuomikoski, 1966;

Hennig, 1970 & 1971; Chvála, 1981). Chvála (1983, p. 9) regarded the Family Empididae as "an unnatural paraphyletic unit" and, depending on the authority, comprised about 11 subfamilies. Chvála suggested splitting the former Empididae into four distinct families; Empididae, Hybotidae, Atelestidae and Microphoridae. These, together with the Dolichopodidae, comprise the superfamily Empidoidea (Fig. 39).

Chvála (1981 & 1983) discussed the phylogenetic patterns of the Empidoidea. As I have previously mentioned in Chapter 4, I have taken his phylogeny and added the two Orapa fossils: *Pseudoacarterus* and the Empid: *Empis orapaensis* (Fig. 39).

The wings of *Pseudoacarterus*, being the only parts available for close study, do not provide sufficient information for changes to be made to the arrangement of groups as shown in Fig. 39. Other morphological details are required (e.g. chaetotaxy of thorax and structure of genitalia). However, the date of the origin of the Hybotidae is considerably earlier than the 70Myr supported by Chvála (1983), at the very least 30Myr prior to this date, but more likely 40Myr or more. Diversification of the Hybotidae coincided with the rise to dominance of the flowering plants. The nectar feeding habit of these flies may indicate a close evolutionary relationship.

Of the three subfamilies of the Hybotidae: Ocydromiinae, Hybotinae and Tachydromiinae, the latter two are more closely related, on the basis of the loss of M_2 (Hennig 1970). Hennig (1970) considered the Ocydromiinae to be a sister group of the Tachydromiinae and Hybotinae.

Trichinites cretaceous (wing illustrated in Fig. 45) was considered by Hennig (1970) and Chvála (1983) to be the forerunner of these three subfamilies, since it displays several of the groundplan characteristics (e.g. a large anal cell, cup). The large anal cell is also assumed to be a part of the groundplan of the Hybotinae. The presence of an even larger anal cell in some genera (e.g. Hybos), and a short anal cell (as in the Ocydromiinae) are derived features (Hennig, 1970). The anal cell of the Orapa fossil is proportionally the same size as that of Trichinites cretaceous (it is as long as the two basal cells), and this primitive feature therefore suggests Pseudoacarterus to be a forerunner of a number of hybotid groups.

Trichinites also displays the plesiomorphic characteristics of having three M veins emitting from the discal cell and having all the venational elements (cells and the points of origin of various veins) nearer the wing base. The veins are thus longer than those of some more recent species. Pseudoacarterus orapaensis, however, exhibits apomorphic character states; it has only two M veins (having lost M_2) and it has the venational elements nearer the wing tip. Veins (for example, M_1 and M_3) are thus shortened.

Pseudoacarcerus excludes the Ocydrominae as a possible descendant as its members have either a very short anal cell, for example the genus *Ocydromia*, or they have three M veins issuing from the discal cell, for example the genus *Stuckenbergia*. The subfamily Tachydrominae is also excluded as it does not have a discal cell.

Members of the subfamily Hybotinae are, therefore, the only descendents of *Pseudoacarterus*. Extant genera which resemble this fossil are, as previously mentioned, *Sabinios*, *Syndyas* and *Acarterus*. As nearly all species of the Hybotinae have swollen and bristled hind femora, a comparatively large anal cell and a distinct vein M between the two basal cells br and bm, I suggest that these characteristics are part of the groundplan of the subfamily. *Pseudoacarterus* does not display all these features, and I therefore do not consider it an ancestor of all Hybotinae genera. The faint M vein between its two basal cells suggests it could be ancestral to *Sabinios* and *Syndyas* as both display this feature; I do not believe that this derived feature arose independently in more than one group. However, these two genera have other derived characters which they do not share with *Pseudoacarterus* such as the shortening of Rs (by the displacement of its point of origin towards the wing tip). *Sabinios* and *Syndyas* have a considerably larger number of apomorphic wing venational characters. In *Acarterus* on the other hand, the portion of vein M between the two basal cells is distinct. I suggest that *Acarterus* branched away from the main line as a separate genus before the appearance of <u>Pseudoacarterus</u>; thereby possibly sharing another more ancient and as yet unknown ancestor. This difference in the venation of the extant and the extinct genus is, however, the only one, and is the main reason I have chosen this generic name.

<u>Trichinites</u> has no distinct swelling or bristling of any of the legs, or a portion of them, and it is not certain whether this was a part of the groundplan of the Hybotidae or of the Empidoidea in general. Swelling of femora or tibiae of the raptorial legs occurs in several groups within the superfamily. For example, the Hemerodrominae of the family Empididae display this condition as do the Hybotinae and Tachydrominae of the Hybotidae. It seems likely that this condition arose independently a number of times. The extant genus <u>Acarterus</u> does not exhibit swelling or bristling, in contrast to <u>Pseudoacarterus</u>, <u>Sabinios</u> and <u>Syndyas</u>. This supports my suggestion that <u>Pseudoacarterus</u> is more closely related to <u>Sabinios</u> and <u>Syndyas</u> than it is to <u>Acarterus</u>, and may indeed be the common ancestor of <u>Sabinios</u> and <u>Syndyas</u>.

Incidently, <u>Trichinites</u> is one of the very few representatives of the Mesozoic Hybotidae to date.

<u>Distribution</u>

At least two thirds of the species of the subfamily Hybotinae are found in the tropics and subtropics of the Oriental and Neotropical regions (Chvála, 1983). Three common southern African genera allied to P. orapaensis are Sabinios, Syndyas and Acarterus. The former two extant genera are found mainly in the Cape coastal region, and Acarterus (with its single species, A. unicolor) is an entirely Afrotropical genus (Smith, 1980) (Fig. 46). Specimens of all three genera have been reported from the southern coastal regions in general, and as far up as Zimbabwe. These regions are moist and often well-wooded. The absence of members of the subfamily in the drier open regions including the Limpopo coastal region is obvious (Smith, 1969).

The morphology of the fossil is so similar to some living dipterans, that I suggest their environmental requirements were the same. The specimen therefore leads me to suggest that humid conditions (and seasonal rainfall?) and forested or well-vegetated surroundings prevailed in or around Orapa during this part of the Cretaceous, substantiating yet again the type of palaeoenvironment indicated by some of the other dipterans.

CHAPTER SIX

FAMILIES ?MYCETOPHILIDAE (SCIAROIDEA)
AND
?RHAGIONIDAE / ?TABANIDAE (TABANOIDEA)

6.1. INTRODUCTION

I have found many dipterans which, although they are well preserved, I cannot identify, even to family level. This is due to the fact that vital diagnostic characteristics (usually wing venation) are not preserved. Here, I deal with three such dipterans which I have assigned to two separate superfamilies within the two suborders, Nematocera and Brachycera. The specimens have tentatively been placed in two, possibly three, families: the first fossil described is suggested to be a member of the Mycetophilidae (Nematocera: Sciaroidea), the second is provisionally placed in the Rhagionidae (Brachycera: Tabanoidea) and the third is possibly a member of this latter family or perhaps (but more unlikely) a representative of the Tabanidae.

6.2. DESCRIPTIONS AND DISCUSSIONS

6.2.1. SPECIMEN 1

Suborder: Nematocera

Infraorder: Bibionomorpha

Superfamily: Sciaroidea

Family: ?Mycetophilidae

Description

The insect, BP/2/22455 (Plate 10A & B; Fig. 47), has been preserved almost in its entirety on a block of greyish-red mudstone. The head (with antennae and most of the mouthparts), thorax and abdomen have been fossilised. The right compound eye is visible, although the facets are indistinct. Both wings are preserved, but venation is unclear as wings overlap. Both halteres are probably absent (a suggestion of one is arrowed in Fig. 47). All six legs are virtually complete, with the exception of the tarsal claws and one or two tarsal segments on two of them. Terminalia are indistinctly preserved. The insect measures 3.2mm in length, with a comparatively broad thorax (1.0mm). The wings, with their basal portions missing, are approximately equal in length to the abdomen (2.2mm).

HEAD. The head is small and is inserted well below the level of the upper margin of the thorax; it is hypognathous, (Plate 10B; Fig. 47), ovoid, and higher than long. The antennae are inserted at the middle of the head. The flagellum consists of approximately 15 articulated flagellomeres and it is as long as the head, thorax and first segment of the abdomen combined. The flagellomeres are narrow, longer than wide, and the flagellum tapers at the distal end. Hairs are abundant but short, approximately equal in length to three-quarters of the flagellomere's width. The scape is large and ovoid, and the pedicel is somewhat smaller but also oval in shape. Above the base of each of the antennae, just anterior to the compound eyes, is a long stout spine of unknown identity. The mouthparts are short, they are half the height of the head. The labellae are large and fleshy. Further details are not distinguishable. The compound eyes are moderately large and ovoid; some individual facets are discernible. Eyes do not meet at the top of the head, and are, in fact, widely separated. The top of the head is strongly arched; on the hump two ocelli are visible.

THORAX. The thorax is strongly arched; seemingly compressed and deep. The pronotum, prescutum and scutum are large, and the delimitations of other segments are not clear. The position of the coxae is indicated in Fig. 47. They are rather large, distinct, rounded structures. The legs are fairly long and slender. The femora are only slightly swollen, with those of the hind legs considerably longer than those of the other legs. The hind legs measure 3.4mm. Tibiae are long and slender, particularly those of the hind legs. Two apical spurs are present on the hind tibiae; one is present on each of the middle and fore tibiae. Tarsi are long and slender; each one a little shorter than the previous one. The legs have a well-developed chaetotaxy, illustrated in the insert of Fig. 47; all segments, particularly the femora and tibiae are densely and regularly covered with short setae (setae approximately a third of the width of the segment).

The wings are broad and long; they are rounded (blunt) distally and they are not hairy. Venation appears to be reduced or is indistinguishable due to poor preservation.

However, as details of other parts of the body are so distinct, the latter option seems unlikely. It appears as though the anterior (and some proximal) veins are thickened and the posterior veins are weakly developed. The costa of the right wing is the only identifiable vein. It is darkly pigmented and ends at the apex of the wing.

ABDOMEN. The abdomen is elongated and stout and consists of approximately eight segments. It tapers slightly from the fifth segment onwards, but ends bluntly. At the third segment the abdomen is the broadest. Genitalia are not distinguishable.

Discussion

Identification

The presence of two, many-segmented antennae and the rounded posterior of the wings indicates that this specimen is a Nematoceran. Of the Nematoceran families, this specimen is most closely similar to the family Mycetophilidae. Characteristics that affiliate the specimen with this family are summarised below. The specimen is slender, long-legged, and has elongated coxae; the widely separated, large and oval eyes do not meet above the antennae; ocelli are present at the top of the head; the antennae are long and slender (only characteristic of some members); the mouthparts are fairly short; wings are bare, long and broad and venation is reduced (a characteristic of only some members of the family), except for the costal vein, which is darkly pigmented and ends at the apex (tip) of the wing; tibial spurs are present. A diagnostic feature of the family that could not be verified in the fossil is the simple, two branched radial sector. An exception, however, is that the antennae of this specimen are situated lower on the head with respect to the compound eyes than is the case in extant Mycetophilidae.

Basing the identification mainly on these gross morphological features, I have come to the following additional conclusions. Although members of the family Sciaridae resemble the fossil closely as well, the eyes in this case form a bridge dorsally. Other morphologically similar families are also ruled out for a number of other reasons: the Axymyidae, Simuliidae, Scatopsidae and Bibionidae have antennae which are very much shorter; the eyes of the Thaumaleidae and Synneuridae are of a different shape and are holoptic; the Cecidomyiidae and Dixidae lack tibial spurs; the Culicidae have mouthparts which are very much more elongated; and the family Anisopodidae also resembles this specimen in many ways but here, the wing venation is distinct and the wing is covered with microtrichia.

Biology of the Mycetophilidae

The common name describing a member of the Mycetophilidae is fungus gnat. This is because the larvae generally feed on the fruiting bodies, spores or hyphae of fleshy or woody fungi but sometimes however, they may be predacious (Barraclough & Londt, 1985). The immatures are mostly terrestrial, (Colless & McAlpine, 1970). Mycetophilid adults have been observed feeding on flower nectar and honeydew on leaves (Vockeroth, 1981) and therefore may be important pollinators.

Certain family groupings can be discerned, for example, Mycetophilidae-Sciaridae-Cecidomyiidae, but a satisfactory scheme of superfamilies is still disputed. Although McAlpine, et al. (1981) distinguish the superfamily as the Sciaroidea, other authors [e.g. Crosskey, et al. (1980)] consider the group as belonging to the (superfamily) Mycetophiloidea.

The family Mycetophilidae is large, consisting of over 3 000 species (Vockeroth, 1981), but, despite this, it is generally poorly known, and has been of little interest until recently. Their neglect has possibly been a result of their small size and unimportance socially and economically (Matile, 1980). Forty-eight genera and 268 species have been recorded in the Afrotropical Region, and, in South Africa, 15 genera and 27 species are known to date. As yet, no comprehensive taxonomic account has been published on the family as a whole. Of the families noted as being similar to the fossil, the Mycetophilidae is the largest (general abundance and species numbers). This, and the fact that the oldest insect bearing sediments often bear Mycetophilidae (as well as Tipulidae) (e.g. Vockeroth, 1981; Jarzembowski, 1984; Jell & Duncan, 1986), make it more probable that the specimen belongs to this family. I suggest that the Mycetophilidae arose early (Jurassic), and survived and evolved successfully as a result of a life cycle which is independent of water. Other families noted as being similar to the fossil, are known from much fewer representatives, e.g. the Sciaridae are only known from about 150 species (Steffan, 1981) and approximately 100 Anisopodidae species are recognised to date (Peterson, 1981).

Distribution

Mycetophilidae members are known from all over the world, in both tropical and temperate regions (Colless & McAlpine, 1970), on all continents, with the exception of the Antarctica. They are abundant in humid areas, especially moist woodland, near stream banks (Vockeroth, 1981).

Fossil record

Various fossils from periods of the Upper Triassic onwards were referred to extinct genera and families of the Sciaroidea (=Fungivoroidea) by Rohdendorf (1974); these were recently revised by Kovalev (1987). Kovalev placed some of these, and other Mesozoic Mycetophiloid Diptera from Jurassic and Lower Cretaceous sediments in the extinct family Pleciofungivoridae, a family considered as ancestor of most modern Mycetophiloid groups. The oldest fossils which are definitely members of the Mycetophilidae are two undescribed species of Sciophilinae from the Cretaceous, one from the Lower Cretaceous clayey Wealden Beds (144-119Myr) of southern England (Jarzembowski, 1984), the other from Upper Cretaceous Canadian amber (Vockeroth, 1981), and one described species of the same subfamily from the Lower

Cretaceous Koonwarra fossil Bed, Victoria (Jell & Duncan, 1986). The fossil from Orapa, if a true member of the Mycetophilidae, is thus among the oldest representatives of the family, but is by no means the oldest. Early Cretaceous extinct forms must, therefore, have given rise to and co-existed temporally with recent families for a considerable length of time. Early Tertiary deposits (e.g. the Redbank Plains Series - see Riek, 1954) and particularly ambers (250 species recorded) are rich in Mycetophilidae; most subfamilies and some recent genera have been reported (Vockeroth, 1981). Spahr (1985) lists others from other ambers derived from Bitterfeld, Burma, China, Columbia, the Dominican Republic, Libanon, Mexico, Sachalin, Siberia, and Sicily.

6.2.2. SPECIMEN 2

Suborder: Brachycera
Infraorder: Tabanomorpha
Superfamily: Tabanoidea
Family: ?Rhagionidae

Description

The fossil wing, BP/2/25896 (Plate 10C; Fig. 48), preserved on red mudstone, is moderately large and broad, somewhat elongated, and measures 3.1mm by 1.3mm at the widest point. Venational elements Sc, R_1 and R_{2+3} are strongly developed, but the other veins less so. The anal lobe and the alula are strongly differentiated. The wing is hyaline and not pigmented. Whether the costal vein (C) continues around the entire wing margin is not clear, it appears as though it does, but it is more weakly developed on the posterior side. Sc_1 ends in the costa, about half way along wing length, distal to the origin of Rs. R is straight and weakly developed just proximal to the cross-vein h. A faint outline of what is possibly the dm cell is distinguishable, it is positioned more or less at the centre of the wing. M is two or three-branched. Rs arises well before the base of cell dm, it is very short, its fork only just beyond crossvein h. It branches into R_1 and $R_{2+3+4+5}$. Cell r_1 is open. R has four branches reaching wing margin, R_1, R_{2+3}, R_4 and R_5. Cross-vein r-m is situated well beyond the fork of Rs, possibly half way along dm. CuA_1, CuA_2 and possibly A_1 reach wing margin. A_2 is absent.

Discussion

Identification

The wing venation is very similar to that of the families Rhagionidae and Anisopodidae. The one very obvious difference between the fossil wing and an anisopodid wing, is that in the Anisopodidae R_{4+5} is not split into R_4 and R_5; and the wing is mostly pigmented. As this is not so in the fossil, I tentatively assign this specimen to the family Rhagionidae. In the Rhagionidae, however, the position of the cross-vein r-m is said to be well before, rarely at the middle, of cell dm; in the fossil wing it occurs at the middle of cell dm. The fossil wing, illustrated in Fig. 48, is not very different from that of the living genus Symphoromyia.

Most of the southern African species were keyed out by Stuckenberg (see references in Stuckenberg, 1980), but with so few details available in this fossil, his keys cannot be used.

Biology of the Rhagionidae

The Rhagionidae, commonly known as the snipe flies, comprise the two subfamilies Rhagioninae and Vermileoninae (Stuckenberg, 1980). Larvae of the Vermileoninae are terrestrial predators and those of the Rhagioninae are probably also all terrestrial. Larvae are found in damp soil, rich in decaying organic matter (James & Turner, 1981). Most adult Rhagionidae are associated with flowers, and, in the Afrotropical Region no adults of any genera are predators. However, adult females of Symphoromyia, a genus found abundantly in the Nearctic Region, suck blood of warm-blooded vertebrates. In some species, where the female is haematophagous, hosts may be amphibians and birds as well as mammals (James & Turner, 1981). I suggest that the fossil probably represents an early pollinator, rather than a predator of early Cretaceous vertebrates, amphibians or reptiles. It is notable that no mammals have been found in the Orapa sediments. It is unfortunate that the mouthparts were not available for study as, in the extant specimens, they are very characteristic of vertebrate feeding flies: i.e. small, evenly-set mandibular teeth and a blade-like maxillary organ armed apically with retrose teeth (Downes, 1978).

Some distinguishing features of the Rhagionidae are: the presence of three pulvilli; a non-annulated flagellum; an antenna never consisting of more than three segments of which the third segment is rounded and bears a long terminal style; calypters that are small or vestigial; a costa which continues around wing margin and an open r_1 cell. However, these features are of no consequence with regards this fossil wing.

Distribution

There are approximately 180 species of Rhagionidae (James & Turner, 1981). In the Afrotropical Region there are four genera with 56 species and, in South Africa, the same four genera are present and they comprise 21 species. Genera in the Afrotropical Region are found mainly in tropical-subtropical environments and in the humid montane parts of this country.

Fossil record

The oldest fossil Rhagionidae date back to the Upper Jurassic, from which three genera are known (Rohdendorf, 1974). Then, follow the Cretaceous representatives, such as the snipe fly from the Early Cretaceous Wealden Beds (Jarzembowski, 1984) which closely resembles that of the recent genus Ptiolina (not found in the Afrotropical Region) and a Rhagionid from the Koonwarra fossil Bed of the same age (Jell & Duncan, 1986) belonging to the genus Atherimorpha. In the Afrotropical Region this genus is represented by two species from South Africa, and two from

Lesotho. The family, and especially Symphoromyia species is evidently well represented in the Oligocene deposits of Baltic amber (Stuckenberg, 1974), and Spahr (1985) notes their presence in ambers from Siberia and the South-West USSR. Melander (1949) reported on some Miocene Rhagionids from the florissant shales in Colorado.

6.2.3. SPECIMEN 3

Suborder: Brachycera

Infraorder: Tabanomorpha

Superfamily: Tabanoidea

Family: ?Rhagionidae/ ?Tabanidae

Description

A medium sized dipteran, BP/2/18217 (Plate 10D; Fig. 49), approximately 9mm long, preserved as a brown deposition of organic matter on cream coloured (buff) sedimentary mudstone. The body is not conspicuously hairy. The specimen is lying ventral side down, and, therefore, only dorsal features can be identified. Although this specimen is fairly well preserved, the lack of wings prevents accurate identification. The specimen is a mature adult.

HEAD. The head is two-thirds of the width of the thorax. The ocelli appear to be absent. The glabrous eyes, which are broadly separated (therefore the specimen is possibly a female), have large facets antero-posteriorly. The antennae are seemingly missing although on the left hand side of the thorax there is a structure made up of three segments which I think may represent an antenna. This may indicate that the antennae are short; the scape and pedicel are rounded, bulbous structures with a short compressed flagellum attached (number of flagellomeres unknown). The mouthparts are not visible. The anterior region between the compound eyes protrudes forward conspicuously.

THORAX. The thorax is robust. The setae on the scutum and scutellum are not discernible. The legs are stout, particularly the femur and tibia, but they are unmodified. No tibial spurs are present, but this is not surprising as only one leg remains. Pectinate claws are preserved (see ?middle left leg in Fig. [illegible] - arrowed); the two claws appear to be equal in length. The wings are missing but one haltere is visible which is labelled in Fig. 49. The knob is large and rounded and the stalk possibly thin; it does not appear to bear setae.

ABDOMEN. The abdomen is a swollen oval and stout structure, tapering only slightly to a blunt end posteriorly; it appears to be relatively bare of setae. The abdomen comprises approximately seven pregenital segments, all of which are approximately of equal width (4.7mm) except for the first and last segments. Segment eight is somewhat modified into rounded and blunt genital structures; their shape indicates that the specimen is probably a male.

Discussion

Preservation

This fossil is the only fossil from cream-coloured matrix; it is also the only fossil which displays some relief, and is not an entirely two-dimensional compression. Its preservation, which is relatively good, is unusual in that most fossils from this buff-coloured matrix are poorly preserved, having been altered during *diagenesis* by groundwaters. The other dipteran fossils, preserved mainly in the grey matrix, are the most distinct with the finest details retained as a result of preservation presumably in deep water, without oxygen. The reddish matrix, which represents shallow water deposition, is partly oxidised, but fortunately the fossils present in these sediments are also fairly well-preserved.

Identification

The specimen is very similar to recent families of the infraorder Tabanomorpha, superfamily Tabanoidea, especially the families Tabanidae and Rhagionidae. These families are the larger ones in the extant Tabanoidea fauna. The length of the individual, its general morphology, size and number of visible abdominal segments are in agreement with its placement in this infraorder. There are no signs of extreme hairiness, thereby ruling out other brachycerous families of this form, for example the Bombyliidae.

Biology of the Tabanidae

A large world-wide family with over 3 000 known species, containing the familiar horse-flies, clegs and deer-flies (Chainey & Oldroyd, 1980). In the Afrotropical Region these authors reported some 700 species. Adult Tabanidae feed on nectar and pollen, but females may suck the blood of mammals and reptiles and are annoying transmitters of a variety of diseases. The majority of tabanid larvae live in wet places, such as wet mud, and the margins of ponds, lakes or streams. They may be predacious or feed on vegetable debris (Chainey & Oldroyd, 1980). Different species show a seasonality of abundance (Glasgow, 1946) and flight times (Goodier, 1966), and, some may be nocturnal (Chainey & Oldroyd, 1980).

Fossils of the family are rare, and only one species has been described from Baltic amber (Stuckenberg, 1975) of the genus Haematopota, and three species representing modern genera have been described from the Miocene deposits of Colorado (Pechuman & Teskey, 1981). This would support its affiliation with the family Rhagionidae rather than Tabanidae.

The specimen also supports predictions of a humid, well-vegetated, and possibly seasonal, Cretaceous Orapa as well as the theory that the Diptera represent major pollinators of the early angiosperms. Variance in flight times of species may also influence specific mate recognition.

CHAPTER SEVEN

UNIDENTIFIED DIPTERANS

7.1. INTRODUCTION

Although the majority of specimens described in the previous chapters are well enough preserved for classification to at least family level (even if sometimes tentative), many of the Orapa dipterans are either in a poor state of preservation, or features essential for classification are absent. In this chapter, I describe and discuss briefly ten such specimens, and their inclusion is essential to illustrate the abundance and variety of the dipteran fauna. For two of the fossils, an attempt has been made to narrow their identity down to at least a few families; however, I have based these identifications on superficial evidence.

7.2. DESCRIPTIONS AND DISCUSSIONS

7.2.1. SPECIMEN 1

This specimen, a fairly small and slender fly, BP/2/26238 (Plate 11A; Fig. 50), measuring 2.9mm in length, is preserved as a lateral compression (left side upwards) in red mudstone. Although the head (with antennae), thorax (with wings and legs) and abdomen are present, preservational quality on the whole is poor.

HEAD. The head is small, subrounded to oblong, and is inserted on the anterior end of the arched thorax. The eyes are not discernible. The tennae emerge just above the middle of the head and are the same length as the head (0.29mm). Individual segments are not visible, except for the scape or pedicel which is large and triangular (Fig. 50). The flagellum is short and pointed, consisting either of a few flagellomeres (and in this case the antennae are of the styllate type) or of many compressed segments. The mouthparts project downwards from the ventral side of the head, indicating the insect is hypognathous; individual components are not discernible.

THORAX. The thorax is arched and approximately as long as high (0.77mm). The scutum is large and rounded, and the narrower pronotum is also distinct.

Legs: all six legs are preserved but most are incomplete and/or indistinct. The legs are long and slender, all segments are elongated and narrow except for the coxae, which, although elongated, are stout, and, the femora which are slightly broader at their distal ends. Overall leg length is longer than the head, thorax and abdomen combined; the longest leg (?hind left) measures 3.1mm. A structure at the distal end of one of the tibiae (Fig. 50) possibly represents a tibial spur.

Wings: both right and left wings are preserved. They are approximately as long as the thorax and abdomen combined and extend beyond the abdomen; they are broad and hyaline. They measure 2.2mm x 1mm and 2.2mm x 0.74mm respectively. The only veins present are faint and are positioned near the anterior and proximal sides of the wing;

this either reflects the poor state of preservation of the specimen or it is a true representation of its reduced venation. Tentative identification of veins in the right wing indicates the presence of C, R_1, R_{2+3}, R_{4+5} and CuA.

ABDOMEN. The abdomen is inserted below the midline of the thorax and arches gently upwards, particularly at its distal end (i.e. the last four segments). It is long (1.84mm) and slender and equal in width throughout. It comprises approximately nine to ten segments. Tergites, sternites and intersegmental membranes are easy to distinguish. Tergites decrease progressively in width distally, whereas the sternites increase in width, suggesting a distal rotation of the abdomen towards the right. The first and second abdominal segments are the longest. The terminalia are not discernible although an unidentified structure (spine-like) is present at the tip of the abdomen.

Discussion

Although it is not possible to assign this dipteran to a particular family with confidence, its overall appearance and gross morphology is similar to that of the following families: Blephariceridae, Pachyneuridae, Mycetophilidae, Trichoceridae, Anisopodidae, Culicidae, and the Vermileonidae. However, each of these have certain features which differ with those displayed by the fossil. Of the above, only the Mycetophilidae and Trichoceridae have naturally upward curving abdomens. The antennae of all the above families, except some members of the Mycetophilidae (which have 'compressed' antennae) and Vermileonidae (which have styliate antennae) are long. The wings of Pachyneuridae, Trichoceridae, and Vermileonidae are considerably narrower than those of the fossil. These few characteristics rule out all but one family, the Mycetophilidae.

Factors supporting the specimen's affinity with the Mycetophilidae are listed below.

(a) Mycetophilidae, often display reduced venation of their wings, where only C, R_1, R_{4+5}, CuA_2, and sometimes R_{2+3}, are strongly developed, with the other veins reduced or missing.

(b) Antennae of this family are variable in length and in number of flagellomeres thereby easily accommodating this fossil specimen.

(c) General body shape of the specimen is similar to some genera of this group (small head and narrow abdomen with respect to thorax; large scutum; large wings in comparison to body; upward curving abdomen; long narrow legs; elongated coxae and slightly thickened distal ends of femora).

(d) The Mycetophilidae have tibial spurs.

(e) The family as a whole is large and common in many parts of the world, and is abundantly represented by fossils (Chapter 6).

A general discussion on the biology and behaviour of this group is found in Chapter 6.

7.2.2. SPECIMEN 2

This specimen is a comparatively stout fly, BP/2/fragment (Plate 11B; Fig. 51), preserved on a reddish-grey fragment of mudstone as a lateral compression (left side upwards). Its total length is [illegible] known as its basal portion is missing, but, up to the third and a half abdominal segment, it measures 3.1mm. The head, thorax and abdomen are poorly preserved and the legs, wings and other appendages are incomplete, distorted and shifted in their relative positions.

HEAD. The head is robust (0.52mm in length) with respect to the size of the thorax. A structure possibly representing the compound eye, is illustrated in Fig. 51; if this is indeed the compound eye, it is large and dichoptic. The anterior-dorsal portion of the head is raised and probably represents the ocellar triangle comprising the ocelli. Appendages at the front of the head are only partly preserved and they may represent the antennae. Possible palps have also been identified and are indicated on Fig. 51; the other segments lying together with the palps, are portions of the specimen's legs.

THORAX. The thorax is about as long as it is high (1.24mm). Although the pronotum and scutum are extremely robust and distinct, no other segments are discernible.

Legs: five incomplete legs and one complete leg are preserved. They are short and narrow in comparison with the body as a whole, the longest or the most complete leg (left ?middle) measuring 2.46mm. None of the segments is noticeably swollen, all are relatively narrow, even the coxae. Tarsomeres of all the legs are small with narrow proximal ends and somewhat enlarged distal ends. A pulvillus of the left (?middle) leg is distinguishable.

Wings: only a portion of one wing is preserved, it is 1.4mm long. It is believed to be the right wing as there is no trace of the proximal region which probably lies under the thorax. Only C and R_1 (and ?Rs) remain, and, there is no trace of pigmentation.

The left halter comprising a small knob with a broad stout stem, measuring 0.67mm, is present (Fig. 51).

ABDOMEN. The abdomen is stout, nearly as broad as the thorax, with individual segments short and broad. The three and a half segments present measure 1.33mm, and, considering that there should be at least about five more which probably decrease progressively in length, the total abdominal length is estimated to be about 3.5mm and total body length about 5.3mm.

7.2.3. SPECIMEN 3

Most of this fairly stout specimen, BP/2/25974 (Plate 11C; Fig. 52), is clearly preserved as a lateral compression (left side upwards), on a block of red mudstone. Unfortunately, the absence of wings and antennae renders its classification to family level impossible, and I can therefore only describe its general morphology. The specimen measures 5.4mm in length.

HEAD. The head is large and rounded [0.64mm (length) x 0.91mm (width)], with dichoptic compound eyes and probably with the ocellar tubercle and ocelli present. The labellum is preserved but not clear; the palps are long (as long as the head) and narrow. The mouthparts are more or less ventrally situated and the specimen is therefore hypognathous.

THORAX. The breadth of the thorax is approximately two-thirds of its length which is 1.5mm. Segments which are discernible are the pronotum, prescutum, scutum, scutellum, a possibly the metatergite; these are illustrated in Fig. 52.

Legs: six legs are preserved, in various states. The most complete leg indicates that the legs are relatively long (approximately equal in length to the thorax and abdomen combined). The longest (the ?hind leg) and the middle leg measure 4.24mm and 3.88mm respectively. They are fairly stout, with the base of the femur and tibia slightly thickened. The tarsomeres are narrow, elongated structures and, what appear to be empodia, are found at the distal ends of two of the legs.

Wings: only the anterior portion of the right wing is preserved. The wing is short (three-quarters of the length of the abdomen) and probably oval in shape (it does not protrude beyond the ventral side of the abdomen); it measures 2.55mm and comprises the veins C, Sc_1, Rs, and R_1. The remaining portion of the wing lies below the body. No trace of pigment is detectable. A section of the left halter is present, and it has a large knob but no stem.

ABDOMEN. The abdomen is stout, elongated (3.27mm in length), straight and comprises nine to ten segments. All segments (except the first and the last) are more or less equal in length. The first five segments are approximately the same width; there is thus no narrowing at the proximal end of the abdomen. The hypopygium is discernible but its individual components are not. Intersegmental areas are clear, but the boundary between the tergites and sternites is not.

7.2.4. SPECIMEN 4

This comparatively slender fossil specimen, BP/2/26852 (Plate 12A; Figs 53 & 54A-D), is preserved as a lateral compression (right side upwards) on red mudstone. It is small, measuring 2.2mm, and comprises the head (without identifiable appendages), thorax (with a few remnants of legs and wings) and the complete abdomen.

HEAD. The head is rounded and large (0.5mm) with respect to the remaining portion of the body. In Fig. 53, a question mark indicates what may represent the mouthparts, and if so, the insect is hypognathous. On the dorsal portion of the head a rounded projection is apparent and I think this represents the ocellar tubercle. No compound eyes or other features are distinguishable. Below the head, the many segmented appendages, are the legs.

THORAX. The stout thorax, probably much broader than in the living form as a great deal of distortion is apparent, measures 0.6mm by 0.9mm. The pronotum, prescutum, scutum and scutellum are distinct. The scutum in particular is well-developed and stout.

Legs: long and slender in comparison to the rest of the body. There is no apparent swelling of any of the segments. Tarsomeres are small and sub- rectangular. The tibia and femur of the ?right hind leg are long and slender; this is the longest of the legs, measuring 1.75mm.

Wings: the wings are large with respect to the specimen's overall size, ending far beyond the abdomen. The basal portion of the right wing and the near-distal portion of the left wing are preserved. I have made an attempt at a composite illustration of these two parts and this is shown in Figs 54A-D; together they measure approximately 1.5mm.

(a) Fig. 54A. The right and left wing portions are joined directly to one another.

(b) Fig. 54B. Right and left wing portions are joined directly, with a few possible additional veins included near their junction. The suggested outline of the wing is also added here, giving the wing a rather broad appearance.

(c) Fig. 54C. Right and left wings are joined with a region of overlap, this makes the wing short, broad and rounded. If the area of overlap is increased even more, it is possible that only two longitudinal veins reach the anterior costal margin, instead of the suggested three.

(d) Fig. 54D. Right and left wing sections are not joined; a missing section between the two may be present implying a longer narrower wing.

In the four illustrations, the fifth longitudinal vein ($?M_{1+2}$) is indistinct distally and its possible ending is variously shown in these figures.

The wing is hyaline and its base is narrow. I suggest Fig. 54C is the most similar to the original wing. Veins C, Sc, R_1, R_{2+3}, $?M_{1+2}$ and CuA are preserved. C, Sc and R_1 are somewhat thickened relative to the other veins.

The right halter is well preserved; it is large and distinctive and comprises a long narrow stem with an elongated, large knob; together they measure 0.3mm. Compression has resulted in the halter splitting in half.

ABDOMEN. The abdomen comprises approximately ten segments and is fairly short (1.1mm) and of the same length as the thorax and head combined. It is narrow basally, where it unites with the thorax; the third segment is the broadest and all the segments thereafter narrow progressively to a rounded, blunt end. Details of the hypopygium are not discernible.

Discussion

From an analysis of the composite illustration of the wings, I suggest that the specimen may belong to the family Anisopodidae (Nematocera). The wing venation resembles that of this group the most closely and this family is therefore discussed in more detail. Similarities also exist between the wing of this specimen and that of members of the Pipunculidae (Brachycera) and Gasterophilidae (Muscoids). However, representatives of the former family have very large heads (composed mostly of eye) - a characteristic not shared with the fossil, and the latter family is believed to have arisen later in the evolution of the Diptera, and representatives are not known from the Cretaceous.

The family Anisopodidae consists of almost 100 species in six genera, of which 18 species in four genera are known from the Afrotropical Region (Hutson, 1980b). Adult flies may be found at flowers or windows and males sometimes perform aerial dances in swarms (Hutson, 1980b) to attract females (Peterson, 1981). Adults are found near larval habitats, i.e. in damp places on decaying or fermenting organic matter, such as in water filled tree-holes, moist rotten wood, bleeding tree-trunks and under bark (Hutson, 1980b; Peterson, 1981). Females oviposit on moist surfaces.

Fossil specimens identified as members of the Anisopodidae are few (Peterson, 1981). McAlpine and Martin (1969) mention one species from Cretaceous Canadian amber. Edwards (1928 <u>in</u> Peterson, 1981) reports on 11 species in three extant genera, three from the Eocene/Oligocene formations of Colorado and Wyoming. Spahr (1985) lists an additional seven species from various ambers including those from Canada, China, Mexico, Sicily and South-West USSR.

A study of extinct and extant species, shows that the wing of the Cretaceous specimen from Orapa resembles the extinct form _Protolbiogaster_ _rhaetica_ (Fig. 55) in many ways, and a list of similarities is given below. _P._ _rhaetica_ Rohdendorf (family Protolbiogastridae) from the Upper Triassic of Central Asia is said to possibly be the nearest fossil relative to the Anisopodidae (Rohdendorf, 1974). Figure 55 illustrates Rohdendorf's original drawing.

(a) The costal field is wide with convexity directly beyond its point of initiation.

(b) Sc is weakly bent anteriorly without branches and transversa veins.

(c) Sc is parallel with R_1 for nearly its entire length.

(d) Rs emerges from R in the first quarter of the wing.

(e) Sc, R_1, R_{2+3} enter the costal vein (C) close together, near the middle of the anterior edge of the wing.

(f) The main trunk of M branches out from CuA in a somewhat thickened form, which thins out distally.

(g) Both M and CuA are almost straight over their entire lengths.

(h) In _P._ _rhaetica_, A is thin and short; this may be a characteristic in common with the Orapa fossil if this vein has been correctly identified in the latter specimen.

Differences observed between the wings of the two fossils are also prevalent and render positive identification impossible, these differences are listed below.

Protolbiogaster	Orapa 'Anisopodid'
(a) Sc and R almost straight.	(a) Sc and R curve anteriorly for most of their length and they are parallel.
(b) The basal part of R is thickened. The common trunk of R distal to the phragma is thick with a short posterior branch terminating freely in the membrane.	(b) R is not noticeably thickened at its base and no posterior branch is present
(c) R_{2+3} originates just proximalto the middle of the wing.	(c) R_{2+3} originates in the first quarter of the wing.
(d) R_{2+3} runs parallel to R_1 especially distally.	(d) R_{2+3} runs parallel to R_1 proximally.

7.2.5. SPECIMEN 5

A poorly preserved specimen with the exception of the wings, BP/2/25248 (Plate 12B; Figs 56 & 57a-c), compressed dorsi-ventrally on a red coarse matrix. The total body length (excluding the palps) is 4.3mm.

HEAD. Possible palps and a compound eye are indicated in Fig. 56; they are distorted and further details are not discernible.

THORAX. The thorax is large, rounded and has rotated over onto its left side. The scutum is discernable on the left size, and it appears to be fairly small; the other segments cannot be identified with certainty.

Legs: the legs are badly preserved and only small portions of three of them remain (Fig. 56); they are believed to be the right hind (RHL), middle (RML) and front legs (RFL). They appear to be rather stout and of medium length (2.8mm). The femur of the ?right middle leg is a little broader distally.

Wings: the left (3.0mm) and right wings (3.9mm) of the specimen are incompletely preserved, as well as an additional wing belonging to another insect near the head of specimen 5 (possibly a dipteran, but lack of detail prevents further identification). Considering only the wings of the fossil concerned: of the left wing the posterior-basal portion is missing, and of the right wing, the posterior-basal and distal sections are missing, and only the anterior portion remains. I have superimposed the left (Fig. 57a) and right wings (Fig. 57b), and the composite is illustrated in Fig. 57c. Venation: the costa is thickened at least up to R_4, and, possibly up to R_5 (it appears to continue a little beyond R_4 in the left wing). Sc and R_1 leave their common base simultaneously and lie parallel to one another for most of their length. Both veins enter the costa close together, in the middle of the anterior edge of the wing. Rs originates in the first quarter of the wing and branches into R_{2+3} and R_{4+5} in the middle of the second quarter. R_{4+5} subsequently branches into R_4 and R_5 in the last quarter of the wing. R_{2+3} and R_{4+5} are long, nearly parallel to one another, diverging only slightly at their distal ends; they enter the costa at the most anterior-distal portion of the blade. Crossveins r-m and m-cu are situated more or less in the middle of the wing resulting in long longitudinal veins. Cells br, bm and cup are long and narrow. The possible presence and shape of cell dm is illustrated in Figs 57a & c, as are the veins M_1, M_2 and ?M_3. CuA_1 is straight until just beyond m-cu whereafter it curves sharply posteriorly, meeting the posterior wing edge close to CuA_2. A possible trace of A_1 is also illustrated.

Both halteres are preserved but only the right one is distinct. It has a very narrow stalk and the knob is large, pear-shaped and split lenghtwise due to compression.

ABDOMEN: A featureless crumpled and distorted structure with no discernible features.

7.2.6. SPECIMEN 6

A poorly preserved specimen, BP/2/25911 (Plate 12C; Fig. 58), of which half the abdomen is missing and the wings are crumpled. It is preserved as a lateral compression (right side upwards) on grey mudstone. It is small measuring 1.5mm in length (from the head to the fifth abdominal segment). It is a slender specimen with long thin legs and narrow elongated wings.

HEAD. The head is small (0.2mm), approximately a third of the size of the thorax from which it projects directly forwards; the specimen is probably hypognathous (an extension on the ventral side of the head, mostly hidden by the right front leg, is present and possibly represents the mouthparts). The compound eye is large and appears to meet its counterpart at the midline of the top of the head, i.e. the specimen may be holoptic. The ocellar tubercle is discernible on the dorsal side of the head. The antennae are directed forwards (inserted anteriorly on the head) and are composed of approximately eight segments, a brachycerous condition, they are approximately 0.38mm long.

THORAX. The thorax is long and narrow (0.5mm x 0.26mm).
Legs: portions of four legs are preserved [the right hind (RHL), middle (RML) and fore legs (RFL) and the left fore leg (LFL)]. The RHL is the most complete, it is 2.42mm long. The legs are long and thin with long, slender femora, tibiae and tarsal segments. None appears thickened and no tibial spurs are present.
Wings: the right wing is complete but it is crumpled and no veins except the costa are preserved; it is 1.6mm long. Only the basal portion of the left wing remains. In the left wing, three longitudinal veins are present which may represent the costal (C), subcostal (Sc) and radial (R) veins. Part of the right halter is preserved (0.2mm); the knob is large and rounded in appearance and the stem appears to be very thin and long.

ABDOMEN. Five abdominal segments are preserved, and up to the fifth segment, the abdomen measures 0.8mm. I estimate the total abdominal length to be a maximum of 1.5mm, with the total insect length about 2.2mm. The abdominal segments are stout with broad intersegmental regions. The third segment is probably the broadest.

Discussion

If the antennae are correctly interpreted, then the dipteran belongs to the brachycerous group whose antennae are usually composed of approximately eight segments. Further identification is impossible.

7.2.7. SPECIMEN 7

A small slender fly, BP/2/25859 (Plate 12D; Fig. 59), measuring 2.3mm in length and preserved as a lateral compression (left side upwards) on a block of grey mudstone. This dipteran is very poorly preserved and is not assignable to any specific superfamily or lower taxon.

HEAD. The head is small (0.3mm long), distorted, and projecting forwards from the thorax. The scape, (?left or right), if correctly interpreted, is the only part of the antennae which is well preserved. This antennal segment is large and rounded. A faint impression of what may have been palps is discernable (Fig. 59); they are long, thin and project antero-ventrally.

THORAX. The thorax is stout and rounded (0.8mm) with a distinct pronotum, scutum and scutellum. Other segments which I have identified but which are not as distinct are the anepisternum, anepimeron, anatergite, katatergite, kepisternum, metatergite, ?metanotum, meron and kepimeron (Fig. 59).

Legs: portions of all six legs are preserved and are scattered randomly around the fossil. The legs are long and slender, probably as long as or longer than the body, the longest (?left hind leg) measuring 2.76mm. The coxae are elongated and narrow, the femora are somewhat stout, in particular those of the hind legs, and the tibiae are very long and slender and slightly thickened distally; a single tibial spur can be observed on two of the tibiae. The tarsomeres are small, elongated and rectangular with an empodium preserved on one of them (?LHL); no details of the empodium are discernible.

Wings: portions of the right and left wings are preserved, but the former is more distinct. The wing is short (approximately 1.51 mm) and broad, probably not exceeding the length of the abdomen. Some veins are discernible which I have interpreted as C, Sc, R, Rs and possibly R_{2+3}, R_{4+5} and CuA (Fig. 59). The costal, subcostal and radial veins are parallel along most of their length (left wing). R branches into ?R_1 and Rs in the first quarter of the wing, Rs branches at least once, in the second quarter (into ?R_{2+3} and R_{4+5}), and ?CuA originates in the first quarter.

ABDOMEN. The abdomen is long and slender with only six segments preserved. The third segment is the longest and broadest, with the segments to follow decreasing progressively in size. The junction between the thorax and abdomen is narrow, as in some Mycetophilidae.

7.2.8. SPECIMEN 8

The fossil specimen, BP/2/22455 (Plate 13A & B; Figs 60 & 61), is a fairly stout dipteran preserved as a lateral compression (right side upwards) on reddish-grey mudstone. It is of medium length, 4.6mm long, and comprises the head (with an incomplete antenna), thorax (with portions of all six legs and both wings), and the abdomen.

HEAD. The head is ovoid without discernible features. It is 0.6mm in length and is partially obscured by the front legs. A small portion of one antenna remains, comprising two flagellomeres which are narrow and elongated (twice as long as broad) (Plate 13B).

THORAX. The thorax is small (1.3mm) in comparison to the head, and, particularly the abdomen. The positions of the pronotum, prescutum, scutum and scutellum are indicated in Fig. 60, as is the possible metanotal segment. Individual segments are not noticeably enlarged.

Legs: portions of all six legs remain, of which the right middle leg is the most complete; it measures approximately 2.8mm. This leg is, however, probably not the longest as, for example, the femur of the right hind leg (Fig. 60) is stouter and longer than that of the right middle leg, as, no doubt, is the overall leg length as well. The legs (particularly the femora) are fairly short and stout with respect to the rest of the body.

Wings: the right wing is the most complete (Figs 60 & 61). It is long, exceeding the length of the abdomen, and is at least 2.9mm in length, but probably as much as 3.7mm if the non-preserved section covering the thorax is added. The wing is relatively broad (approximately 1.2mm) but I could not obtain the exact measurement as the posterior margin is not discernible. I have attempted to identify some of the veins of the right wing (Fig. 61), since in the left wing, only the proximal portions of the three anterior veins remain, i.e. C, Sc and R. The longitudinal veins: C, R (and parts of $?R_1$ and $?R_{4+5}$) and M are well developed. All other veins are slightly narrower, more reduced or less well-preserved. The costa, C, is thickened up to $?R_{4+5}$, and only slightly less so up until it disappears from view (where the wing overlies the abdomen). Sc is weakly preserved but its presence is discernible to just beyond mid-wing length. $?R_1$ may reach the wing margin in the costa at two-thirds of the wing's length along. $?R_{4+5}$ reaches the costa just prior to the wing apex. M splits into $?M_{1+2}$ and $?M_3$ (which reach the wing's edge just posterior to its apex) and CuA divides into CuA_1 and CuA_2. Only one anal branch (?A) is discernible.

ABDOMEN. The abdomen is large and stout and measures 2.7mm in length; it comprises approximately eight segments which broaden successively posteriorly, up to the fifth segment. The abdomen ends bluntly; no genitalia are discernible.

7.2.9. SPECIMEN 9

A stout, poorly preserved dipteran, BP/2/26872 (Plate 13C; Fig. 62), preserved as a lateral compression (left side upwards) on a block of red mudstone. The specimen is small, and is 2.1mm long.

HEAD. The head is stout and rounded and is 0.5mm in length. There is a faint impression of what probably represents the mouthparts at the antero-ventral side of the head (Fig. 62), details cannot be distinguished. No other features can be identified either. At the ventral side of the head, there are very faint impressions of portions of the legs.

THORAX. The thorax is robust and wider than long (0.6mm x 0.86mm). I have identified the pronotum, prescutum, scutum and scutelium; all are stout.

Legs: portions of all six legs are faintly preserved. They appear to be short, thin and frail in comparison to the body of the specimen. I estimate the longest to be approximately 1.16mm.

Wings: both the left and right wings are preserved, and they measure 1.78mm and and 1.46mm respectively. I cannot account for the discrepancy in size. At least seven veins reach the wing margin in the left wing, and six in the right wing, and these I interpret as SC, R_1, R_2, R_3, R_{4+5}, $M_?$, CuA, and possibly $A_?$. All are long, approximately a third of the total wing length. Crossveins are either few or not preserved. The costa continues to just before the apex of the wing, at vein R_{4+5}. Four veins (Sc, R_1, R_2, and R_3) enter the costa in the anterior margin. No halteres are preserved.

ABDOMEN. The abdomen is short and stubby (1.0mm long), with approximately eight compacted segments, which end bluntly. The genitalia are not distinguishable. The tergites appear to be completely separate from the sternites, and segmental divisions are relatively distinct between the tergites, but less so between the sternites.

7.2.10. SPECIMEN 10

A small, rather dainty specimen, BP/2/26238 (Plate 13D; Fig. 63), measuring 3mm in total, preserved on red mudstone as a lateral compression (right side upwards). Although the head (with portions of the antennae), thorax (with both wings and all six legs) and the abdomen remain, fine details (particularly wing venation), are not distinct.

HEAD. The head is tiny in comparison to the thorax and abdomen. It is broader than long (0.22mm x 0.38mm), and somewhat elliptical in shape, the dorsal side a bit more rounded than the distinctly pointed antero-ventral region, where the mouthparts are situated. Details of the latter are not discernible. A compound eye is observable, it does not reach as far as the top of the head, and the specimen is therefore dichoptic. The distal portions of both the left and right antennae are visible, they are much longer than the head, and approximately equal in length to the thorax (0.62mm). They are long and slender consisting of an unknown number of elongated flagellomeres; these are at least twice as lon as they are broad.

THORAX. The thorax is relatively small, subrounded and measures 0.65mm x 0.89mm. Only the scutum is distinct, and I cannot identify any other segments with confidence.

Legs: all six legs are long and slender, longer than the head, thorax and abdomen combined. The longest leg, one of the hind legs, measures 3.39mm in length. All individual segments are slender except for the slightly thickened femora of the fore, middle and hind legs, and the dist ends of the tibiae. The femora of the hind legs nearly twice as long as those of the front legs; the middle legs have femora of intermediate length. Delimitations between tarsal segments are not clear, nor are the extremities of the fore tibiae.

Wings: the wings are long and broad (2.32mm x 0.89mm for the ?right wing); they do not exceed the abdomen in length, but their rounded ends are exactly in line with the end of the abdomen. They are hyaline without trace of pigmentation. Venation: the costa, C, does not reach the apex of the wing, but disappears in the last quarter. Sc is long and straight, curving anteriorly only at its very distal end, terminating in the costa in the distal third of the blade; it is parallel to C throughout its length. The proximal portion of R is missing, but the distal part is also long and straight until just prior to its anterior curve into the costa. Three branches emerge from R, they are all parallel to one another, and head towards the postero-distal margin of the wing. Their identity is uncertain, and it is also not known whether they are complete. ?Cu is also parallel to these three branches and also disappears before reaching the margin. I do not know whether the venation is reduced or badly preserved.

ABDOMEN. The abdomen is long and slender, and measures 2.16mm. It comprises approximately ten segments; the delimitation between the first segment and the distal side of the thorax are difficult to distinguish. The third segment is the longest and broadest, whereafter the abdomen narrows progressively until the tenth segment which expands sligthly forming a rounded, blunt end. The genitalia, here, are not discernible.

7.3. DISCUSSION

I have been able to suggest families for two of the ten specimens. I have only been able to describe the other eight. What I am sure about is that the ten specimens are from a number of different families. They indicate that the dipteran fauna of Orapa was extremely varied. Further collections may produce well preserved specimens which, on the basis of comparative morphology, will permit some of these specimens to be placed in families with confidence.

CHAPTER EIGHT

FAMILY BIBIONIDAE

8.1. INTRODUCTION

In this chapter, four members of the Bibionidae are described. Of the entire dipteran fauna these were the only specimens previously studied (Rayner, 1987). I wish to redescribe the specimens for two reasons. Firstly, my study would be incomplete without them; indeed, having four representatives it is the second largest family present in the Orapa deposits (Fig. 68). Secondly, my descriptions and illustrations are more detailed than those in the previous investigation. I have also endeavoured to key out the specimens further than was done previously and, as a consequence, I have had to assign them to a new genus and species. All four specimens belong to the same species.

8.2. DIAGNOSIS AND DESCRIPTIONS

Infraorder: Bibionomorpha
Superfamily: Bibionoidea
Family: Bibionidae
Subfamily: ?Bibioninae
Genus: Cretobibionida gen. nov.

Type Species

Cretobibionida anticus gen. et sp. nov., with four representatives (Plate 14A,B,C & D; Figs 64, 65, 66 & 67).

The specimens are preserved on grey mudstone; specimens 1 (BP/2/22454) and 2 (BP/2/22453) as ventral compressions and specimens 3 (BP/2/22455) and 4 (BP/2/22456) as lateral compressions.

Derivation of generic and specific epithet

From Latin creta = chalk + Bibionidae, and anticus = old, ancient.

Diagnosis for species

Medium size, 3.2-4.8mm. Head: antennae short with short crowded flagellomeres, blunt ended; large compound eyes. Thorax: pronotum well-developed with lateral enlargement; scutum conspicuously raised, dome-like; scutellum small; legs: hairy, hairs short and dense; tibia with apical spurs; empodium and pulvilli strongly developed. Wing up to or greater than 3.4mm; fairly broad and long, approximately equal to length of thorax and abdomen combined; hyaline with stigmata on tip of R_1. Wing venation: C extending beyond R_{4+5}, two-thirds of the way to M_1, ending near wing tip; Sc three-quarters of wing length, ?complete; R with two branches, R_1 and R_{4+5}; Rs simple, R_{2+3} absent; R_1, R_{4+5} and M strongly developed, Sc to a lesser extent; R_1 extending shortly beyond Sc; M with two branches, M_1 and M_2; d absent; br and bm closed; br long, one-third to half wing length; bm long, >two-thirds wing length; m_2 and cup open to wing margin; r-m absent, Rs joins M at point of origin of M_{1+2} and R_{4+5}; bm-cu at fork of M_1 and M_2; extra longitudinal vein between M and CuA; M_1, M_2, CuP, CuA_1 and CuA_2 weakly developed; CuA_1 and CuA_2 extending to margin; CuP lies along side CuA_2 for two-thirds of its length, then disappears; cubital cell wide open; A_1 weakly developed, appears not to reach wing margin; A_2 absent; anal lobe undeveloped. Halter: small, rounded knob; very narrow stalk. Abdomen: long, fairly stout, turned ventrally distally; well developed tergites and sternites; tergite nine reduced, incorporated in genitalia. Female genitalia: eighth sternum divided into two plates, obtuse lobes on inner margin; two long oval cerci enveloped laterally and ventrally by tergite nine. Male genitalia: unknown.

Diagnosis for genus as for species

Descriptions

8.2.1. *SPECIMEN* 1

The specimen, BP/2/22454 (Plate 14C; Fig. 64), measures approximately 4.5mm in length. The right wing is better preserved than the left; they measure 3.4mm and 3.2mm in length respectively. Both wings are incomplete, with the posterior and proximal sides of each missing.

HEAD. No features are distinct although Rayner (1987) indicated the position of a compound eye, I find this doubtful (I interpret this structure as the left front femur). No ocelli are distinguishable. The antennae are short with short, compacted flagellomeres; the number of flagellomeres is not discernible.

THORAX. It is large, robust and rounded. Only the scutum can be distinguished with certainty. It is large and strongly arched. Four legs are preserved (two hind and two front legs) and these are mostly incomplete. Legs are fairly stout, particularly the femora. The femora of the front legs are especially swollen and these legs have very short and broad tibiae (RFL). The tibia of the right hind leg is nearly three times this length. No tibial spurs have been observed on this specimen.

Wings: completely hyaline except for the pterostigma near the distal end of R_1. The costa is thickened until beyond R_{4+5}. Sc appears to be complete and reaches the wing margin half way along the wing's length; it is weakly developed especially its distal end. R_1 reaches wing margin two-thirds of the wing's length along. Rs is unbranched, its origin is also half way along the wing's length. Rs joins M where M_{1+2} and R_{4+5} originate. M_{1+2}, M_1, CuA_1, and CuA_2 are preserved incompletely. Halteres are missing.

ABDOMEN. It is fairly stout throughout its length. It narrows only slightly between segments one and two and at segment eight. The abdomen is somewhat flattened dorso-ventrally. It probably consists of nine segments of which the ninth is very small, altered and incorporated as part of the genitalia. The genitalia (Fig. 64 - see inset) resemble those of a female. The ninth tergum extends around the sides and the ventral portion of the genitalia. The cerci are large, elongated and oval in shape and are at least twice as long as they are wide. The eighth sternum is divided into two large, rather square, plates, with the inner margin of the left plate with a large obtuse lobe at its apex.

8.2.2. SPECIMEN 2

The specimen, BP/2/22453 (Plate 14A; Fig. 65), is approximately 4.6mm in length. As the head is folded ventrally and is partially obscured, this measurement may not be quite accurate and should indeed be longer. Both wings are well preserved although, as with all the others, the basal region is missing. The left and right wings measure 3.0mm and 3.7mm respectively; this measurement should also be longer considering the basal region is absent.

HEAD. No features [including the compound eye noted by Rayner (1987)] are discernible.

THORAX. It is large, robust and arched. The possible positions of the pronotum, prescutum, scutum and scutellum are indicated on Fig. 65. Legs: approximately three or four relatively stout legs are present (e.g. the stout right hind leg, particularly the femur, and, the leg arrowed at the center of the specimen). On one of the legs, the tibia is produced apically to form two large spurs. Five tarsal segments are discernible on this same leg. I believe this is the front leg with the femur positioned as indicated in Fig. 65.

Wings, venation: hyaline except for stigmata at distal end of R_1. C is thickened to wing tip, beyond R_{4+5}, two-thirds of the way to M_1. Sc appears to be nearly complete or indeed complete; R_1 ends in the margin two-thirds of the wing's length along. Rs is unbranched. Stem of R_{4+5} originates directly at the origin of M_{1+2}; Rs ends where R_{4+5} and M_{1+2} arise, crossvein r-m is thereby obliterated; there is an extra longitudinal vein between M and CuA; it ends just a little posteriorly to the fork of M_{1+2}. M_{1+2} branches once, into M_1 and M_2, at a point in line with the pterostigma. m-cu also originates at this point and is recurrent. CuA_1 and CuA_2 reach the wing margin. CuP lies along side CuA_2 for two-thirds of its length, then disappears. The cubital cell is wide open. A_1 is present but weak and probably does not reach the wing margin. A halter is present at the base of the right wing, it is incomplete. It comprises a small and rounded knob with a very (?long) narrow stem.

ABDOMEN. It is large, robust, and narrows distally to a rather blunt end. The abdomen curves ventrally at its distal end. It consists of about nine segments. The genitalia comprise the same bilobate structures seen in the previous specimen, and these probably represent a pair of long, elongated and oval cerci indicating that the specimen is an adult female. Additional details were not discernible.

8.2.3. SPECIMEN 3

The specimen, BP/2/22455 (Plate 14B; Fig. 66), measures 4.8mm in length. Portions of both wings are preserved although poorly so; the right wing is the most complete and measures 3.4mm in length. Portions of four legs are preserved.

HEAD. The head is somewhat elongated, but distorted. The compound eyes are faintly visible but the distance separating them is not clear. No ocelli are discernible. The antennae are fairly short with short and crowded flagellomeres, they end bluntly. The number of flagellomeres is not known. No palps are visible.

THORAX. The scutum is conspicuously raised and dome-like. The possible position of the pronotum (with lateral enlargement), prescutum and scutellum are indicated in Fig. 66. Legs: they are hairy and the tarsal segments particularly, are covered densely with short hairs (see Fig 1E in Rayner, 1987). The legs are fairly stout, particularly the femora. The most swollen femora are those of the two front legs. A single tibial spur can be distinguished on each of the two hind legs; the left front leg however displays two spurs on the tibia. Five tarsal segments are visible on each leg. The first segment is about twice as long as the others with the exception of the fourth; this segment is much smaller than segments two, three and five. The empodium and pulvilli are strongly developed (all legs have certain portions of these structures). There are two distinct claws visible on the leg emerging from under the head.

Wings, venation: hyaline except for stigma at the tip of R_1. C thickened to wing tip, nearly to M_1 (left wing). Sc weakly developed, particularly distally. Sc appears to reach wing margin and does so just prior to stigma. Rs joins M where M_{1+2} and R_{4+5} originate. Portions of M_{1+2}, M_1, M_2 and CuA_1 are preserved. The fork of M_{1+2} is at the same point where m-cu joins; in line with tip of R_1. Halteres are missing.

ABDOMEN. It is stout, tapering distally to a fairly pointed end, with segment five being the largest. There are nine tergites and sternites which are all well developed except tergite nine which is reduced. The genitalia, which are seen from the side, do not have identifiable details. In general appearance however, they differ from those in the other three specimens in that there are no large oval appendages; instead, there is a rather square structure of unknown identity (?possibly a clasper). In addition, tergite nine is not reduced dorsally (and medially), and, the genital structures are directed upwards, unlike the other specimens.

8.2.4. SPECIMEN 4

The specimen, BP/2/22456 (Plate 14D; Fig. 67), is 3.2mm in length. The right wing is the most complete, and measures approximately 2.2mm; the left wing is incomplete. The specimen overlies another insect of unknown identity.

HEAD. The head is rounded and has two large separate compound eyes which nearly meet at the dorsal midline. No ocelli are distinguishable. The antennae are fairly short, and the flagellomeres are short and compacted. The individual flagellomeres are not discernable. The antennae are approximately 0.5mm long. The head overlaps with the two front legs and therefore the mouthparts are not distinguishable.

THORAX. The thorax is robust and rounded. Only the dorsal segments are distinct, that is the prescutum, scutum, scutellum and mediotergite. The pronotum is well developed with prominent lateral enlargement; the scutum is conspicuously raised and dome-like; the scutellum is small.
Legs: all legs but particularly the front legs are stout, the front legs also have enlarged femora. The tibiae are with tibial spurs (RFL in Fig. 67).
The front tibiae are short in comparison to those of the ?hind legs.
Wings: Hyaline except for pterostigma near distal end of R_1. C is thickened to wing tip, about two-thirds of the distance to M_1. R_1 is parallel to the costa, it is complete and meets the margin at the stigma or pigment spot. Rs is present and emerges approximately half way along the length of R_1, it joins R_{4+5} at the same point where M_{1+2} leaves. M_{1+2} splits once, into M_1 and M_2, in line with the stigma. Crossvein r-m is absent. CuA_1 is only faintly preserved, it curves posteriorly at a point in line with the stigma. R_{4+5} is complete and ends in the costa just prior to where

the costa becomes thinner. No halteres are distinguishable.

ABDOMEN. It is relatively stout and consists of nine segments. The fifth tergite is the longest, broadest and largest; prior to and after segment five, the segments progressively narrow and shorten. Segment nine forms part of the genitalia. It is extremely narrow dorsally, widening medially and extending around the genitalia ventrally. The genital structures appear to be those of a female; there are two long and oval lobes, the left only just visible behind the right (as this is a side view). I interpret them as a pair of cerci as described in specimen 1. They curve towards the ventral side of the insect. At the tip of these lobes are three structures which I can not identify. Perhaps they are emerging, or clinging eggs, or perhaps even pollen grains.

8.3. DISCUSSION

Biology

The family Bibionidae consists of about 700 species distributed throughout the world (Hardy, 1981), of which 77 have been recorded from the Afrotropical Region (Hardy, 1980). Hardy (1980) predicted that there are many more however, maybe up to 150 undescribed species. Most of the Bibionidae are found in the tropics especially Plecia. In southern Africa, the majority are from the South West Cape, and somewhat fewer in the Eastern Cape.

Two subfamilies are represented in the Afrotropical Region, namely Bibioninae and Pleciinae (Hardy, 1960 & 1980). In the Nearctic Region Hesperininae is also present, but it is only represented by a single genus *Hesperinus* (Hardy, 1981). The Pleciinae are poorly represented in South Africa, with only two species in the genus *Plecia* (Hardy, 1960 & 1980). This genus is, however, well represented elsewhere in the Afrotropical Region. In the Neartic Region the *Penthetria* is another genus of this subfamily. In the Bibioninae, the genus *Bibio* is the best represented in South Africa with nine known species (Hardy, 1960 & 1980); the genus *Dilophus* (previously known as *Philia*) is the next largest with five species (Hardy, 1960 & 1980). *Bibiodes* has not been found in the Afrotropical Region.

The Bibionidae are herbivorous and are known pollinators (Colless & McAlpine, 1970; Hardy, 1980). For example, adults of *Dilophus* are frequently found on blossoms and are seemingly nectar feeders (Hardy, 1980). Their ample presence in the Cretaceous indicates that they may have been important pollinators of some of the Orapa angiosperms. Interestingly, living Bibionidae form important prey items of carabids (Coleoptera: Carabidae) (McKay, pers. comm.) and empids, both of which have been found at Orapa. *Plecia* and *Bibio* representatives are known to hover in large swarms consisting mainly of males (Hardy, 1980 & 1981). In the Nearctic Region swarming is most common in spring, when mating occurs; this indicates seasonality. Larvae of the Bibionidae are mainly scavengers on decaying organic materials in soils rich in humus and among roots of grasses and other plants, manures, decaying leaves and forest litter (Hardy, 1960 & 1981; Colless & McAlpine, 1970). Most adult species inhabit forests (Colless & McAlpine, 1970).

Identification

In an attempt to classify the fossil Bibionidae from Orapa, I have looked at much of Hardy's work (Hardy, 1948, 1949, 1950a, 1950b, 1951a, 1951b, 1952a, 1952b, 1960, 1961, 1962, 1971, 1980 & 1981). Unfortunately, Hardy's keys concern mainly colouration and genital structure of species and not wing venation; this has made their usefulness in terms of these fossils limited. His key comprising other gross morphological features of genera (Hardy, 1981) is the main reference used for identification.

The Bibioninae and the Pleciinae have compacted flagellomeres, and their antennae are therefore fairly short. The Hesperininae on the other hand, have long antennae with long individual flagellomeres. Since the Orapa fossils have short stubby antennae, I do not consider them members of the Hesperininae.

In the Pleciinae and Hesperininae Rs is branched to form R_{2+3} and R_{4+5}. This is not the case in the Bibioninae nor in the fossil specimens, where Rs is unbranched and only R_{4+5} is present. As the branching of Rs is considered an important diagnostic character in the distinction between these subfamilies (Hardy, 1981), the four specimens may belong to the Bibioninae. Other venational features of the fossils, however, negate this.

Considering the Bibioninae only, further identification involves the characteristic tibiae. Bibiodes and Bibio have the fore tibiae produced apically to form two large apical spurs. Dilophus has a ring of spines at the apex and one or two sets of spines above the apex of the tibiae. The fossils have distinctly preserved spurs on three of the four specimens, which indicates their affinity with the former two groups.

The reason why I can not directly place them into either Bibio or Bibiodes is that the fossil wings have one basic but very characteristic difference from either genera, and various other inconsistencies. Unlike the two extant genera, the crossvein r-m in the fossil wing is missing and therefore Rs ends at a point coinciding directly with the origins of veins R_{4+5} and M_{1+2}. The only specimens with a shortened crossvein r-m are B. upembensis (Hardy, 1952a) and B. hortulanus (Hardy, 1950b), but, indeed, in no specimen is it missing completely; this feature is not found in any modern species. As it is a rather distinctive and unusual character unique to the fossils, the specimens warrant placement in a genus of their own. Another peculiarity of the Orapa specimens is that Sc appears to be complete; this vein is incomplete in Bibio and Bibiodes but is a character common to all the other subfamilies. There is also an extra, weakly developed longitudinal vein between M and CuA; its point of origin is unknown but it ends just posterior to the fork of M_{1+2} (specimen 2 only, left wing particularly - implying that it is probably an aberration in the venation, an occurrence common throughout the Diptera). Most interestingly, a trait also unique to the Orapa Bibionidae is the length of the costa, C is longer than in any of the extant members of the family. In modern Bibionidae, in the genera <u>Bibio</u> and <u>Bibiodes</u>, the costa ends just beyond R_{4+5}. In other groups (e.g. <u>Plecia</u>, <u>Dilophus</u>, <u>Hesperinus</u> and <u>Penthetria</u>) the costa extends to at least about a third to half way along, between R_{4+5} and M_1. In the fossils, where the tip of the wing is preserved (specimens 2, 3 & 4), the costa stretches two-thirds of the way between R_{4+5} and M_1. This marks the specimens as more primitive or plesiomorphic than its extant descendants. It was previously noted (Chapter 5), and reinforced by Ennos (1989), that, as the dipteran wing evolved, the leading edge (as well as the other longitudinal veins) shortened. Also, the basic venational elements (for example the bifurcation of the media) were brought nearer the wing base creating longer emmiting veins, and, allowing for greater ventral flexion. Changes in wing structure in flies (hand-in-hand with changes in the thorax) have been very important in the evolution of faster, more manoeuvrable and more precise flight (Ennos, 1989). I measured the position of these venational elements with respect to the length of the longitudinal veins emitted but found that, with the exception of the longer costa, these ratios were the same as those in modern forms.

Strangely, the genitalia of the fossils (specimens 1, 2 & 4 particularly) resemble those of some modern Plecia species, which possess two large round cerci, a reduced ninth tergum and an eighth sternum comprising two plates which are said to function as egg guides (Hardy, 1948 & 1952b). However, none has such enlarged and elongated paired lobes as those observed in the fossils.

The conflicting evidence above seems to point to a possible need for erecting a new subfamily as diagnostic characters of Cretobibionida anticus are either indicative of affiliations with more than one subfamily or are entirely unique, or primitive. The new subfamily would, as a consequence, represent an extinct group.

Fossil Representatives

These four specimens are the first fossil Bibionidae from Africa and they are also the oldest ever found. The earliest identified Bibionid prior to the Orapa find is Plecia myersi Peterson from Canadian amber of upper Cretaceous age (72-73 Myr) (Peterson, 1975). Except for this record, all fossils definitely known to belong to this family are from the Cainozoic era. From the Tertiary are a larval bibionid from the Eocene (Harris, 1983); some Oligocene representatives (Lewis, 1971; Rice, 1959); Plecia pristina from the Oligocene-Miocene boundary in Mexican amber (Hardy, 1971); representatives from the Miocene (James, 1937); and a bibionid specimen from Siberian amber (Spahr, 1985).

CHAPTER NINE

DISCUSSION

9.1. INTRODUCTION

My interest in the assemblage of fossil Diptera from Orapa has centred around them as once-living organisms. Taxonomy has inevitably been a major part of this study, since it is vital to name and assess the affinities of specimens before any progress can be made in understanding their biology. In the following section I shall elaborate on my taxonomic observations, and place the specimens in their living context. It is first necessary to appreciate how the Diptera became fossilised.

9.2. DIPTERAN PRESERVATION AT ORAPA

All fossil Diptera from Orapa are coalified compressions, with perhaps the exception of the rhagionid/?tabanid. The specimens are entirely two-dimensional as result of burial in a fine-grained, highly compressible matrix. The rhagionid/?tabanid (Chapter 6) displays some relief as a result of burial in a coarse matrix which is less compressible, and its organic matter appears to have been at least partially oxidised. In addition, this specimen was found at a higher elevation than the others, and may be less compressed for this reason.

The larvae of the Tipulidae and Ceratopogonidae (and other animals besides insects) are known to leave traces in sediments (examples in Moussa, 1970; Ekdale & Picard, 1985; Metz, 1987), but, even after careful investigation of the Orapa sediments, we have found no evidence of such traces. Indeed, no larvae at all have been found. This supports the notion that the lake waters were inhospitable to animal life.

During sedimentation specimens come to rest in a position in which their centre of gravity is lowest, and their shortest axis is vertical (Walton, 1936). Therefore, the most extended surface will be parallel to the bedding plane. This explains clearly why all Orapa Diptera were preserved lengthways, lying either on their dorsal, ventral or lateral sides, but never with their anterior or posterior sides facing upwards. Few specimens have been found in contorted positions, indicating a passive death (perhaps from poisoning), rather than a struggle to escape entrapment.

Soft tissues such as legs, antennae or even abdomens, are often present on the Orapa fossils (even the softer-bodied insects, such as a whole aphid, have been preserved). Among many possible reasons, this may be a result of rapid anoxic burial, leaving little time for destruction by physical or chemical agents and exposure to scavengers or decomposer organisms. Fossilisation, like burial, was thus rapid. The preservation of fine structures (for example the chaetotaxy of many of the Diptera) may indicate a lack of transport away from the original life-setting, which suggests that the flies resided in, on, or near the crater lake and its immediate perimeter, i.e. the preserved fauna was mainly of a local origin.

9.3. FORMATION OF THE ORAPA FOSSIL ASSEMBLAGE

The collection of fossils from Orapa is large and diverse. The Diptera, however, form an important part of the assemblage in terms of numbers of specimens, quality of preservation and biological importance. Diptera at Orapa are limited almost entirely to laminated and unlaminated shales in the centre of the sedimentary basin. This suggests that the organisms were not transported into the lake by mud or debris flows, but flew there.

As certain plant and insect fragments are consistently found together, and since burial of material or deposition of sediments was rapid, and transportation minimal, I suggest they were once part of the same biological community. Indeed, there is evidence that living carabids feed on bibionid and other dipteran larvae [e.g. Ceratopogonidae and Culicidae (Downes. 1978)], and some empids prey on bibionids and other Diptera (all these have been found at Orapa). I suggest these associations had all been established in the Cretaceous. In addition, I have already mentioned the possibility of some of the Diptera acting as pollinators.

9.4. THE PALAEOENVIRONMENT OF ORAPA

An added bonus from my and my co-workers' studies is that the fossils allow a fairly complete reconstruction of the palaeoenvironment of Orapa. The lack of large leaves (angiosperms and gymnosperms) indicates that forests were not present in the crater (Bamford, 1989). The insect fauna, for example, some of the Coleoptera (McKay, 1987), and particularly some of the Diptera, however, indicate that there must have been a lush (?non-forest) vegetation in the crater for the insects to have been able to complete their life cycles and reproduce. The abundance of Diptera within the fossiliferous sediments reinforces this, since their larval stages in particular are dependent on wet and vegetated conditions. I suggest that there were forests in the area, but these were distant, and were unable to colonise the area within the crater.

9.5. SPECIES CONCEPTS

As once living organisms, these Diptera were members of genetic species. They highlight, for me, the major problems of dealing with fossil taxa.

Palaeontologists define their species almost completely on the morphology of individual fossils (types) and their relationship to the morphologies of the other individuals in collections (Rayner, 1988). Problems arise, however, when palaeontologists attempt to discuss processes of evolution with neontologists, since the morphological and genetic species concepts are often incompatible. Also, particularly in the fossil record of insects, palaeoentomologists are frequently faced with small collections of fragmented specimens. Species defined on the basis of incomplete material may lead to highly subjective groupings, which do not necessarily represent populations of evolutionary or even biological significance.

Most neontologists, on the other hand, use a genetic species concept, where species are defined in terms of gene exchange. The most commonly used concept is based on reproductive isolation, where species are "groups of populations the gene exchange between which is limited or prevented in nature by one or a combination of several reproductive isolating mechanisms" (Dobzhansky, 1951, p262). An alternative approach, and one I favour, defines species as groups of individuals which share a common set of fertilisation mechanisms (Paterson, 1978, 1980, 1981, 1982a & b, 1984; Masters, 1985); a subset of these includes the means by which potential breeding partners (or their cells) recognise each other (Paterson, 1984). The gene pool boundaries are therefore determined by measurable signals and responses (i.e. the specific-mate recognition system), and reproductive isolation is merely an incidental effect of this recognition. The recognition concept has greater explanatory power, and it is logically more correct (Masters et al., 1987). In addition, it allows morphology to be seen in an entirely different light. If we examine fossils from the point of view of the recognition concept, morphology may often be implicated in specific-mate recognition, and, when it is, it will be subjected to intense stabilising selection. We therefore have direct and consistent markers of genetic species in taxa where gene exchange is effected by means of morphological recognition systems (Rayner, in press). Some of the Diptera have preserved morphological mate recognition signals, such as male genitalic structures or wing pigmentation.

Recognition can, however, involve signals and reponses at many different levels (Masters, 1985); visual, chemical and acoustical means may be employed in locating conspecific mates. Insects, including the Diptera, may engage in one or more of these forms of recognition in order to find their mating partners.

In the case of the bibionids and empids, living representatives swarm, and recognition is visually mediated. In the former group, their pigmented wings function as signals, and in the latter group, their silken balloons enclosing prey, serve as attractants. In the bibionids, if an individual is born without wing spots, or the spots are a different colour or are located in a different position, the prediction is that the individual will not be recognised as a conspecific mate. It will not breed and cannot pass on its abnormal signal. Similarly, within empid species which produce courtship balloons, the females will not recognise mates without balloons. This very selective elimination of mating partners provides for the strongest stabilising selection, and is an explanation for stasis.

9.6. STASIS

Some of the fossil Diptera collected from the Cretaceous sedimentary material from Orapa show remarkable morphological stasis. Indeed, the members of the two genera, Helius and Empis are virtually identical to extant representatives. This is even more remarkable when I consider the number and degree of changes in other organisms since the Cretaceous. The conservative nature of the genus Helius was noted by Savtshenko (1966), who described the "slow evolutionary progress" for the group (Tipulidae) as a whole. In addition, I have been able to place Empis (s.s.) orapaensis in an extant subgenus. A subgenus that is as old as 93 Myr is remarkable in terms of the evolutionary duration of a lower taxon, and is superb evidence for stasis. Differences between extant and extinct species may be as small as those between recent species.

Fossil evidence for punctuated evolution, is demonstrated by the discovery of these Diptera. Changes in morphology appear few and negligible. The Diptera appeared abruptly and have changed little since then. The evolution of the group was probably concentrated in a limited number of rapid speciation events. This is in accordance with Stanley's view (1982) that a segment of phylogeny comprising several identical species and persisting with little overall change for a long interval of time provides testimony for stasis, as do single lineages that survive for long periods with little change.

In order to assert that a species has been static, correct diagnosis of the species is essential. It is vital to assess how closely the fossil dipteran morphological species reflect true genetical species, based simply on wing morphology. Modern dipterologists group extant Diptera principally on the basis of their male genitalic structures (e.g. the Bibionidae). Basing a classification on reproductive characters makes for a natural grouping. Although identification usually requires examination of the hypopygium, most species have equally distinctive non-genitalic characters (especially useful if the specimen is a female). Wing venation, body colouration, ratio of sizes of various body parts to one another and various other characters may be used together for reliable identification, but, wing venation on its own is considered practically as significant as the hypopygium for reliable classification. Indeed, classification of the Tipulidae, for example, is based nearly entirely on the wings. It is fortunate, therefore, that many of the fossil specimens (at least 50%) have retained their wings during fossilisation with fairly distinct venation.

Knowledge of the history and/or correct phylogenetic positions of fossils are also essential for determining species stability. The fossil record of the dipterans is fairly well known. Most living groups have been trac back into the Mesozoic and their relationships have been well studied (Hennig, 1981) - at least more so than other insects (Hennig, 1981; Remm, 1976). Most lines of descent are therefore reasonably well understood.

In my material, where only one or two differences are recognisable between the Cretaceous fossil and the related living species, it is obvious that morphological changes occur only rarely. The data provided by the Botswanan fossils are insufficient to determine the longevities of individual species, but they do provide insight into the duration of higher taxa. A morphological change or two (in the overall morphology of an individual) every 100 Myr, implies that each morph or species has a life-time of, on average, 30 Myr if, and only if, they were purely temporally separated. Spatial and temporal separation would increase this estimate. Temporal separation is unlikely, however. Rather than the complete transformation of a species in a specific geological time (gradualism), it seems more likely a matter of the displacement of one species by another in the same time period. This is substantiated by some of the extinct and extant Mycetophilidae which co-existed during the early Cretaceous (Chapter 6).

Schopf (1982) identified four biases employed by palaeontologists when estimating the duration of a static period, which automatically lengthens it. I believe he is correct, and, although they are sometimes unavoidable, such biases should be taken into account when an estimation is made. He summarised (p.1155) these biases as follows:

(a) absence of preserved morphological complexity makes organisms appear to evolve more slowly (more taxa are mistakenly placed with other taxa);

(b) common taxa are fewer, but longer-lived than the much more numerous but more rarely collected shorter-lived taxa;

(c) durations of taxa are based on durations of geological stages, thus presetting a minimum duration;

(d) the polytypic (lumper's) species concept prevails; shorter lived taxa (e.g. sibling species) are pushed into longer lived taxa.

Some other fossil finds at Orapa, from various other insect orders, demonstrate similar stability of form; for example an aphid (Rayner and Waters, 1989; Appendix 4) which shows a remarkable resemblance to a number of extant species of the Siphonoroides family. Fossil aphids (Cretaceous and particularly Tertiary) resemble the recent aphid fauna strikingly (Heie, 1987). For example, Heie mentioned that species of <u>Mindarus</u> (Mindaridae) in the early Tertiary are identical to extant species of this group. Some other insects show that unique forms existed in the Cretaceous, and have become extinct.

The flora of Cretaceous Orapa, however comprises new forms (Bamford, 1989). Indeed, Bamford descibed twenty-seven genera and 28 species of angiosperm leaves, three genera and three species of flowers, and 13 genera and 14 species of seeds and fruits. Of these, only one leaf genus had previously been described, all other taxa being newly erected. Stasis, in other words, is not reflected in the fossil flora.

I have already mentioned that such stasis is predictable if morphology is connected to reproduction. In addition, I would also like to consider briefly stasis in habitat preference.

9.7. HABITAT TRACKING

Predictions of the Concept of Recognition of Species may also explain the present distribution of many of the extant relatives of the Orapa fossils. Diptera, which were apparently fairly common at Orapa in the Mesozoic, are virtually unknown there today. Indeed, the drier open regions of the Central District of Botswana today support few representatives of the dipteran families described here. At present, these families are restricted mainly to the southern regions of southern Africa, such as the Cape coast.

Organisms' reproductive systems are seriously affected by changes in environment, but remain stable as long as animals remain in their preferred habitat; in other words, the SMRS of a species is closely linked or adapted to the habitat in which speciation occurred (Paterson, 1982a & b; Masters et al., 1987). The Recognition Concept predic that characters linked to the SMRS will remain constant in time, and throughout the species' geographical range (Lambert & Paterson, 1984). Thus, insects which are trapped in changing conditions, rather than being allowed to shift their geographical range in pursuit of their favoured habitat, are likely to become extinct, or, very rarely, these conditions may induce speciation. Habitat tracking, similar to that described for Coleoptera by Coope (1979), is the usual response to climatic fluctuations. Organisms will follow, or actively seek or 'track', their preferred habitat for as long as possible, rather than passively suffer drastic environmental changes (Paterson, 1982a). Habitat tracking of up to 7 000km have been recorded.

The shift in the geographical distributions of certain families of Diptera, of a distance of 2 000km or more, may be explained by the fact that, at the time when deposition of the sediments in the Orapa crater was taking place, the African continent was approximately 15° to the south of its present position - in other words, Orapa was about where Cape Town is today. As morphological differences of the 93 Myr species, are so slight and so few compared with the extant species in the genera *Helius* and *Empis*, it seems likely that they differed little on a reproductive or physiological level as well. This makes it credible to assume their environmental tolerances were very similar, and leads us to assume that the environment of Orapa then and Cape Town now, were similar too.

It appears that as the African continent moved northwards and Orapa shifted from its earlier relative position to its present one, the particular climate affecting the area, slowly changed at any defined point on the continent. In particular, the moist environment of Cretaceous Orapa was experienced further south. Simultaneously, the present arid conditions of the region were becoming prevalent. As the continent moved northwards, the insects' geographical range gradually shifted southwards, necessitating the tracking of their favoured humid environment and preferred ecological surroundings.

9.8. DIPTERA AND POLLINATION

The most significant aspect of the discovery of these Diptera at Orapa for me, however, is their association with early angiosperms.

The most spectacular biological activity of some of these Diptera is that they probably were pollinators. The evolution of this form of plant/insect relationship, whereby the plant harnesses the mobility of the insect in exchange for food, is the *climax* of an ancient association. Indeed there is evidence from the Lower Palaeozoic to show that interrelationships between land plants and arthropods existed from the beginning of land-colonisation (Thomas & Spicer, 1986). These authors noted that, as early as the Silurian, some predatory arthropod forms have been found in empty sporangia, which they probably occupied following spore eating, and that stems of other plants also show evidence of attacks by arthropods or other small animals. Evidence from the Rhynie Chert also shows that arthropods (including a hexapod) were associated with early land plants (Rolfe, 1980).

The average height of plants increased during the Devonian and this was accompanied or preceded by the development of flying insects which probably fed off the spores and even dispersed them (Thomas & Spicer, 1986). In the Carboniferous some insects' food may have been fleshy sporophylls and possibly even spores, as they had biting jaws rather than mouthparts adapted for sucking nectar (Scagel <u>et</u> <u>al</u>., 1969).

It was not until the Lower and, particularly, the Upper Cretaceous that flowering plants diversified, clearly following the appearance of many of the modern orders of insects. Indeed, the Late Jurassic and Early Cretaceous marks the advent of dipteran diversification, and by the Late Cretaceous most dipteran forms existing today were represented by very similar forms. Extant representatives of the dipteran families Empididae, Hybotidae, Tipulidae, Bibionidae, Mycetophilidae and Anisopodidae are all pollen or nectar feeders and serve effectively as pollinating agents; the same is assumed for their Cretaceous ancestors. Aphididae (Rayner & Waters, 1989), Hymenoptera and Coleoptera (McKay, 1990) (representatives of which have been recovered from the Orapa sediments) may also have been important pollinators at the time.

It is almost certain that the intimate association between flowers and their insect visitors began during the Cretaceous and that these relationships stimulated the development of independent forms, which, together provided for new ecologies (Thomas & Spicer, 1986). Diversification of Diptera, undoubtedly, played a major role in the expansion and evolution of the Angiosperm group.

Pollination and Diversification of Early Angiosperms

Entomophily (insect-pollination) is one of three pollination modes, wind and bird pollination being the other two types. The earliest seed plants were probably wind pollinated, as are most extant gymnosperms (Scagel et al., 1969). However, in many angiosperms there is good evidence that wind pollination has been secondarily acquired and that the flowers probably have been derived from entomophilous ancestors (Scagel et al., 1969).

Flower types typically visited by flies

Insects are particular in their choice of flowers, and will visit specific forms depending on the floral structure, colour, size or scent of the bloom. Entomophilous flowers have been divided into a number of types by, for example, Scagel et al. (1969), who named three: Hymenoptera flowers, Lepidoptera flowers and Diptera flowers. Examples of dipterous flowers range from herbs and shrubs to trees, from xerophytes to hydrophytes, and from monocots to dicots. (Gymnosperms may also provide nourishment to certain fly families, e.g. Cecidomyiidae). A list of some flowers visited by flies follows below (this list is by no means complete and it is taken from McAlpine, 1981; Downes, 1958 & 1978; Hesse, 1938; Scagel _et_ _al_., 1969).

Rosaceae (e.g. _Crataegus_, _Rubus_, _Spiraea_, _Prunus_, _Potentilla_, _Rorippa_). The nectar of the blooms may serve as a food source for Stratiomyidae, Culicidae, Ceratopogonidae.
Compositae. Visited by Blephariceridae, Bombyliidae, and Stratiomyidae.
Apiaceae (e.g. Umbelliferae). Ceratopogonidae, Vermileonidae and Stratiomyidae.
Caryophyllaceae (e.g. _Silene_). Ceratopogonidae.
Onagraceae (e.g. _Epilobium_). Culicidae.
Celastraceae (e.g. _Euonymous_). Culicidae/Ceratopogonidae.
Proteaceae. Bombyliidae.
Orchidaceae (e.g. _Habenaria_). Culicidae.
Aristolochiaceae (e.g. _Aristolochia_).
Asclepiadaceae (e.g. _Stapelia_).
Scrophulariaceae (e.g. _Veronica_).
Ericaceae (e.g. _Rhododendron_, _Vaccinium_). Simuliidae and Culicidae.
Saxifragaceae (e.g. _Saxifraga_). Ceratopogonidae.
Caprifoliaceae (e.g. _Sambucus_). Ceratopogonidae.
Salicaceae (e.g._Salix_). Culicidae, Ceratopogonidae, Hilarimorphidae and Stratiomyidae.
Anacardiaceae (e.g. mangoes). Simuliidae, Bombyliidae.
Mesembryanthemaceae. Bombyliidae.
Arecaceae/ Palmae (e.g. date flowers). Simuliidae.
Araceae (e.g. _Arum_). Culicidae.
Cyperaceae (e.g. _Carex_). Stratiomyidae.
Typhaceae (e.g. _Typha_). Stratiomyidae.

Other dipterans known to feed off nectar (or honeydew, water or ripe fruit) of flowering plants are the Tabanidae, Tipulidae, Bibionidae, Chironomidae, Coenomyiidae, Acroceridae, Rhagionidae, Cecidomyiidae, Mydidae, Therevidae, Athericidae, Pelecorhychidae, Mycetophilidae, Sciaridae and Anisopodidae.

The above angiosperm groups nearly always have flowers which are bisexual, rarely unisexual; they are usually very small and situated close together. If unisexual, the flowers are arranged in, for example, a spadix, with the male flowers in the upper part of the spathe, and the female ones in the basal half (e.g. Araceae and Arecaceae); in the case of *Arum*, the initial attraction to the spadix is due to the unpleasant odour it gives off. Pollination results from a necessity for the fly to pass by the male flowers to reach nectar, thereby dusting pollen off onto its body, which may rub off in subsequent female flowers visited. (*Aristolochia*, the dutchman's pipe, is a bisexual flower where pollination takes place in a similar way to the *Arum*, but here a single flower is involved rather than an inflorescence). *Stapelia* flowers produce a stench resembling that of rotten meat to which Diptera are attracted. When flowers are unisexual, they may also be arranged in a spike (Typhaceae) or glume (Cyperaceae) where the female flowers lie in the lower regions with the male flowers just above these, or, they may simply be clustered close together in a spike or catkin (Salicaceae). Flies are compelled to pass by male flowers and their pollen in search of nectar in female flowers. In bisexual flowers, the small flowers may be arranged in the form of dense spikes (*Habenaria*, Proteaceae); racemes (Proteaceae, *Veronica*, *Vaccinium*, *Aristolochia*); peduncles (Proteaceaea, *Stapelia*); panicles or corymbs (Proteaceae, *Saxifraga*); cymes or fascicles (*Euonymous*); or grouped together in heads (Compositae, Onagraceae) or umbels (Scrophulariaceae, Umbelliferae). Flies are thus in contact with many flowers - male and female - in a single feeding session allowing for pollination. In a very few cases the flowers may be solitary (Aristolochia, Orchidaceae).

Such sophisticated relationships have evolved as a consequence of the inter-dependance of the insects and angiosperms. We have some evidence that faithful pollination existed in the Cretaceous in that funnel shaped flowers have been found (Bamford, 1989), along with Diptera with mouthparts apparently adapted for sucking (_Helius botswanensis_). If the long rostrum of _H._ _orapaensis_ is an adaptation in the strict sense (evolved under the action of natural selection to solve a life problem - _sensu_ Williams, 1966), then it is adapted for feeding at funnel flowers and was a faithful pollinator.

Diptera are found throughout the world, and have evolved into a bewildering number and variety of forms. I hope my contribution has added to our understanding of this remarkable group of animals, and its relationship to flowering plants.

CONCLUSIONS

1. Insect fossils are preserved in the majority as compressions or sometimes impressions. Preservation is good and many of the original structures have been retained.

2. Dipteran fossils, particularly those of the family Tipulidae, superfamily Empidoidea (families Empididae and Hybotidae) and family Bibionidae, are abundant in the middle Cretaceous sedimentary deposits at Orapa. Species were reliably diagnosed using wing venation as the vital diagnostic character.

3. Fossil Diptera from the middle Cretaceous are very similar, virtually identical, to living species, demonstrating their stability as individual species over long periods of geological time.

4. Phylogenetic conclusions: ages of many dipteran families, genera or other taxa have been underestimated. The families Empididae and Hybotidae for example, originated at least 40 million years prior to the last prediction made.

5. Stability in morphology over millions of years reflects a constancy in their environments, but a radical change in their geographical distribution.

6. In response to climatic fluctuations over the past 100 million years, as the African continent moved northwards,

dipteran species have altered their geographical ranges so that the whereabouts of species today (in this case the Cape coastal regions), can be traced back up to Orapa (15° north of the Cape) 93 Million years previously.

7. Habitat tracking of insects is evident in the dipterans described. Despite changing climatic conditions, an insect species may keep living conditions constant by following the shifting habitat.

8. The environments of the Cape today and Orapa 93 Myrs ago can be equated. Moist, well-wooded, seasonal, with spring and summer rainfall.

9. The recognition that species morphology may remain relatively constant over long periods of geological time (i.e. long-term stasis and short-term transformation) is in direct support of the punctuational model of evolution.

10. The Diptera were significant early pollinators.

REFERENCES

Alexander, C.P., 1917. The Crane flies of South Africa in the South African Museum (Diptera: Tipulidae). Part I. Annals of the South African Museum, 17: 139-184.

Alexander, C.P., 1920. New or little known Tipulidae (Diptera). 1. Ethiopian species. AnnalsandMagazine of Natural History, (9)5: 53-62.

Alexander, C.P., 1931. Crane flies of the Baltic Amber (Diptera). Bernstein Forsch, 2: 1-135.

Alexander, C.P., 1945. Helius (Helius) dugaldi. Proceedings of the Royal Entomological Society of London (B, Taxonomy). 18: 100-101.

Alexander, C.P., 1949. Helius (Helius) paramorosus. Proceedings of the Royal Entomological Society of London (B, Taxonomy). 18: 154-155.

Alexander, C.P., 1956. Tipulidae. Ruwenzori Expedition 1934-35 Part I: 129-380.

Alexander, C.P., 1964. Diptera (Nematocera) Tanyderidae, Phychopteridae, Tipulidae. In B. Hanström, P. Brinck and G. Rudebeck (Eds) South African Animal Life 10:229-441. Stockholm: Swedish Natural Science Research Council.

Alexander, C.P., 1975. New or insufficiently known African Crane flies. IV. (Tipulidae: Diptera). Studia Entomologica (n.s.), 18: 259-312.

Alexander, C.P. & Byers, G.W., 1981. Chapter 7: Tipulidae. In J.F. McAlpine, B.V. Peterson, G.E. Shewell, H.J. Teskey, J.R. Vockeroth and D.M. Wood (Eds) Manual of Nearctic Diptera 1:153-159. Hull, Quebec: Agriculture Canada.

Allen, H.E., 1981. Development of Orapa and Lethakane diamond mines, Botswana. Transactions of the Institution of Mining and Metallurgy (Section A: Mining Industry) 90: 177-191.

Bamford, M.C., 1989. The Angiosperm Palaeoflora from the Orapa Pipe, Botswana. Doctoral Thesis, University of the Witwatersrand, Johannesburg, South Africa.

Barraclough, D.A. & Londt, J.G.H., 1985. Diptera. In Scholtz, C.H. & Holm, E. (Eds): Insects of Southern Africa 283-326. Butterworths, Durban.

Carpenter, F.M.; Folsom, J.W.; Essig, E.O.; Kinsey, A.C.; Brues, C.T.; Boesel, M.W. & Ewing, H.E., 1937. Insects and Arachnids from Canadian Amber. University of Toronto, Studies in Geology, 40: 7-62.

Chainey, J.E. & Oldroyd, H., 1980. 21. Family Tabanidae. In R.W. Crosskey (Ed.). Catalogue of the Diptera of the Afrotropical Region 275-307. British Museum (Natural History): London.

Chvála, M., 1976. Swarming, mating and feeding habits in the Empididae (Diptera), and their significance in the evolution of the family. Acta Entomologica Bohemoslovaca, 73: 353-356.

Chvála, M., 1981. Classification and phylogeny of Empididae, with a presumed origin of Dolichopodidae (Diptera). Entomologica Scandinavica Supplement, 15: 225-236.

Chvála, M., 1983. The Empidoidea (Diptera) of Fennoscandia and Denmark. II. General part. The Families Hybotidae, Atelestidae and Microphoridae. Fauna Entomologica Scandinavica, 12: 9-257.

Colless, D.H., 1963. An Australian species of Microphorella (Diptera: Empididae), with notes on the phylogenetic significance of the genus. Procedings of the Linnaean Society of New South Wales, 88 (3): 320-323.

Colless, D.H. & McAlpine, D.K., 1970. Diptera. In CSIRO, Insects of Australia. Melbourne: Melbourne University Press, pp. 656-740.

Coope, G.R., 1979. Late Cenozoic fossil Coleoptera: evolution, biogeography and ecology. *Annual Review of Ecology and Systematics*, 10:247-267.

Crosskey, R.W.; Cogan, B.H.; Freeman, P.; Pont, A.C.; Smith, K.G.V. & Oldroyd, H., 1980, Catalogue of the Diptera of the Afrotropical Region. Introduction, p13-14. 1st edition, British Museum (Natural History), London.

Davis, G.L., 1977. The ages and Uranium contents from Kimberlites and associated rocks. *Extended abstracts 2nd international Kimberlite conference*, Santa Fe.

Dobbs, P., 1978. The distribution of kimberlitic mass flow sediments in the Orapa crater (2125 A/K1). *DeBeers (Botswana) Mining Company Limited. Internal report number 105/17/15 (16)*.

Dobzhansky, T., 1951. *Genetics and the Origin of Species*. 3rd ed. Columbia University Press, New York.

Downes, J.A., 1958. The Feeding Habits of Biting Flies and their Significance in Classification. *Annual Review of Entomology*, 3: 249-266.

Downes, J.A., 1968. Notes on the organs and processes of sperm-transfer in the lower Diptera. Canadian Entomologist, 100: 606-616.

Downes, J.A., 1970. The feeding and mating behaviour of the specialised Empidinae (Diptera); Observations on four species of Rhamphomyia in the High Arctic and a general discussion. Canadian Entomologist, 102 (7): 769-791.

Downes, J.A., 1978. Feeding and Mating in the insectivorous Ceratopogoninae (Diptera). Memoirs of the Entomological Society of Canada, 104: 1-62.

Downes, J.A. & Smith, S.M., 1969. New or little known feeding habits in Empididae (Diptera). Canadian Entomologist, 101 404-408.

Ekdale, A.A. & Picard, M.D., 1985. Trace fossils in a Jurassic Eolianite, Entrada Sandstone, Utah, U.S.A. Special Publications. Society of Economic Palaeontologists and Minerologists, Tulsa. 35: 3-12.

Eltringham, H., 1928. On the production of silk by species of the genus Hilara Meigen (Diptera). Proceedings of the Royal Society of London, Series B. 102: 327-334.

Ennos, A.R. 1989. Comparative functional morphology of the wings of Diptera. *Zoological Journal of the Linnean Society* 96: 27-47.

Gentilini, G., 1984. Limoniidae and Trichoceridae (Diptera: Nematocera) from the Upper Miocene of Monte Castellaro (Pesaro, Central Italy). *Bollettino Museo Civico di Storia Naturale di Verona*, 11: 171-190.

Glasgow, J.P., 1946. The Seasonal Abundance of blood-sucking flies in a grassed woodland area in central Tanganyika. *Journal of Animal Ecology*, 15: 93-103.

Goodier, R., 1966. Observations on the Seasonal Incidence and Distribution of Tabanidae (Diptera) in Southern Rhodesia. *Entomologist's Monthly Magazine*, 101: 230-239.

Griffiths, G.C.D., 1972. *The Phylogenetic Classification of Diptera Cyclorrhapha, with Special Reference to the Structure of the Male Postabdomen*. Dr. W.Junk, N.V., The Hague.

Haggerty, S.E., Raber, E. & Naeser, C.W., 1983. Fission track dating of kimberlite zircons. *Earth and Planetary Science Letters*, 63:41-50.

Hardy, D.E., 1948. 6. Bibionidae. <u>Ruwenzori Expedition:</u> 1934-35. Under the auspices of the British Museum (Natural History). I: 109-127.

Hardy, D.E., 1949. New Bibionidae from Madagascar. <u>Journal of the Kansas Entomological Society</u> 22: 94-96.

Hardy, D.E., 1950a. Bibionidae (Diptera: Nematocera). Institute National pour la Conservation de la Nature de la Republique du Zaire. Exploration du Parc National Albert. I. Mission G.F. de Witte 1933-1935. Fascicule 65: 1-23.

Hardy, D.E., 1950b. A Monographic Study of the African Bibionidae (Diptera). Part I: Introduction and genus <u>Bibio</u> Geoffroy. <u>Journal of the Kansas Entomological Society</u> 23: 137-153.

Hardy, D.E., 1951a. The Bibionidae (Diptera) of Madagascar, Part II: <u>Memoires de L'Institute Scientifique de Madagascar</u> (A) 5: 323-331.

Hardy, D.E., 1951b. A Monographic Study of the African Bibionidae (Diptera). Part II: Genus <u>Philia</u> Meigen. <u>Journal of the Kansas Entomological Society</u> 24: 74-94.

Hardy, D.E., 1952a. Bibionidae and Dorilaidae (Diptera). Institute National pour la Conservation de la Nature de la Republique du Zaire. Exploration du Parc National de L' Upemba. I. Mission G.F. de Witte. Fascicule 8 (5): 57-71.

Hardy, D.E., 1952b. A Monographic Study of the African Bibionidae (Diptera). Part III: Genus _Plecia_ Wiedemann. _Journal of the Kansas Entomological Society_ 25: 72-91.

Hardy, D.E., 1960. Chapter XI. Diptera (Nematocera): Bibionidae. In B. Hanström, P. Brinck and G. Rudebeck (Eds) _South African Animal Life_, 7: 210-215. Stockholm: Swedish Natural Science Research Council.

Hardy, D.E., 1961. Bibionidae. Institute National pour la Conservation de la Nature de la Republique du Zaire. Parc National de la Garamba. Mission H. de Saeger. Fascicule 24 (3): 111-115.

Hardy, D.E., 1962. The Bibionidae (Diptera) of Madagascar, Part III. _Verh. naturf. Ges. Basel_ 73: 149-170.

Hardy, D.E., 1971. A New _Plecia_ (Diptera: Bibionidae) from Mexican Amber. _Californian University Publications in Entomology_. 63: 65-67.

Hardy, D.E., 1980. 14. Family Bibionidae. *In* R.W. Crosskey (Ed.) *Catalogue of the Diptera of the Afrotropical Region* 213-215. British Museum (Natural History): London.

Hardy, D.E., 1981. Chapter 13. Bibionidae. In J.F. McAlpine, B.V. Peterson, G.E. Shewell, H.J. Teskey, J.R. Vockeroth and D.M. Wood (Eds) *Manual of Nearctic Diptera* 1: 217-222. Hull, Quebec: Agriculture Canada.

Hardy, G.H., 1951a. The Reticulation Theory of Wing Venation in Diptera. *Journal of the Society of British Entomology*, *4*: 27-36.

Hardy, G.H., 1951b. The Phylogeny of Diptera. *Entomological Monthly Magazine*, 87: 140-141.

Harris, A.C., 1983. An Eocene larval insect fossil (Diptera: Bibionidae) from North Otago, New Zealand. *Journal of the Royal Society of New Zealand* 13 (3): 93-102.

Heie, O.E., 1987. Palaeontology and Phylogeny. *In* Minks, A.K. and Harrewijn, P. (eds). *Aphids. Their Biology, Natural Enemies and Control*, Volume A: 367-391. Elsevier, Netherlands.

Hennig, W., 1950. *Die Larvenformen der Dipteren. Eine Uebersicht über die bisher bekannten Jugendstadien der Zweiflügeligen Insecten*. Volume 2. Berlin: Akademie-Verlag.

Hennig, W., 1954. Flügelgeäder und System der Dipteren und Berücksichtigung der aus dem Mesozoikum beshriebenen fossilien. *Beitrage zur Entemologie*, 4: 246-388.

Hennig, W., 1970. Insektenfossilien aus der unteren Kreide. II. Empididae (Diptera, Brachycera). *Stuttgarter Beitragungen zur Naturkunde*, 214: 1-12.

Hennig, W., 1971. Insektenfossilien aus der unteren Kreide. III. Empidiformia ("Microphorinae") aus der unteren Kreide und aus dem Baltischen Bernstein; ein Vertreter der Cyclorrhapha aus der unteren Kreide. *Stuttgarter Beitragung zur Naturkunde*, 232: 1-28.

Hennig, W., 1973. 31. Diptera Zwei-flugler. *Handbuch der Zoologie, Berlin*. 4 (2): 1-200.

Hennig, W., 1981. *Insect Phylogeny*. New York: Wiley. 514pp.

Hesse, A.J., 1938. A Revision of the Bombyliidae (Diptera) of Southern Africa. Annals of the South African Museum, 34: 1-1053.

Hutson, A.M., 1980a. 1. Family Tipulidae. *In* R.W.Crosskey, *et al.* (Ed.) *Catalogue of the Diptera of the Afrotropical Region*, 47-91. British Museum (Natural History): London.

Hutson, A.M., 1980b. 13. Family Anisopodidae. *In* R.W. Crosskey, *et al.* (Ed.) *catalogue of the Diptera of the Afrotropical Region*, 211-212. British Museum (Natural History): London.

James, M.T., 1937. A preliminary review of certain families of Diptera from the Florissant Miocene Beds. *Journal of Palaeontology* 11: 241-249.

James, M.T. & Turner, W.J., 1981. 33. Rhagionidae. *In* McAlpine, J.F. *et al.* *eds.* *Manual of Nearctic Diptera.* Vol. 1. Ottawa: Agriculture Canada. (monograph 27). pp 483-488.

Jarzembowski, E.A., 1984. Early Cretaceous Insects from Southern England. *Modern Geologist*, 9: 71-93.

Jell, P.A. & Duncan, P.M., 1986. Order Diptera. In Jell, P.A. & Roberts, J. (eds). Plants and Invertebrates from the Lower Cretaceous Koonwarra Fossil Bed, South Gippsland, Victoria. Association of Australian Palaeontologists Memoir 3: 163-182.

Kessel, E.L., 1955. The mating activities of balloon flies. Systematic Zoology, 4: 97-104.

Kessel, E.L., 1959. Introducing H.wheeleri Melander as a balloon maker, and notes on other North American Balloon flies (Diptera: Empididae). The Wasmann Journal of Biology, 17 (2): 221-230.

Knizeski, Jr.H.M. & Sullivan, D.J., 1984. Temporal Distribution of Crane Flies (Diptera: Tipulidae) in a Southern New York Woodland. Canadian Entomologist, 116 (8): 1137-1144.

Kovalev, V.G., 1974. A New Genus of the Family Empididae (Diptera) and its Phylogenetic Relationships. Palaeontological Journal, 8 (2): 196-204.

Kovalev, V.G., 1978. A New Fly Genus (Empididae) from the Late Cretaceous Retinites of the Taymyr. Palaeontological Journal, 12 (3): 351-356.

Kovalev, V.G., 1987. The Mesozoic Mycetophiloid Diptera of the Family Pleciofungivoridae. Palaeontological Journal, 21 (2): 67-79..

Krzemiński, W., 1985. Limoniidae (Diptera: Nematocera) from Baltic amber (in the collection of the Museum of the Earth in Warsaw). Part I. Subfamily Limoniinae. Prace Muzeum Ziemi, 37: 113-117.

Lambert, D.M. & Paterson, H.E.H., 1984. On 'bridging the gap between race and species': The Isolation Concept and an Alternative. Proceedings of the Linnaean Society of New South Wales, 107: 501-514.

Latreille, P.A., Le Peletier, A.L.M., Serville, J.G.A. & Guerin-Meneville, F.E., 1828. Entemologie, ou Histoire Naturelle des Crustacés, des Arachnides et des Insectes. In Encyclopedie methodique. Histoire Naturelle, 10 (Part 2): 345-833, Agasse, Paris.

Laurence, B.R., 1955. The Empididae (Diptera) of a Yorkshire Stream. Entomological Monthly Magazine, 91: 220-224.

Le Peletier, A.L.M. & Serville, J.G.A., 1828. See Latreille, P.A. et al., 1828.

Lewis, S.E., 1971. Three new species of fossil Diptera (Bibionidae) from the Ruby River Basin (Oligocene) of South Western Montana. Annals of the Entomological Society of America 64: 1464-1466.

Masters, J.C., 1985. Species within the Taxon *Galago crassicaudates* E.Geoffroy. Unpublished Doctoral Thesis, University of the Witwatersrand, Johannesburg, South Africa.

Masters, J.C.; Rayner, R.J.; McKay, I.J.; Potts, A.D.; Nails, D.; Ferguson, J.W.H.; Weissenbacher, B.K.H.; Allsopp, M.H. & Anderson, M.L., 1987. The concept of species: Recognition versus Isolation. South African Journal of Science, 83: 534-537.

Matile, L., 1980. 15. Family Mycetophilidae. *In* R.W. Crosskey (Ed.). Catalogue of the Diptera of the Afrotropical Region 216-227. British Museum (Natural History): London.

McAlpine, J.F., 1981. 2. Morphology and terminology - adults. *In*: McAlpine, J.F. *et al.* (eds). Manual of Nearctic Diptera. Vol. 1. Ottawa: Agriculture Canada. (Monograph 27). pp 9-63.

McAlpine, J.F. & Martin, J.E.H., 1969. Canadian Amber: A Palaeontological Treasure Chest. Canadian Entomologist 101: 819-838.

McAlpine, J.F.; Peterson, B.V.; Shewell, G.E.; Teskey, H.T.; Vockeroth, J.R. & Wood, D.M., 1981. 1. Introduction. Manual of Nearctic Diptera. Vol 1. Ottawa: Agriculture Canada. (Monograph 27), 9-63.

McKay, I.J., 1987. Cretaceous Carabidae (Coleoptera) from Orapa, Botswana. Unpublished Masters Thesis, University of the Witwatersrand, Johannesburg, South Africa.

McKay, I.J., 1990. Cretaceous Carabidae (Coleoptera) from Orapa, Botswana. Unpublished Doctoral Thesis, University of the Witwatersrand, Johannesburg, South Africa.

McKay, I.J. & Rayner, R.J., 1986. Cretaceous fossil insects from Orapa, Botswana. South African Journal of Entomology, 49, 7-17.

Melander, A.L., 1928. Diptera, Family Empididae. Genera Insect., 185: 1-434.

Melander, A.L., 1949. A Report on some Miocene Diptera from Florissant, Colorado. American Museum Novitates, 14-07: 1-63.

Metz, R., 1987. Sinusoidal Trail formed by a Recent Biting Midge (Family: Ceratopogonidae): Trace fossil Implications. Journal of Palaeontology, 61 (2): 312-314.

Moussa, M.T., 1970. Nematode Fossil Trails from the Green River Formation (Eocene) in the Uinta Basin, Utah. *Journal of Palaeontology*, 44: 304-307.

Negrobov, O.P., 1978. Flies of the Superfamily Empidoidea (Diptera) from Cretaceous Retinite in Northern Siberia. *Palaeontological Journal*, 12 (2): 221-228.

Paterson, H.E.H., 1978. More evidence against speciation by reinforcement. *South African Journal of Science*, 74: 369-371.

Paterson, H.E.H., 1980. A comment on 'mate recognition systems'. *Evolution*, 34: 330-331.

Paterson, H.E.H., 1981. The continuing search for the unknown and unknowable: a critique of contemporary ideas on speciation. *South African Journal of Science*, 78: 113-119.

Paterson, H.E.H., 1982a. Perspective on speciation by reinforcement. *South African Journal of Science*, 78: 53-57.

Paterson, H.E.H., 1982b. Darwin and the origin of species. *South African Journal of Science*, 78: 272-275.

Paterson, H.E.H., 1984. The Recognition concept of species. *South African Journal of species*, 80: 312-318.

Pechuman, L.L. & Teskey, H.J., 1981. 31: Tabanidae. In McAlpine, et al. (eds). Manual of Nearctic Diptera. Vol 1. Ottawa: Agriculture Canada. (Monograph 27), 463-479.

Peterson, B.V., 1975. A New Cretaceous Bibionid from Canadian Amber (Diptera: Bibionidae). Canadian Entomologist 107: 711-716.

Peterson, B.V., 1981. 19: Anisopodidae. In McAlpine, J.F. et al. eds. Manual of Nearctic Diptera. Vol. 1. Ottawa: Agriculture Canada. (monograph 27), pp 305-312.

Poulton, E.B., 1907. Predaceous Insects and their Prey. Transactions of the Entomological Society of London, 1096: 323-409.

Poulton, E.B., 1913. Empididae and their Prey in Relation to Courtship. Entomological Monthly Magazine, 49: 177-180.

Pritchard, G., 1980. Life Budgets for a Population of Tipula sacra (Diptera: Tipulidae). Ecological Entomology, 5: 165-173.

Pritchard, G., 1983. Biology of Tipulidae. Annual review of Entomology, 28: 1-22.

Rayner, R.J., 1987. March flies from an African Cretaceous Springtime. Lethaia, 20:123-127.

Rayner, R.J., in press. The genetic Species Concept and the Fossil Record. A Chapter for the Recognition Concept of Species: Essays in honour of H.E.H. Paterson.

Rayner, R.J. & McKay I.J., 1986. The treasure chest of the Orapa diamond mine. Botswana Notes and Records, 18: 55-61.

Rayner, R.J. & Waters, S.B., 1989. A new Aphid from the Cretaceous of Botswana. Palaeontology, 32: 669-673.

Rayner, R.J. & Waters, S.B., 1990. A Cretaceous Crane fly (Diptera: Tipulidae): 93 million years of stasis. Zoological Journal of the Linnaean Society of London, in press.

Remm, Kh. Ya., 1976. Late Cretaceous biting midges (Diptera: Ceratopogonidae) from fossil resins of the Khatanga depression. Palaeontological Journal, 10: 344-351.

Rice, H.M.A., 1959. Fossil Bibionidae (Diptera) from British Columbia. Bulletin of the Geological Survey in Canada 55: 1-24.

Riedel, M.P., 1914. Nematocera, polyneura. *Resultats Scientifiques du Voyage de Ch. Alluaud et R. Jeannel en Afrique Orientale 1911-1912* (*Diptera*), 3: 68-99.

Riek, E.F., 1954. The fossil Diptera of the Tertiary Redbank Plains Series, Queensland. *Linnaean Society of New South Wales* (*Proceedings*), 79 (3-4): 58-60.

Rohdendorf, B., 1974. *The Historical Development of Diptera*. University of Alberta Press; Alberta.

Rolfe, W.D.I., 1980. Early Invertebrate Terrestrial faunas. *In* Panchen, A.L. (ed.). *The Terrestrial Environment and the Origin of Land Vertebrates*. Academic Press, London.

Savtshenko, E.N., 1966. [*Fauna Ukraini*, 14 (1): 63-88]. Translation by Theowald, B. and Theischinger, G., 1979. Phylogenie und systematik der Tipulidae. *Tijdschrift voor Entomologia*, 122: 91-126.

Savtchenko, E.N., 1983. Diptera. Volume 2, part 1-2. Crane flies of the family Tipulidae. General part and beginning of the systematic part. *Fauna SSSR* (*New Series*) 127: 1-585 (in Russian).

Scagel, R.F., Bandoni, R.J., Rouse, G.E., Schofield, W.B., Stein, J.R. & Taylor, T.M.C., 1969. *Plant Diversity: An Evolutionary Approach*. Wadsworth Publ. Co., Belmont, California. 460p.

Schopf, T.J.M., 1982. A critical assessment of punctuated equilibria. I. Duration of taxa. *Evolution*, 36 (6): 1144-1157.

Scudder, S.M., 1894. Tertiary Tipulidae, with Special Reference to those of Florissant, Colorado [Abstract]. *American Journal of Science*, Series 3: 481.

Smith, K.G.V., 1969. The Empididae of Southern Africa. *Annals of the Natal Museum*, 19: 1-347.

Smith, K.G.V., 1980. 32. Family Empididae. *In* R.W. Crosskey (Ed.). *Catalogue of the Diptera of the Afrotropical Region* 431-442. British Museum (natural History): London.

Smith, R.M., 1986. Sedimentation and Palaeoenvironments of Late Cretaceous Crater-Lake Deposits in Bushmanland, South Africa. *Sedimentology*, 33: 369-386.

Spahr, U., 1985. Erganzungen und Berichtungen zu R. KEILBACHs Bibliographie und Liste der Bernsteinfossilien - Ordnung Diptera. *Stuttgarter Beitragung zur Naturkunde Serie B (Geologie und Palaeontologie)*, 111: 1-146.

Stanley, S.M., 1982. Macroevolution and the fossil record. *Evolution*, 36 (3): 460-473.

Steffan, W.A., 1981. 15. Sciaridae. *In* McAlpine, J.F. *et al. eds*. *Manual of Nearctic Diptera*. Vol. 1. Ottawa: Agriculture Canada. (monograph 27). pp 247-256.

Steyskal, G.C., 1974. Recent Advances in the Primary Classification of the Diptera. *Annals of the Entomological Society of America*, 67: 513-517.

Steyskal, G.C. & Knutson, L.V., 1981. 47. Empididae. *In* McAlpine, J.F. *et al. eds*. *Manual of Nearctic Diptera*. Vol. 1. Ottawa: Agriculture Canada. (monograph 27). pp 607-625.

Stuckenberg, B.R., 1974. A Genus and two New Species of Athericidae (Diptera) in Baltic Amber. *Annals of the Natal Museum*, 21: 455-464.

Stuckenberg, B.R., 1975. New Fossil Species of *Phlebotomus* and *Haematopota* in Baltic Amber (Diptera: Psychodidae, Tabanidae). *Annals of the Natal Museum*, 21: 649-673.

Stuckenberg, B.R., 1980. 22. Family Rhagionidae. *In* R.W. Crosskey (Ed.). *Catalogue of the Diptera of the Afrotropical Region* 309-311. British Museum (Natural History): London.

Theowald, B.R., 1977. Die Tipuliden von Makaronesien (Insecta: Diptera, Tipulidae). Ein Systematischer und Zoogeographischer Beitrag zur Kenntnis von Inselfaunen. Beaufortia, 26: 153-204.

Thomas, B.A. & Spicer, R.A., 1986. The evolution and Palaeobiology of land plants. T.R. Dudley (ed.), Dioscorides Press, London, Sydney, 309pp.

Tillyard, R.J., 1929. Permian Diptera from Warner's Bay, New South Wales. Nature, 123: 778-779.

Tillyard, R.J., 1937. The ancestors of the Diptera. Nature, 139: 66-67.

Tuomikoski, R., 1966. The Ocydromiinae group of subfamilies (Diptera, Empididae). Annale Entomologica Fennoscandia, 32 (4): 282-294.

Vockeroth, J.R., 1981. 14. Mycetophilidae. In McAlpine, J.F. et al. eds. Manual of Nearctic Diptera. Vol. 1. Ottawa: Agriculture Canada. Monograph 27). pp 223-246.

Walton, J., 1936. On the factors which influence the external form of fossil plants, with descriptions of the foliage of some species of the Palaeozoic Equisetalean Genus Annularia Sternberg. Philosophical transactions of the Royal Society of London (Series B), 226: 219-237.

Waters, S.B., 1989a. A Cretaceous Dance Fly (Diptera: Empididae) From Botswana. Systematic Entomology, 14: 233-241.

Waters, S.B., 1989b. A new hybotine fly from the Cretaceous of Botswana. Palaeontology, 32: 657-667.

Wighton, D.C., 1980. New species of Tipulidae from the Paleocene of Central Alberta, Canada. Canadian Entomologist, 112: 621-628.

Williams, G.C. 1966. Adaptation and Natural Selection. Princeton University Press, Princeton, New Jersey.

CRETACEOUS DIPTERA FROM ORAPA, BOTSWANA

VOLUME TWO

SASKIA WATERS

A DISSERTATION SUBMITTED TO THE FACULTY OF SCIENCE, UNIVERSITY OF THE WITWATERSRAND, JOHANNESBURG, FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

JOHANNESBURG, 1990

FIGURE 1

Map of Southern Africa showing geographical location of Orapa. Inset: Details of the Orapa region.

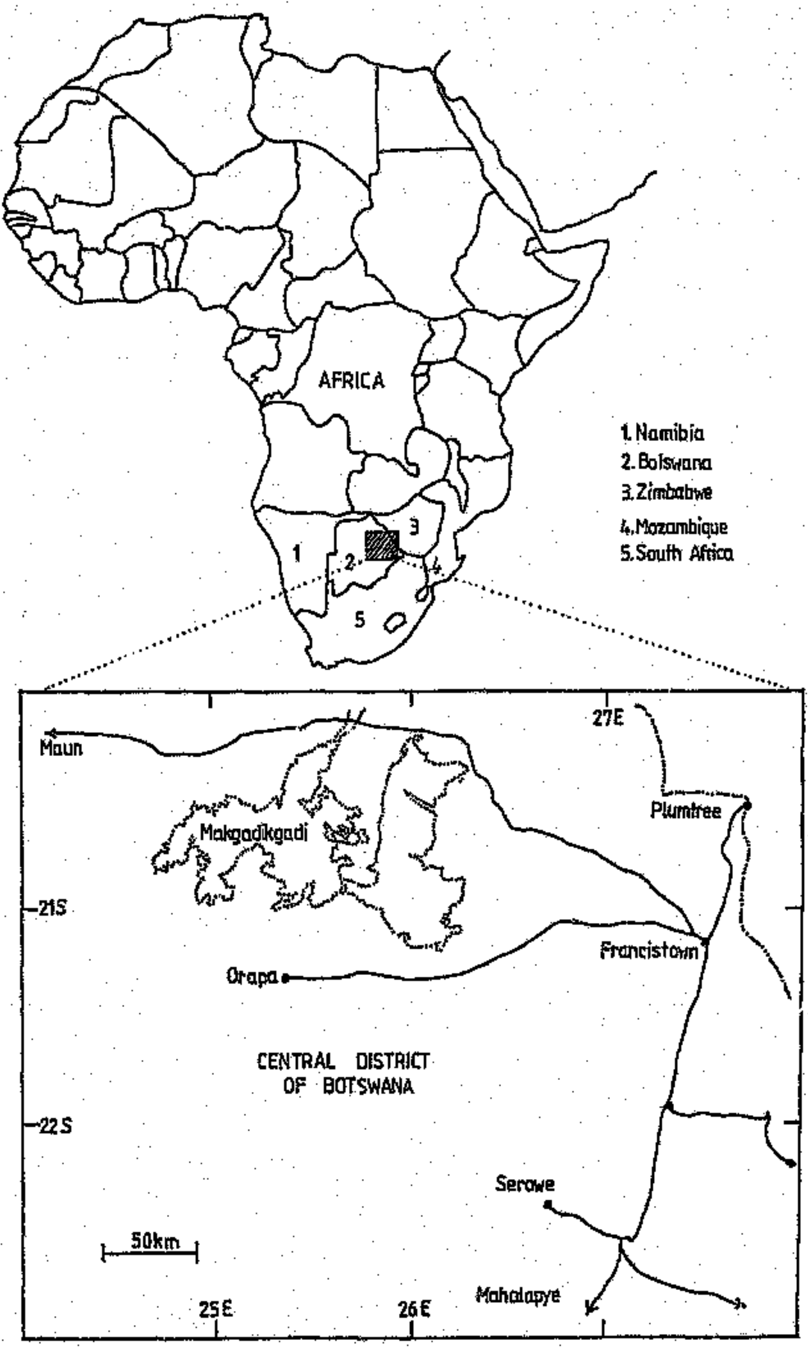

AFRICA
1. Namibia
2. Botswana
3. Zimbabwe
4. Mozambique
5. South Africa
1
2
3
4
5
Maun
27E
Plumtree
Makgadikgadi
21S
Francistown
Orapa
CENTRAL DISTRICT
OF BOTSWANA
22S
Serowe
50km
Mahalapye
25E
26E

FIGURE 1

FIGURE 2

Plan of the Orapa Mine 2125 A/K1 showing restricted area of fossiliferous sediments within the pipe.

——	Outline of the Orapa pipe.
▨	TKB (Exposed tuffaceous kimberlitic breccia).
░	Total area of shales and sandstones within the mine.
▒	Fossiliferous material was collected from this area - from various sites at various different levels. (These levels change continuously as excavation takes place).

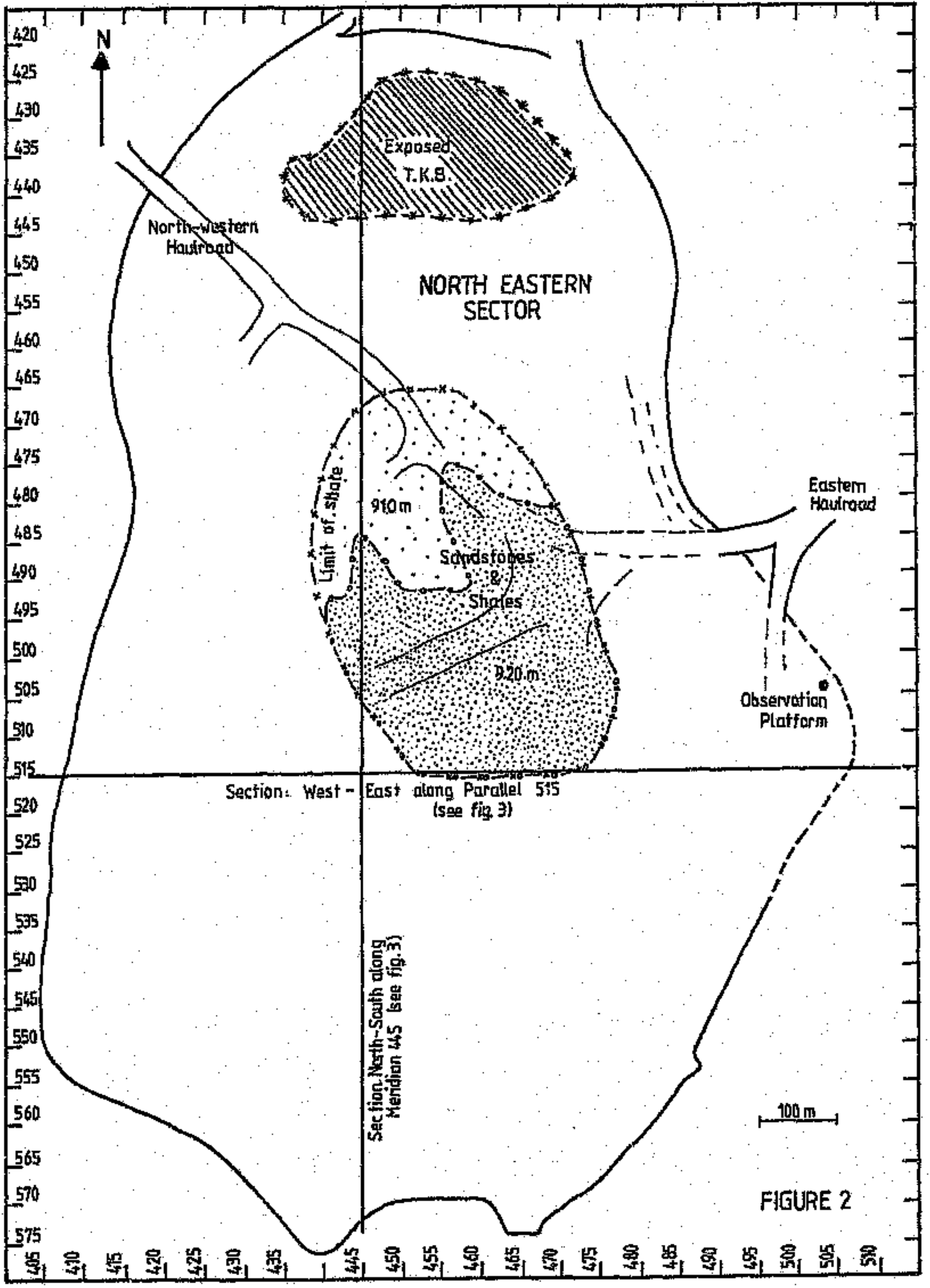

N
Exposed
T.K.B.
North-western
Haulroad
NORTH EASTERN
SECTOR
Limit of shale
910 m
Sandstones
&
Shales
920 m
Eastern
Haulroad
Observation
Platform
Section: West - East along Parallel 515
(see fig. 3)
Section North-South along
Meridian 445 (see fig. 3)
100 m
420
425
430
435
440
445
450
455
460
465
470
475
480
485
490
495
500
505
510
515
520
525
530
535
540
545
550
555
560
565
570
575
405
410
415
420
425
430
435
445
450
455
460
465
470
475
480
485
490
495
500
505
510

FIGURE 2

FIGURE 3

A 3-Dimensional representation of the north-eastern sector of the Orapa pipe 2125 A/K1 as it is at present, 1989, showing surface features and vertical sections along Meridian 445 and Parallel 515.

SURFACE FEATURES

▭ 10m Elevation.

◌ Limit of exposed TKB (1989).

◌ Limit of sandstone and shale area.

◍ Limit of fossil collection sites.

VERTICAL SECTIONS

▒ Sandstones and shales - fossil bearing material.

▦ Mass flow deposits <15% basalt clasts.

▥ Mass flow deposits and breccias >20% basalt clasts.

▨ Mass flow deposits <5% basalt clasts.

▩ Interbedded mass flow deposits, relatively unaltered.

⁂ TKB - diamond bearing tuffaceous kimberlitic breccia.

▓ Basalt wall rock.

▤ Ntane Sandstone.

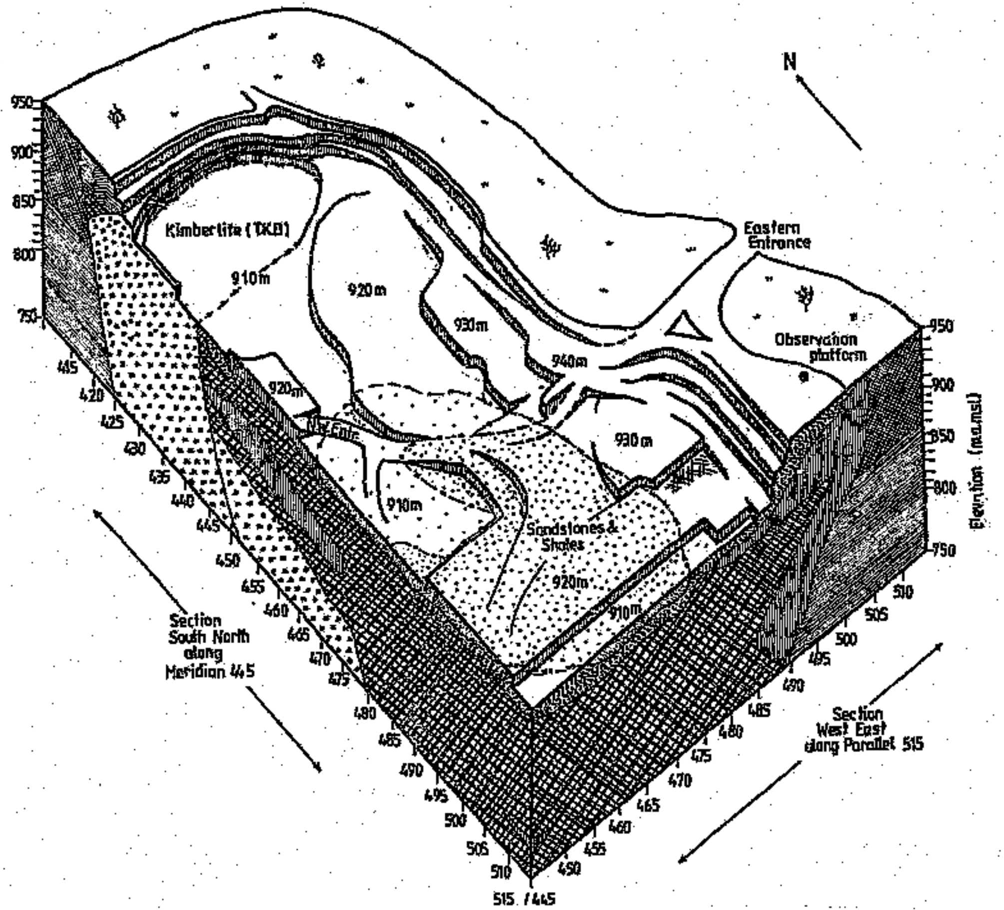

N
Kimberlite (TKB)
910m
920m
930m
940m
920m
W Entr.
930m
910m
Sandstones & Shales
920m
910m
Eastern Entrance
Observation platform
950
900
850
800
750
445
420
425
430
435
440
445
450
455
460
465
470
475
480
485
490
495
500
505
510
515 / 445
450
455
460
465
470
475
480
485
490
495
500
505
510
950
900
850
800
750
Elevation (m a.msl)
Section South North along Meridian 445
Section West East along Parallel 515

FIGURE 3

FIGURE 4

A reconstruction of Ora[illegible] during the Cretaceous including surface and cross-sectional data. The figure represents the north-eastern sector of the erupted pipe and spans an area of about 700m x 500m. The illustration shows a lushly vegetated crater of loose rocky ground with a crater lake at its centre; it is indicated below where the fossiliferous material was found.

(a) Volcanic cone: Volcanogenic and talus slope deposits. Dip >20.
(b) Debris flow deposits: dip 5.
(c) Granular mass flows: dip <5. Fossil wood fragments found here, as well as a few insect remains.
(d) Sedimentation within the lake with plant fragments and insect remains. Plant fragments occured more frequently in top layers suggesting crater vegetation developed slowly.
(e) Wave action on shore line: aggregations of insects were found here.
(f) Surrounding vegetation consisting of pteridophytes, conifers and angiosperms.

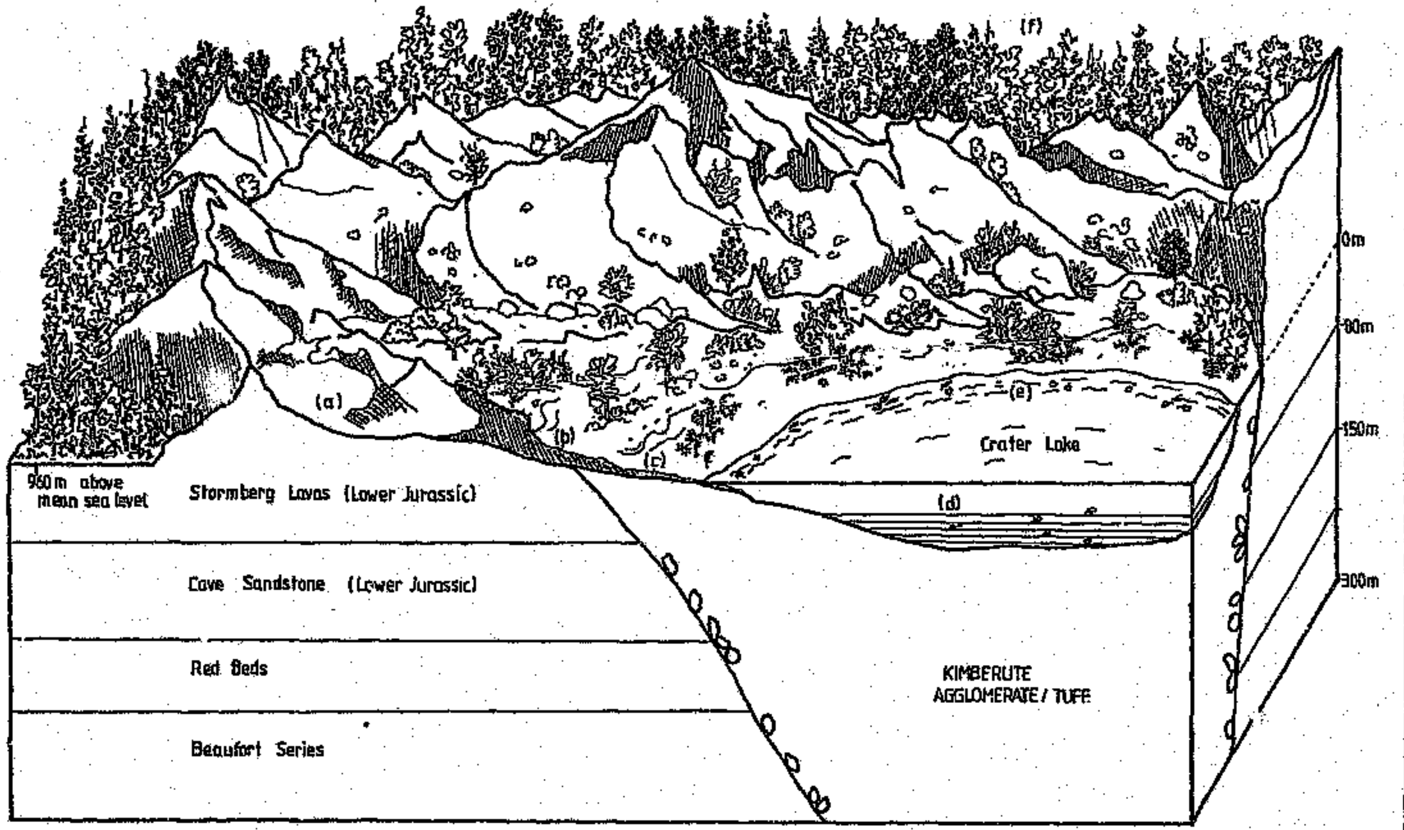

(f)
(a)
(b)
(c)
(e)
Crater Lake
(d)
960 m above mean sea level
Stormberg Lavas (Lower Jurassic)
Cave Sandstone (Lower Jurassic)
Red Beds
Beaufort Series
KIMBERLITE AGGLOMERATE / TUFF
0m
80m
150m
300m

FIGURE 4

FIGURE 5

A generalised dipteran *Tabanus americanus* Forster, to show orientation and anatomical planes and general parts (in part after McAlpine, 1981). Inset: vertical section through distal portion of right mid tibia to show external surfaces.

Abbreviations: RFL, right fore leg; LFL, left fore leg; RML, right middle leg; LML, left middle leg; RHL, right hind leg; LHL, left hind leg; RW, right wing; LW, left wing; a, anterior; av, anteroventral; ad, anterodorsal; d, dorsal; p, posterior; pd, posterodorsal; pv, posteroventral; v, ventral.

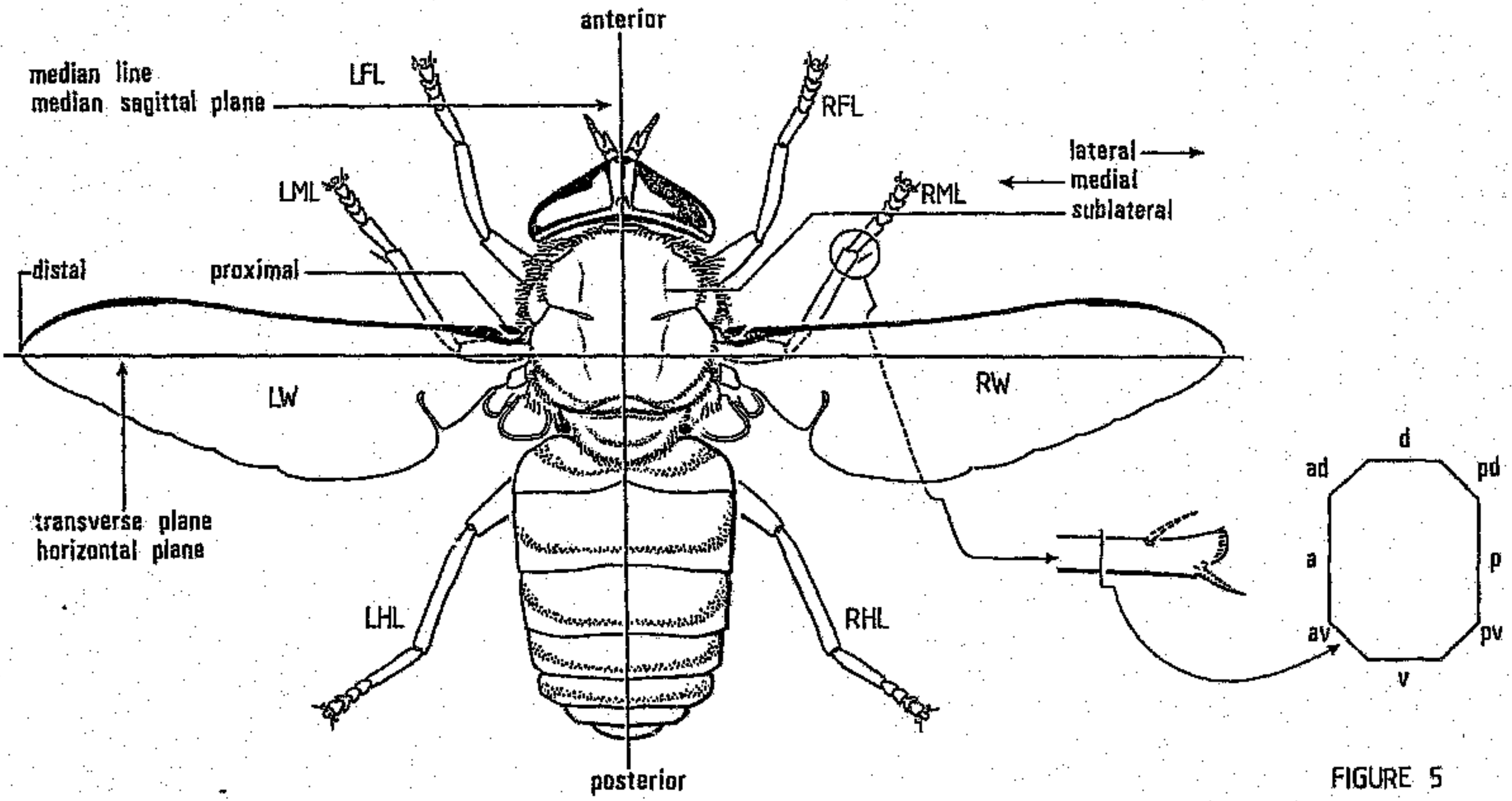

anterior
median line
median sagittal plane
LFL
RFL
LML
RML
lateral
medial
sublateral
distal
proximal
LW
RW
transverse plane
horizontal plane
d
ad
pd
a
p
av
pv
v
LHL
RHL
posterior

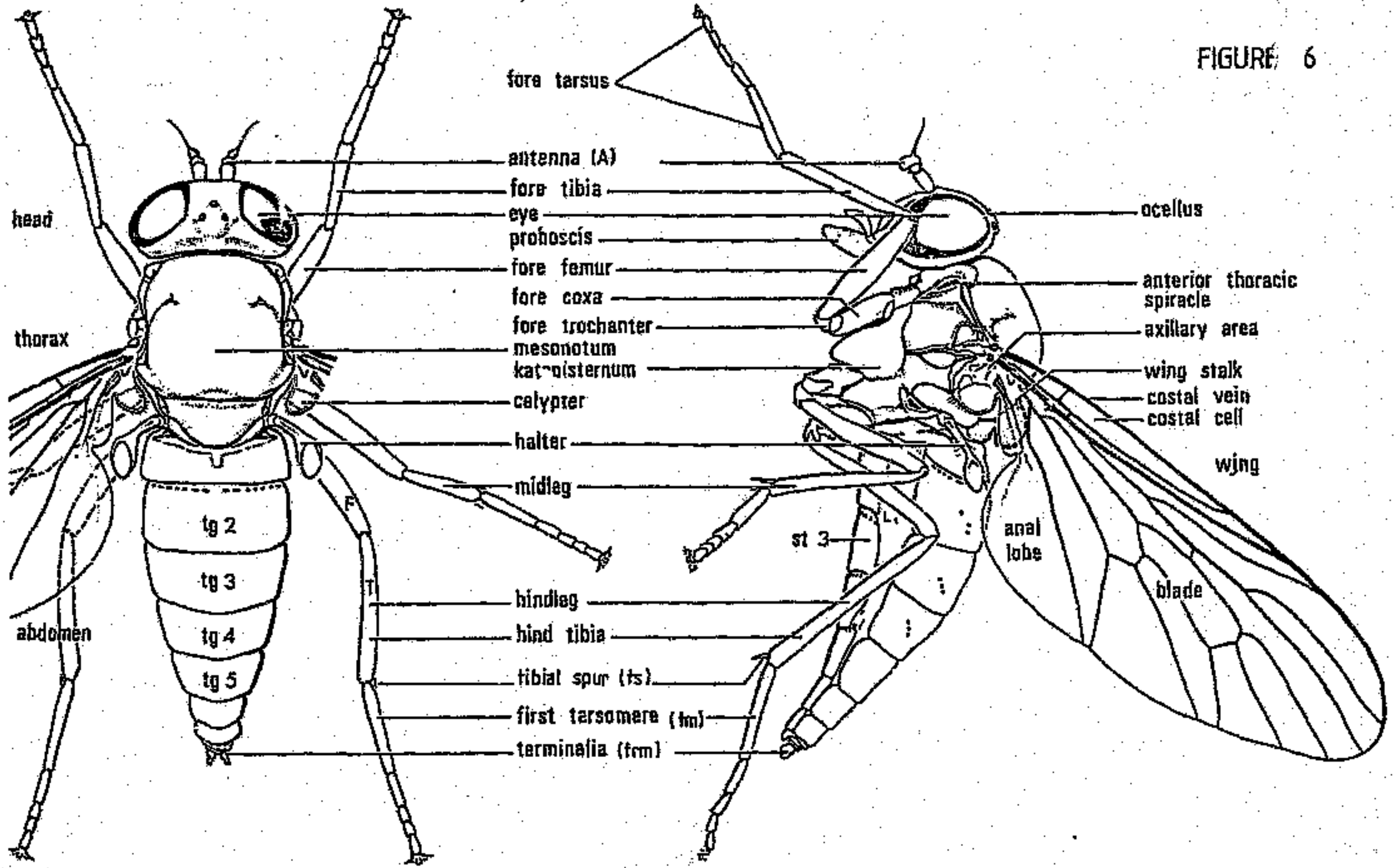
FIGURE 5

FIGURE 6

Main divisions and parts of the Diptera. (a) dorsal and (b) lateral view of Symphoromyia montana, Aldrich, to show main anatomical divisions and parts. (after McAlpine, 1981).

Abbreviations: st, sternite; tg, tergite; F, femur; T, tibia.

FIGURE 6



(a) Symphoromyia montana ♀

(b) Symphoromyia montana ♀

FIGURE 7

Morphology and Terminology of head and thorax of *Tipula trivittata* Say, lateral view (after McAlpine, 1981).

Abbreviations:

a bas, anterior basalare
abd tg, abdominal tergite
anatg, anatergite
anepm, anepimeron
anepst, anepisternum
aprn, antepronotum
a spr, anterior spiracle
cerv scl, cervical sclerite
comp eye, compound eye
cx, coxa
flgm, flagellomere
hlt, halter
kepm, katepimeron
kepst, katepisternum
ktg, katatergite
lbl, labellum
l par sut, lateral parapsidal suture
ltg, laterotergite
mr, meron
mtanepst, metanepisternum
mtepm, metepimeron
mtg, mediotergite
mtkepst, metakatepisternum
mtn, metanotum
patg, paratergite
p bas, posterior basalare
ped, pedicel
plp, palpus
plrtrcn, pleurotrochantin
plr wg proc, pleural wing process
pprn, postpronotum
presct, prescutum
presct pit, prescutal pit
presct sut, prescutal suture
prn, pronotum
prpl, propleuron
prst, prosternum
rst, rostrum
sbal scl, subalar sclerite
scp, scape
sct, scutum
sctl, scutellum
trn sut, transverse suture
wg, wing

FIGURE 7

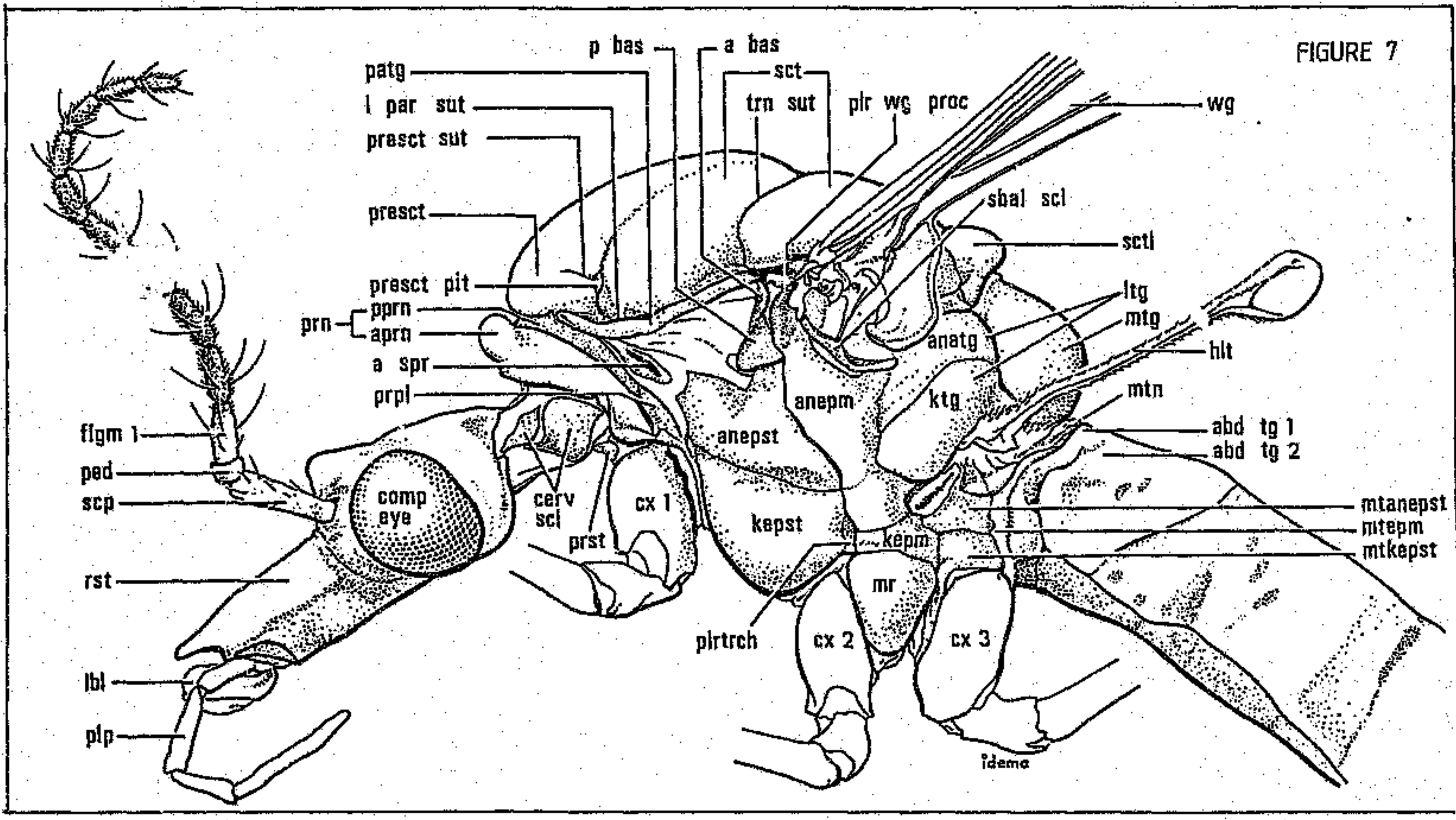

p bas
a bas
patg
sct
l par sut
trn sut
plr wg proc
wg
presct sut
sbal scl
presct
sctl
presct pit
ltg
prn
pprn
aprn
mtg
a spr
hlt
prpl
mtn
flgm 1
abd tg 1
abd tg 2
ped
scp
mtanepst
mtepm
mtkepst
rst
lbl
plp
comp eye
cerv scl
prst
cx 1
anepst
anepm
anatg
ktg
kepst
kepm
mr
plrtrch
cx 2
cx 3
idema

FIGURE 8

Ground plan of Dipteran wing (after McAlpine, 1981). Hypothetical primitive Diptera.

Abbreviations. Veins: A_1, A_2, branches of anal vein; C, costa; CuA_1, CuA_2, anterior branches of cubitus; CuP, posterior branch of cubitus; M_1, M_2, M_3, M_4, posterior (sectoral) branches of media; MA, anterior branch of media; R_1, anterior branch of radius; R_2, R_3, R_4, R_5, posterior (sectoral) branches of radius; Sc, subcosta. Cells: a_1, a_2, anal; bc, basal costal; bm, basal medial; br, basal radial; c, costal; cua, anterior cubital fork; cup, posterior cubital fork; d, discal; m_1, m_2, m_3, medial; r_1, r_2, r_3, r_4, r_5, radial; sc, subcostal. Crossveins: h, humeral; m-cu, medial cubital; m-m, medial, r-m, radial medial; sc-r, subcostal radial.

FIGURE 9

Ground plan of the venation of the Diptera (after Hennig, 1954 & 1981). Abbreviations as for figure 8.

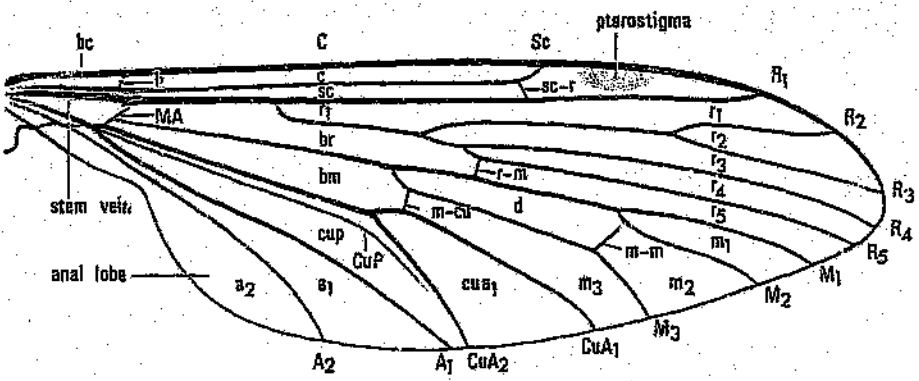


FIGURE 8

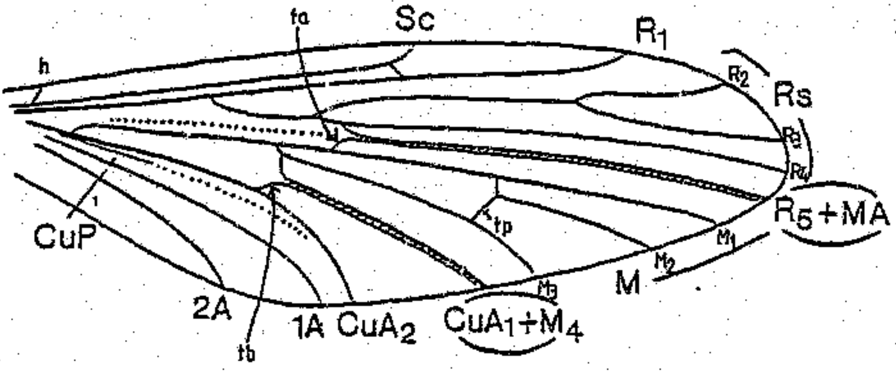


FIGURE 9

FIGURE 10

Phylogenetic scheme of relationships amongst the Diptera (after Hennig, 1981). 1, *Architipula radiata* Rohdendorf; 2, *Tanyderophryne*; 3. Architendipedidae; 4, *Rhaetomyia*, *Protorhyphus*, *Protolbiogaster*. A, Tipulomorpha ('Polyneura'); B, 'Oligoneura'; B1, Psychodomorpha; B2, unnamed group; B2a, Culicomorpha; B2b, Bibionomorpha + Brachycera.

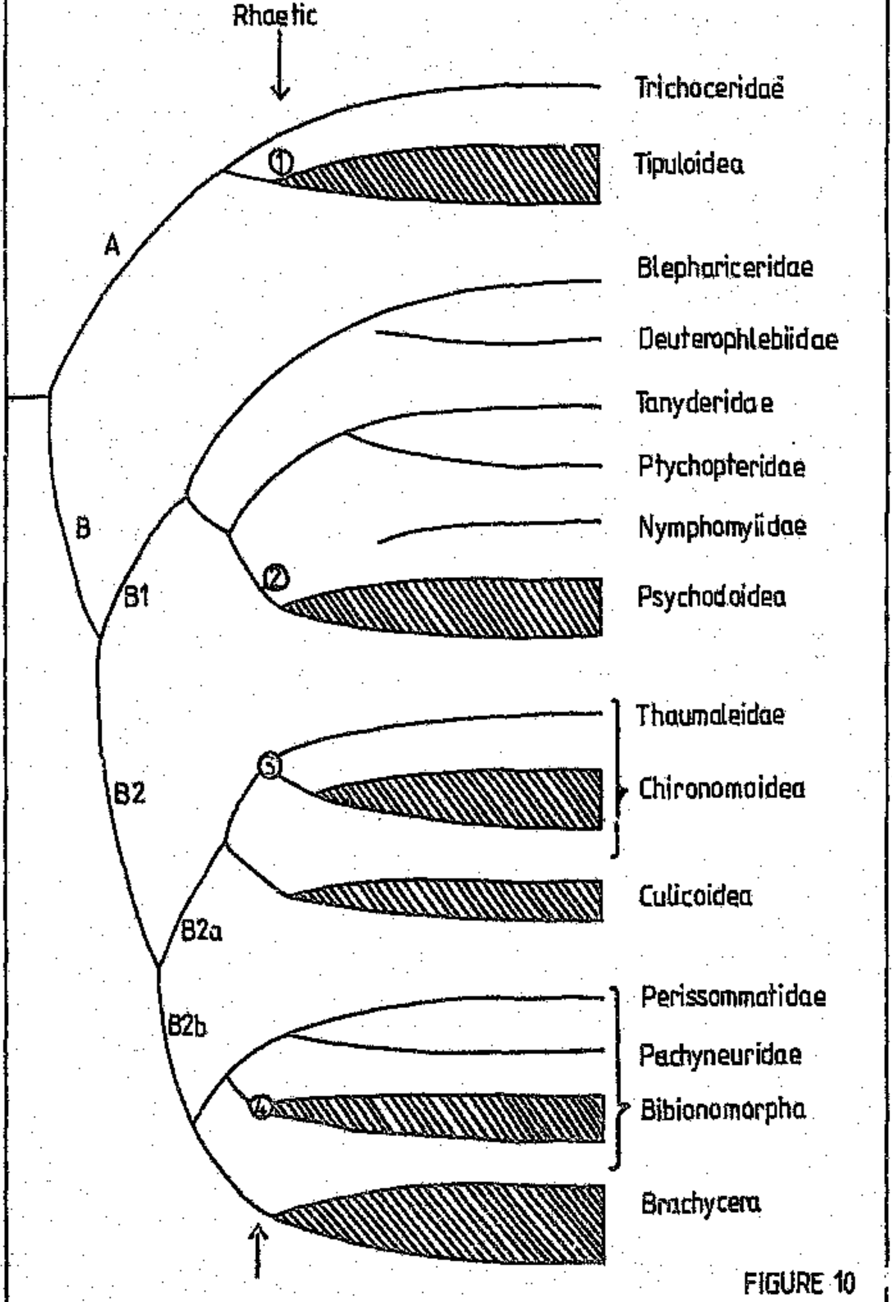

Rhaetic
Trichoceridae
Tipuloidea
①
A
Blephariceridae
Deuterophlebiidae
Tanyderidae
Ptychopteridae
Nymphomyiidae
Psychodoidea
②
B
B1
Thaumaleidae
Chironomoidea
③
B2
Culicoidea
B2a
Perissommatidae
Pachyneuridae
Bibionomorpha
④
B2b
Brachycera

FIGURE 10

FIGURES 11–14

Family TIPULIDAE

Subfamily LIMONIINAE

Tribe LIMONIINI

Genus Helius LePeletier & Serville 1828

Helius botswanensis sp. nov.

BP/2/26000a and b

11. Wing venation, combining details from both part and counterpart; scale bar = 0.5mm (x24.4).
12. Complete specimen; scale bar = 1mm (x5.3).
13. Rostrum, antennae and eyes; scale bar = 0.1mm (x87.0).
14. Details of the hypopygium; scale bar = 0.1mm (x58.8).

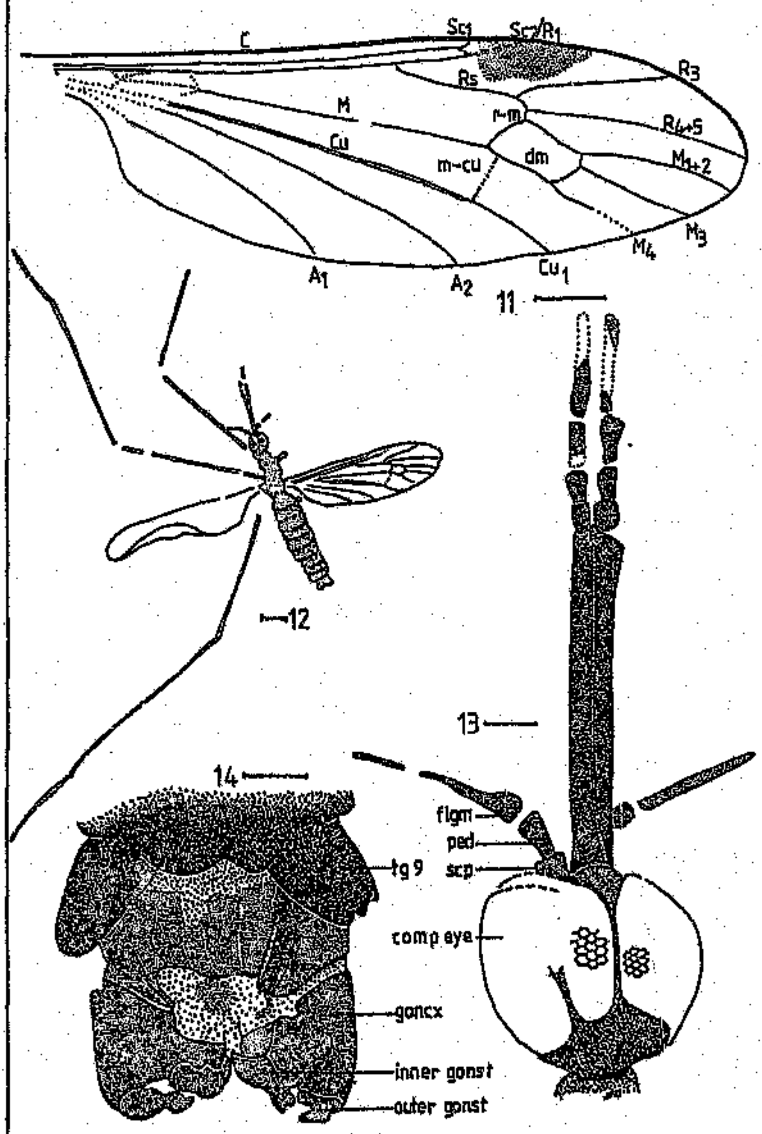

C
Sc1
Sc2/R1
R3
Rs
M
r-m
R4+5
Cu
dm
M1+2
m-cu
M3
M4
A1
A2
Cu1
11
12
13
14
flgm
ped
scp
tg 9
comp eye
goncx
inner gonst
outer gonst

FIGURE 11-14

FIGURE 15

Family TIPULIDAE

SPECIMEN 1: (BP/2/27578a - part), whole specimen (x17.3).

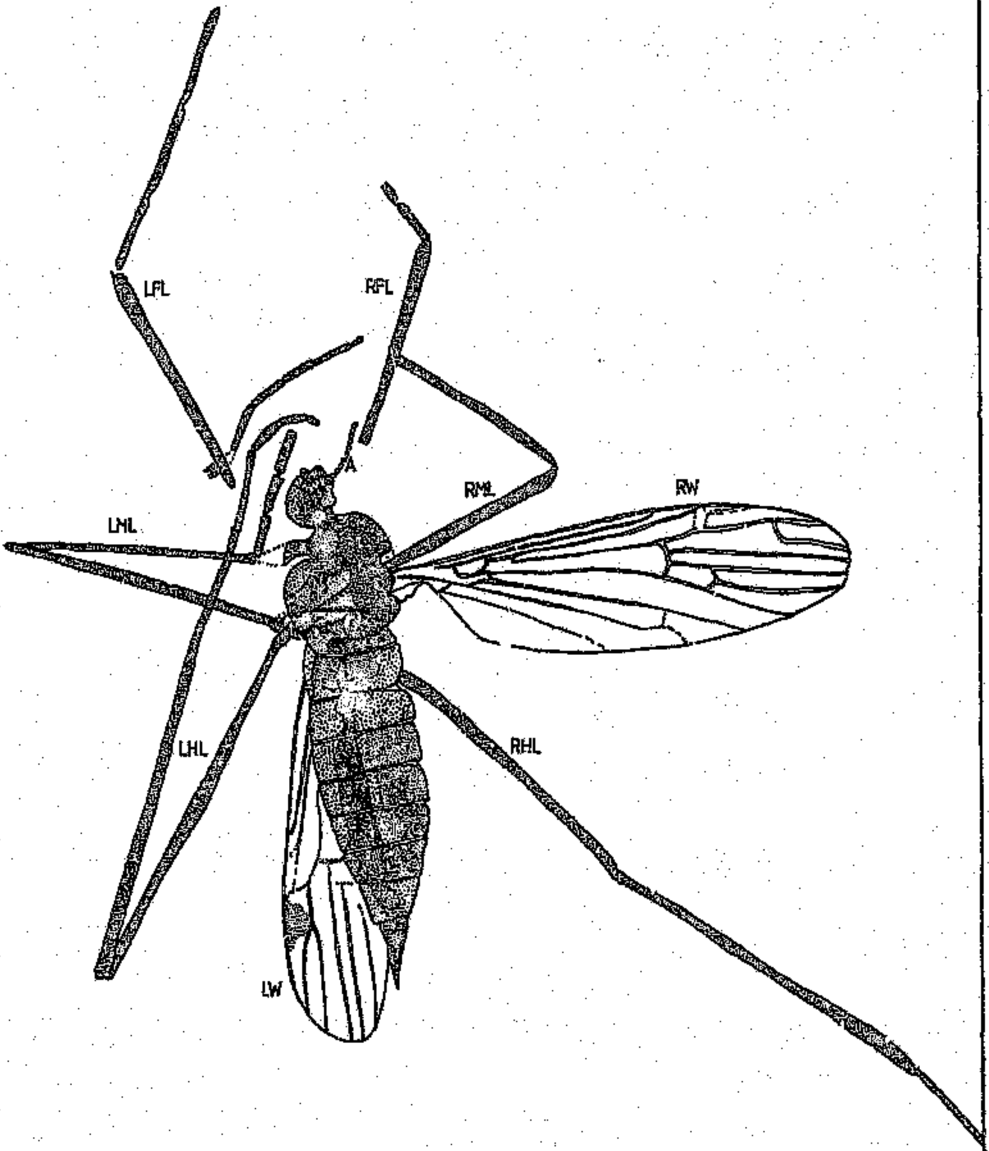


FIGURE 15

FIGURE 16

Family TIPULIDAE

SPECIMEN 1: (BP/2/27578b - counterpart), whole specimen (x15.5).

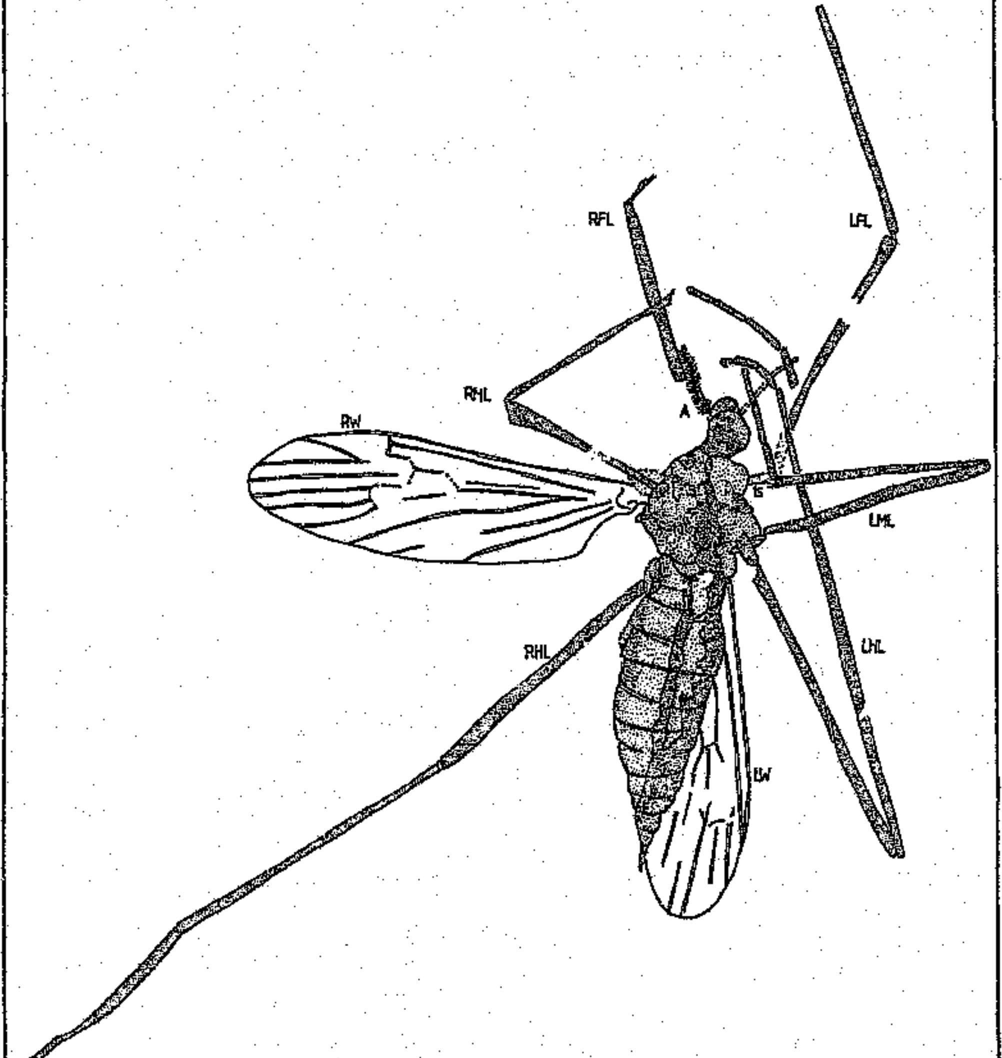


FIGURE 16

FIGURE 17

Family TIPULIDAE

SPECIMEN 1: (BP/2/27578a - part), wing (x54.3).

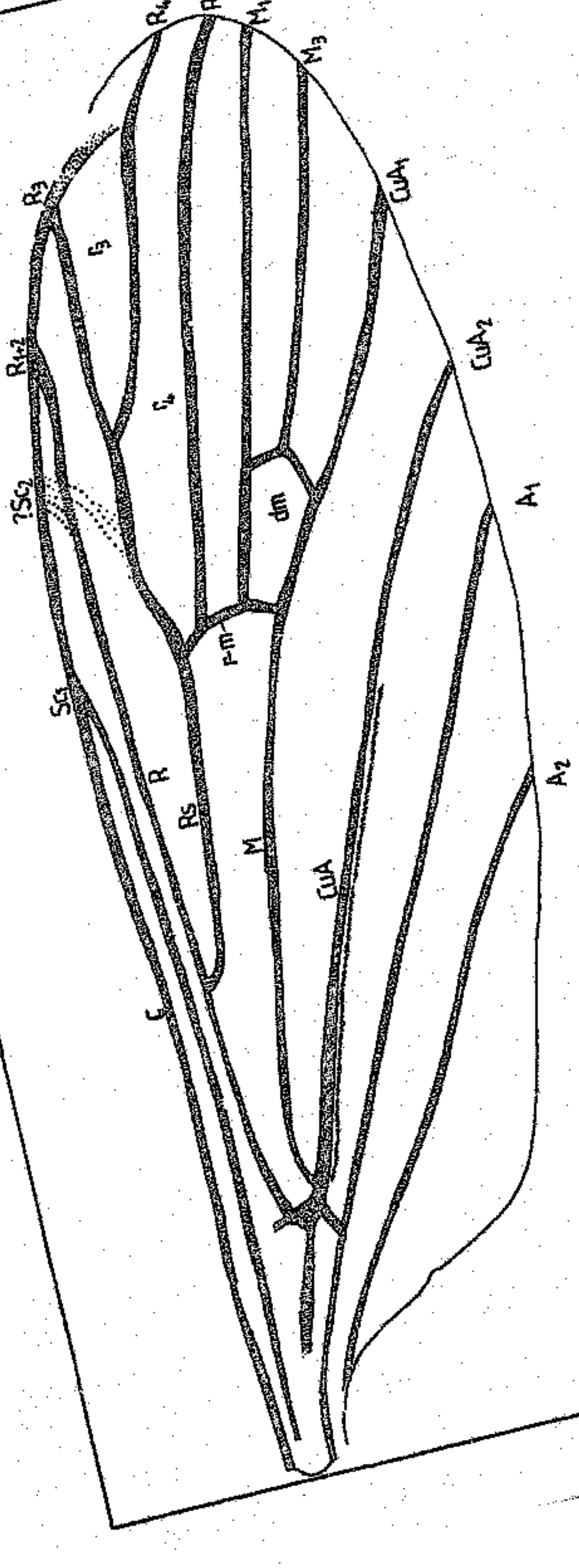


FIGURE 17

FIGURE 18

Family TIPULIDAE

SPECIMEN 1: (BP/2/27578b - counterpart), wing (x51.3).

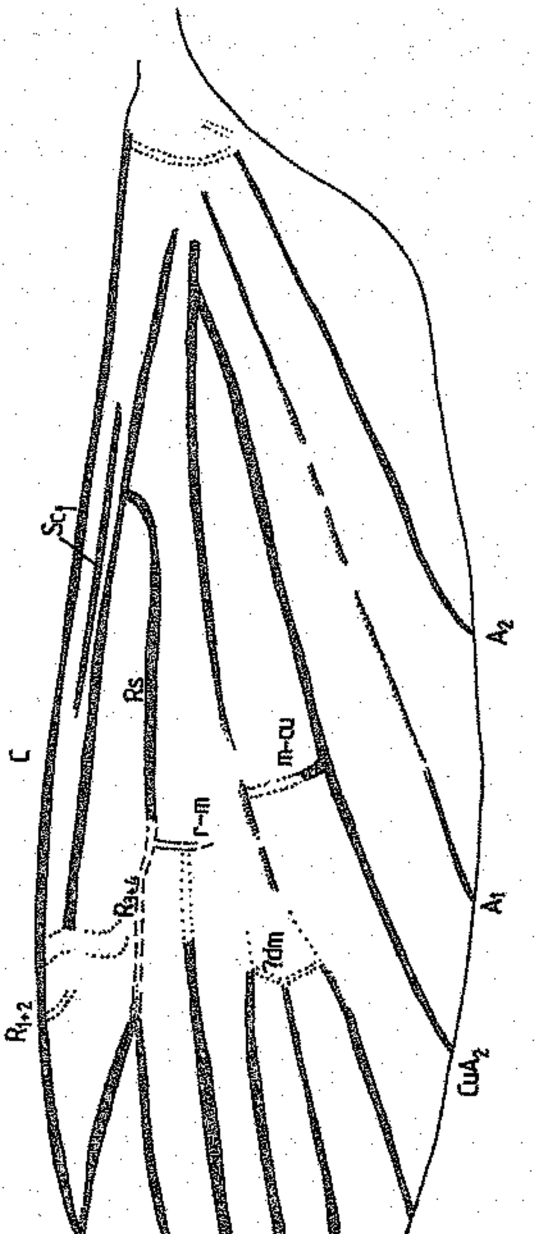


FIGURE 18

FIGURE 19

Family TIPULIDAE

SPECIMEN 2: (BP/2/25228), whole specimen (x24.0).

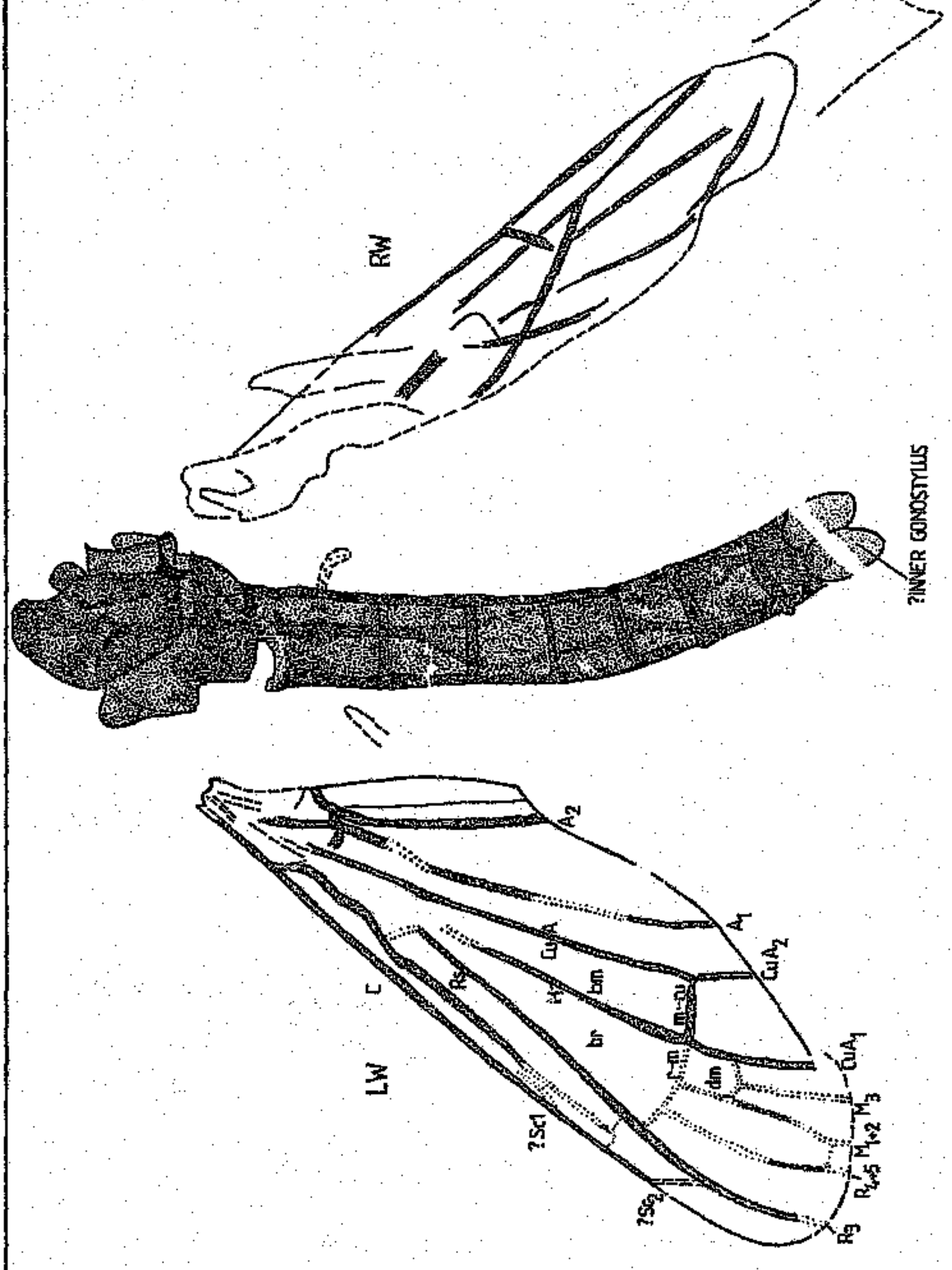

RW
?INNER GONOSTYLUS
LW
C
Rs
CuA
bm
br
m-cu
r-m
dm
A2
A1
CuA2
CuA1
M3
M1+2
R4+5
R3
?Sc1
?Sc2

FIGURE 19

FIGURE 20

Family TIPULIDAE

SPECIMEN 3: (BP/2/25843), whole specimen (x63.2).

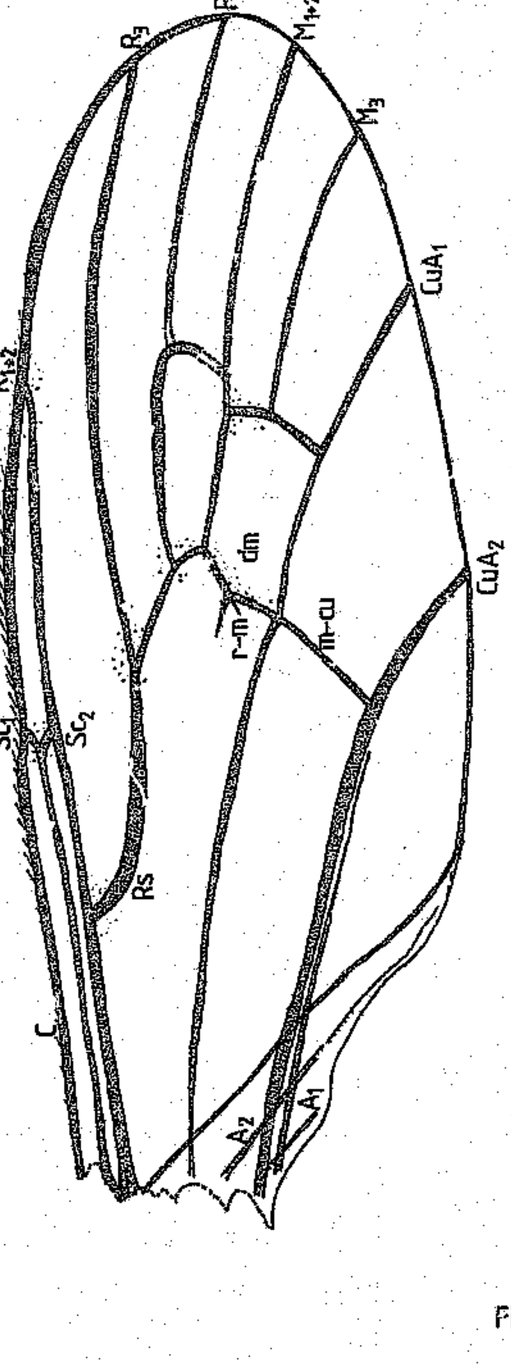


FIGURE 20

FIGURE 21

Atarba capensis Alexander

(after Alexander, 1964).

FIGURE 22

Limonia (*Dicranomyia* Stephens) *marleyi*

(after Alexander, 1917).

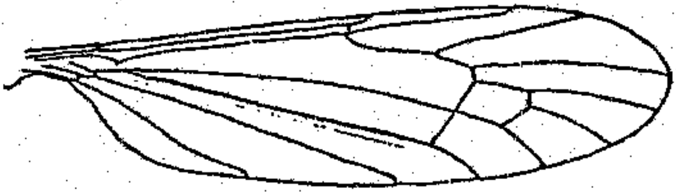


FIGURE 21

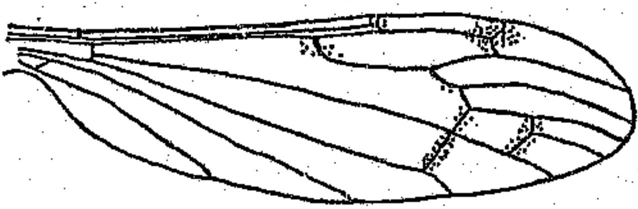


FIGURE 22

FIGURE 23

Family TIPULIDAE

SPECIMEN 4: (BP/2/25939), whole specimen (x19.8).

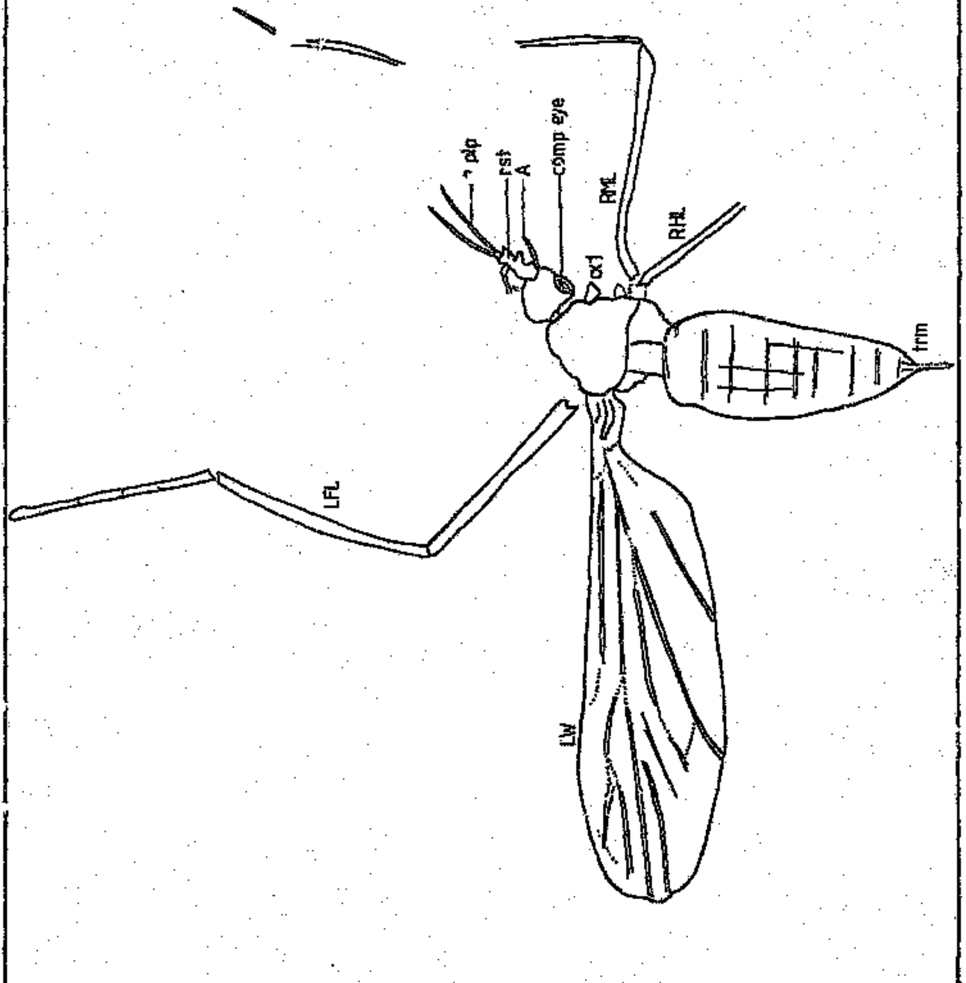


FIGURE 23

FIGURE 24

Family TIPULIDAE

SPECIMEN 4: (BP/2/25939), details of left wing (x36.7).

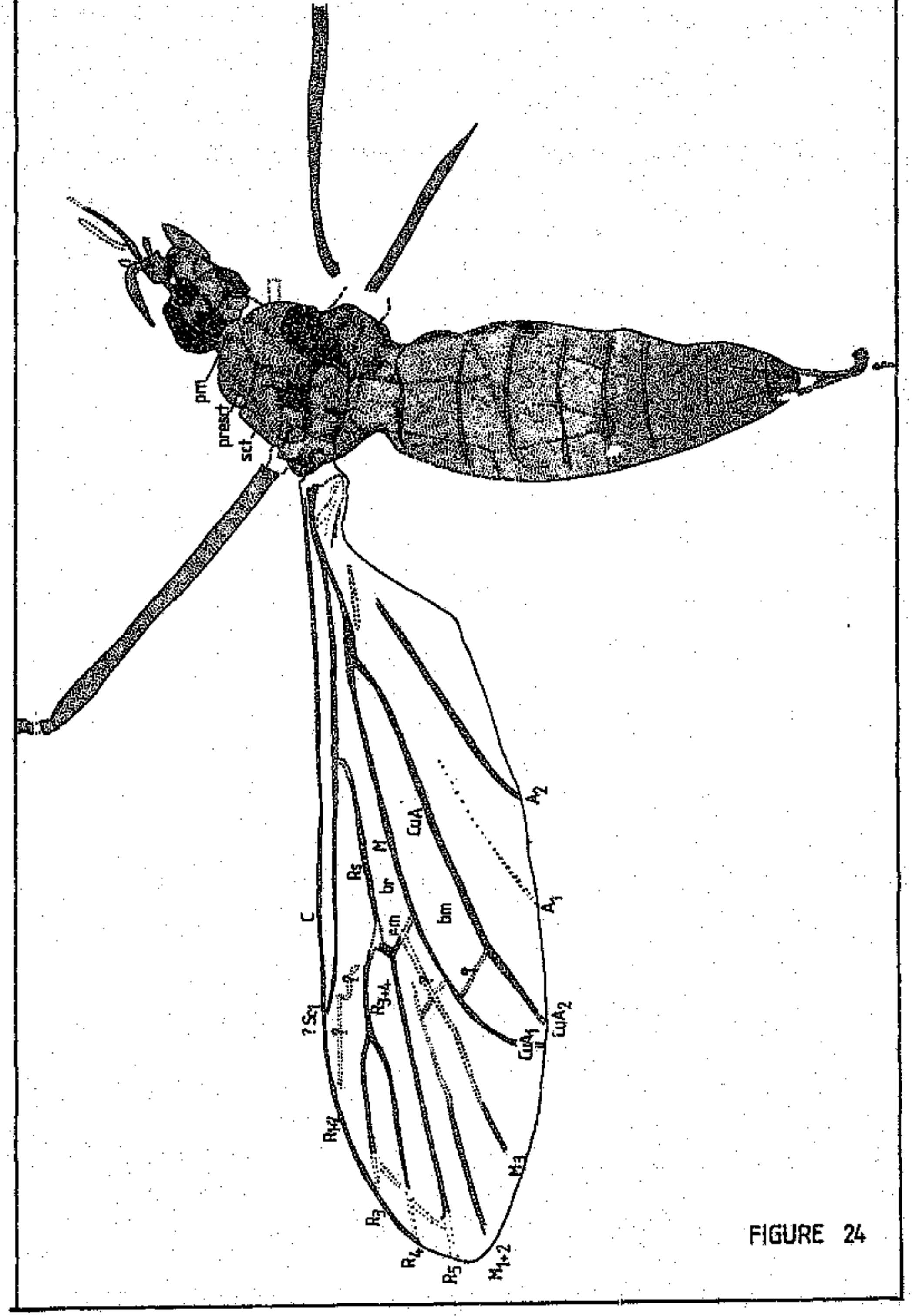

pm
presct
sct
C
Rs
M
br
CuA
bm
A2
A1
rm
?Sc1
R3+4
CuA1
CuA2
R1+2
M3
R3
R4
R5
M1+2

FIGURE 24

FIGURE 25

Family TIPULIDAE

SPECIMEN 5: (BP/2/25948), whole specimen (x20.8).

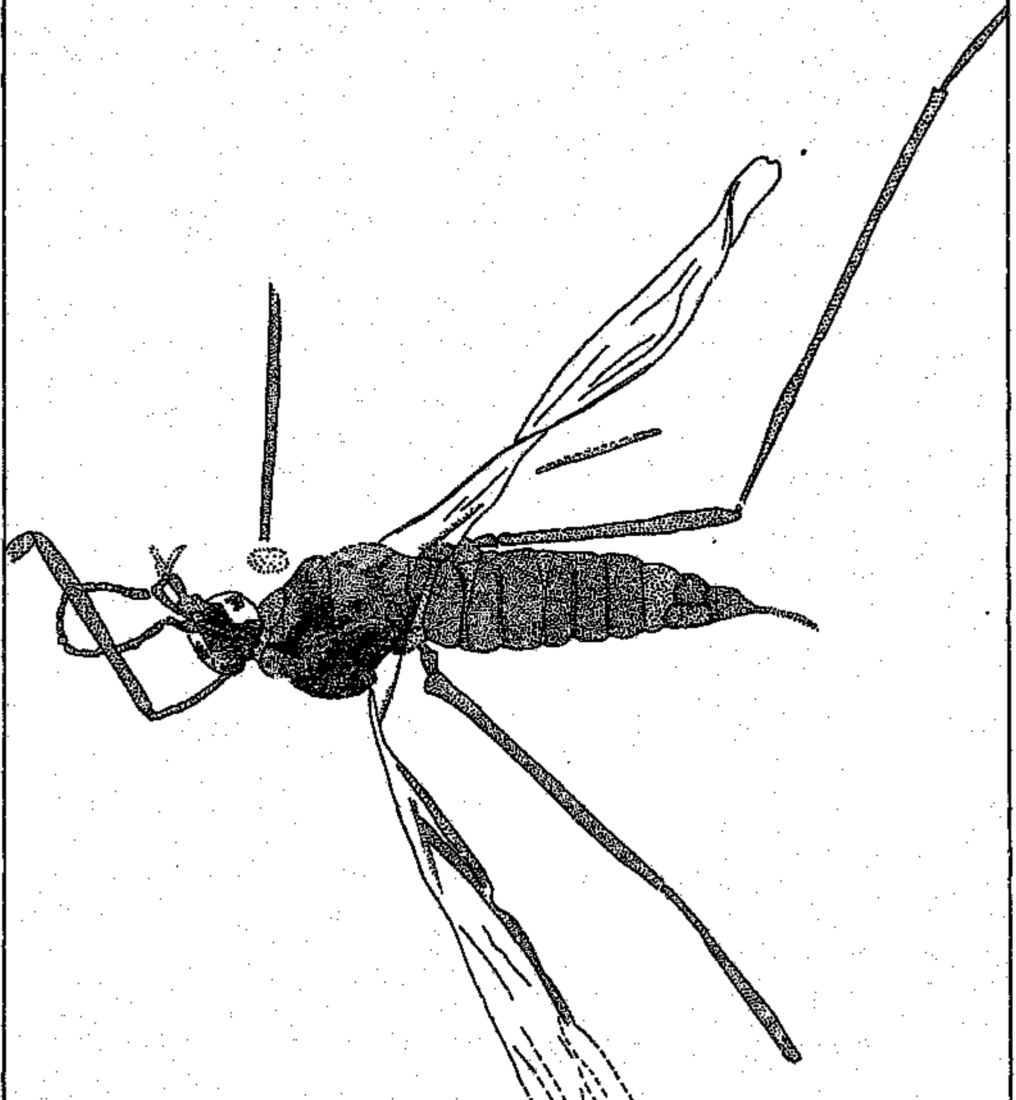


FIGURE 25

FIGURE 26

Family TIPULIDAE

SPECIMEN 5: (BP/2/25948), details of head and thorax (x32.1).

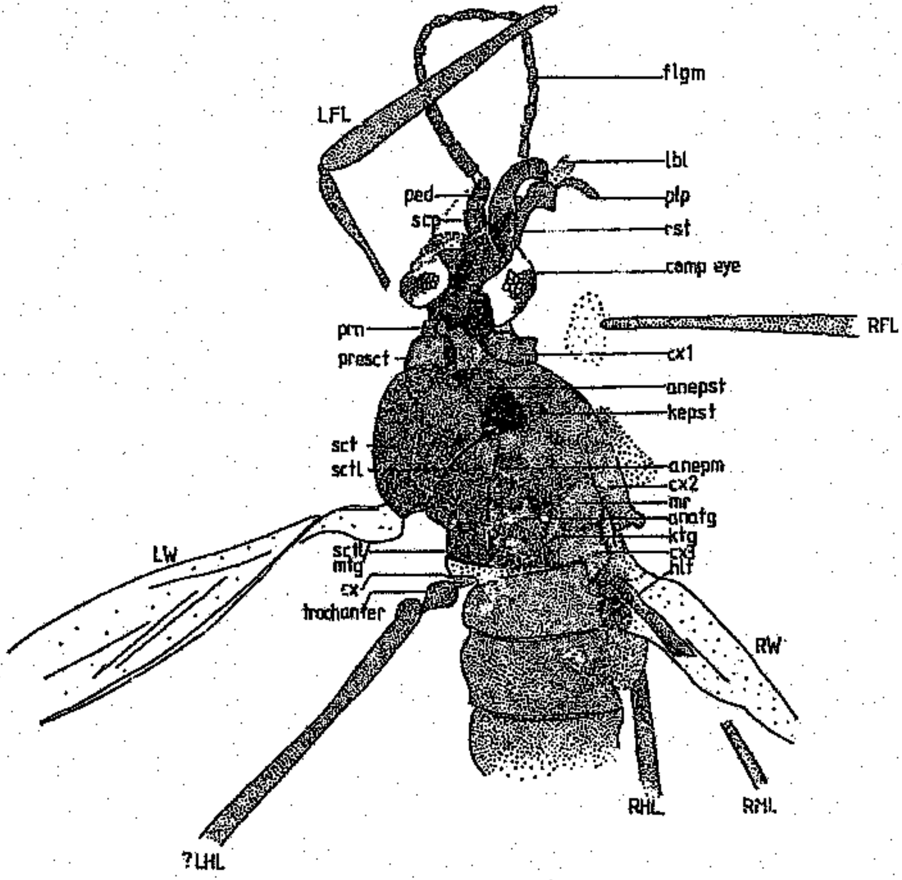

flgm
LFL
lbl
ped
plp
scp
rst
comp eye
RFL
pm
presct
cx1
anepst
kepst
sct
sctl
anepm
cx2
mr
anatg
ktg
LW
sctl
cx3
mtg
hlt
cx
trochanter
RW
RHL
RML
?LHL

FIGURE 26

FIGURE 27

Family TIPULIDAE

SPECIMEN 6; (BP/2/26717), whole specimen (x38.6).

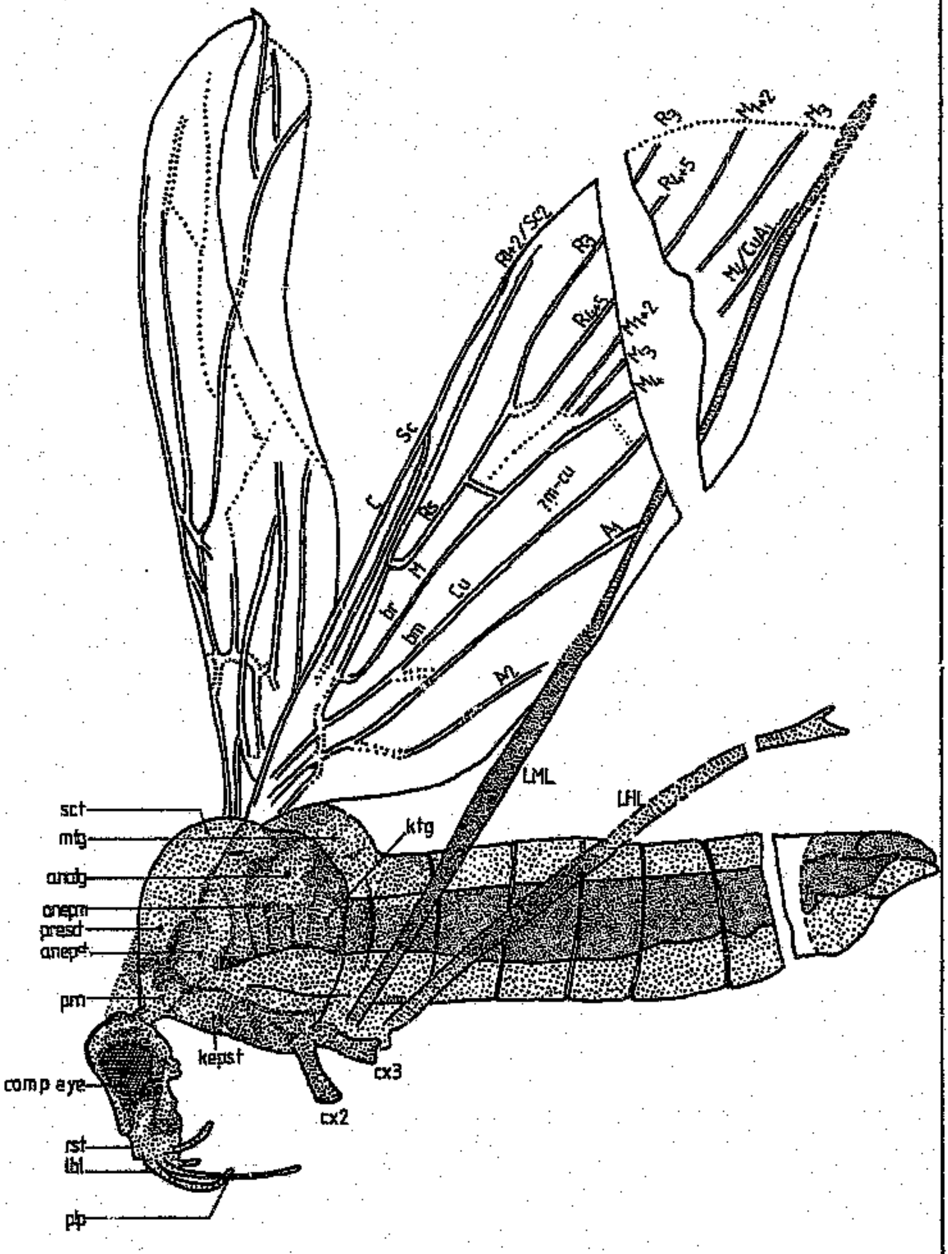

R3
M1+2
M3
R4+5
M4/CuA1
R1+2/Sc2
R3
R4+5
M1+2
M3
M4
Sc
C
Rs
dm-cu
A1
M
br
Cu
bm
A2
LML
LHL
sct
mtg
anctg
anepm
presct
anepst
pm
ktg
kepst
cx3
cx2
comp eye
rst
lbl
plp

FIGURE 27

FIGURE 26

Family TIPULIDAE

SPECIMEN 7: (BP/2/25871), whole specimen (x35.1).

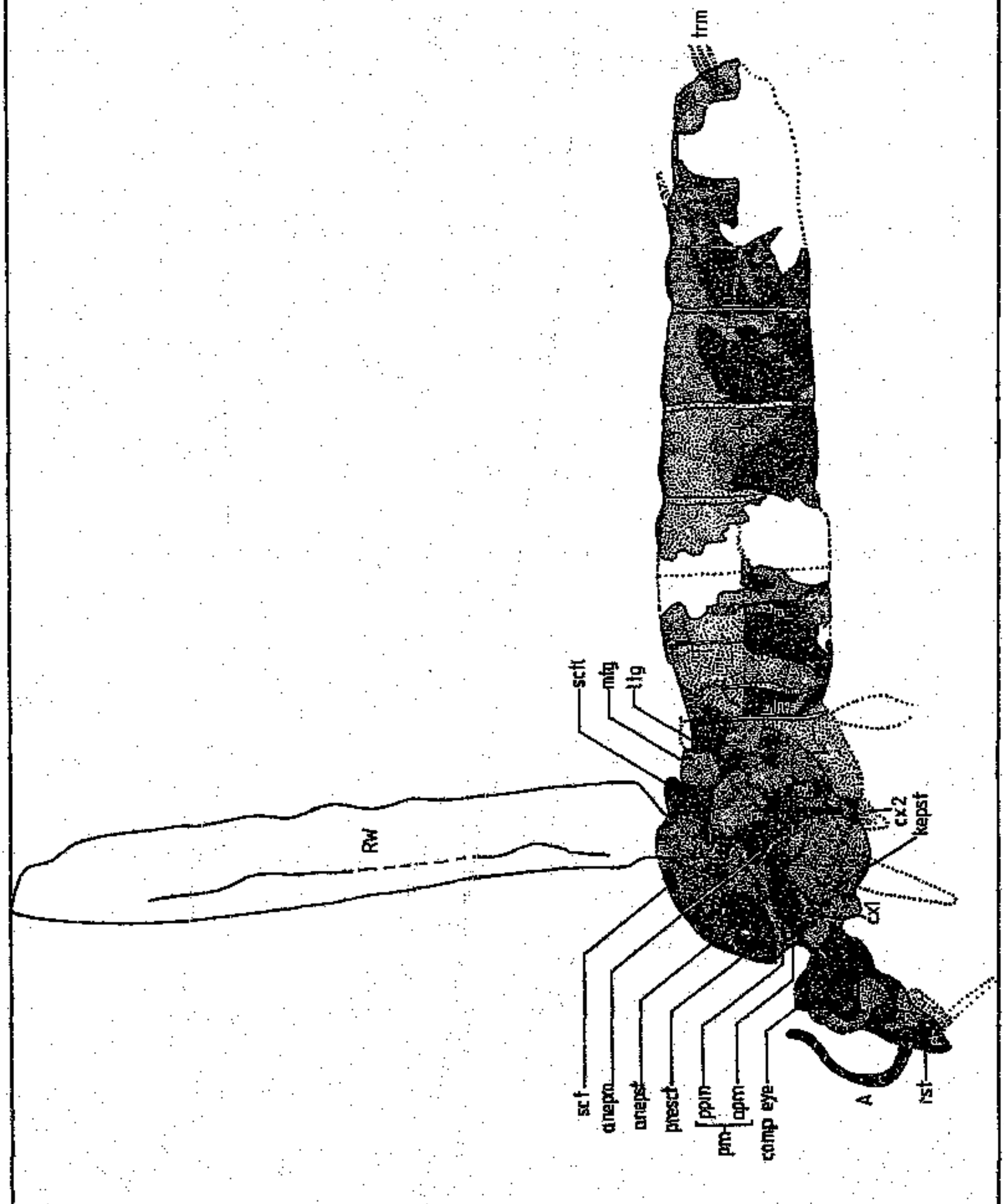

trm
sctl
mtg
ttg
Rw
cx2
kepst
cx1
sct
anepm
anepst
presct
ppm
apm
pm
comp eye
A
rst

FIGURE 28

FIGURE 29

Family TIPULIDAE

SPECIMEN 8: (BP/2/25919), whole specimen (x30.7).

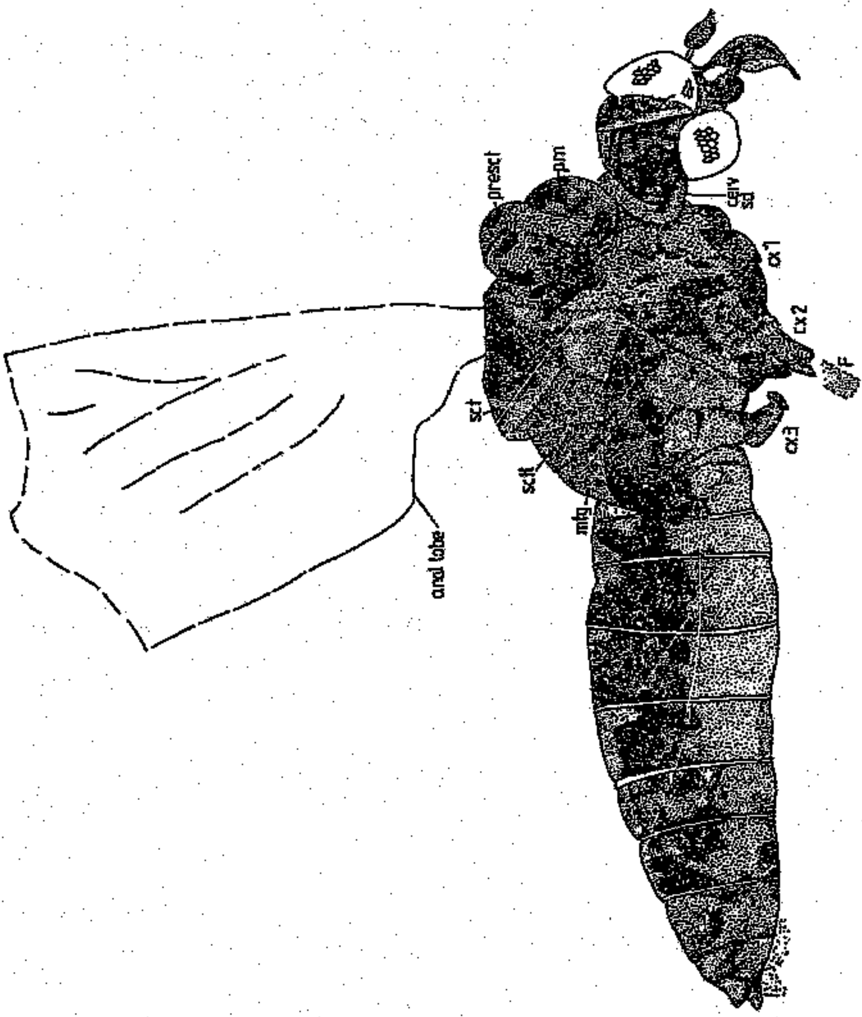


FIGURE 29

FIGURE 30

Family TIPULIDAE

SPECIMEN 8: (BP/2/25919), details of head (x68.1).

Abbreviations: lab, labium; hyphar, hypopharynx.

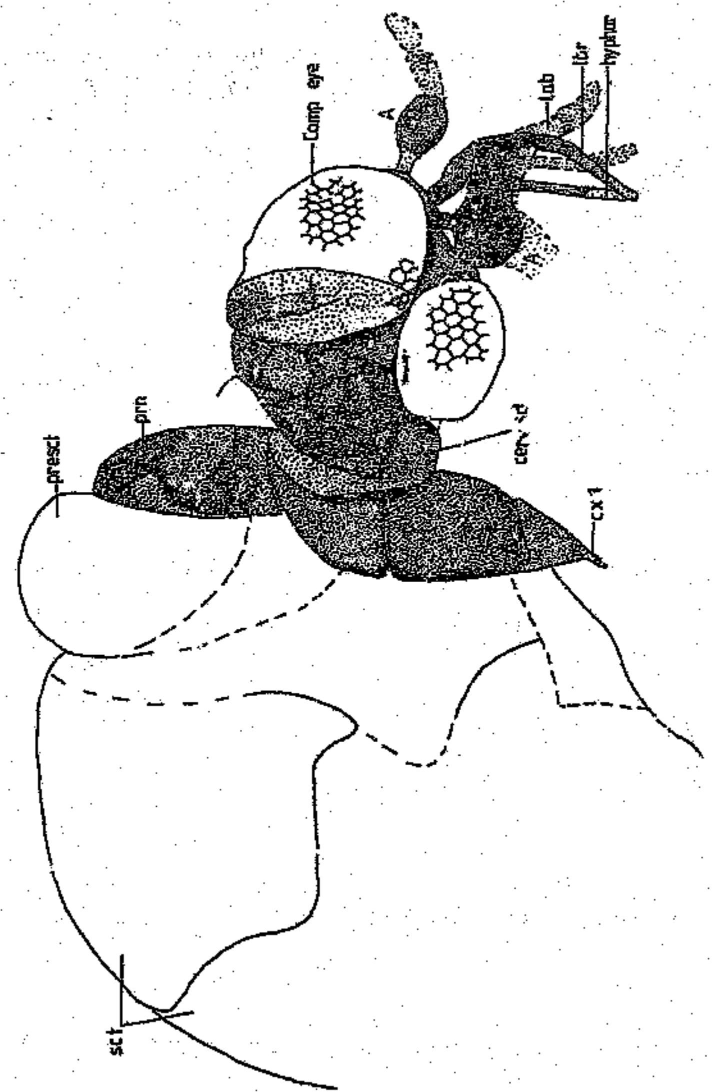


FIGURE 30

FIGURE 31

Family TIPULIDAE

SPECIMEN 9: (BP/2/25269), whole specimen (x27.3).

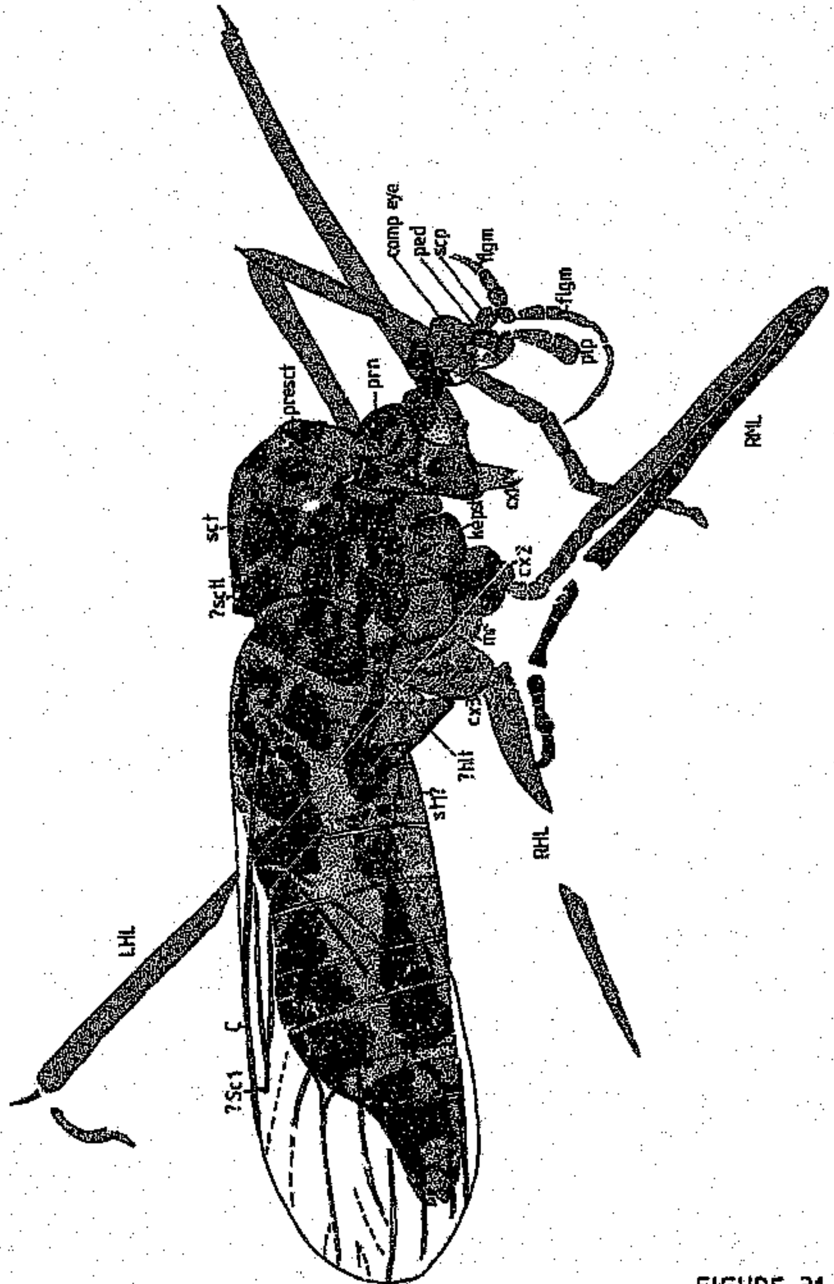

comp eye
ped
scp
flgm
flgm
plp
prn
presct
sct
?sctl
kepst
cx1
cx2
m
cx3
?hlt
sh?
RHL
RHL
LHL
C
?Sc1

FIGURE 31

FIGURE 32

Family TIPULIDAE

SPECIMEN 9: (BP/2/25269), details of head (x70.4).

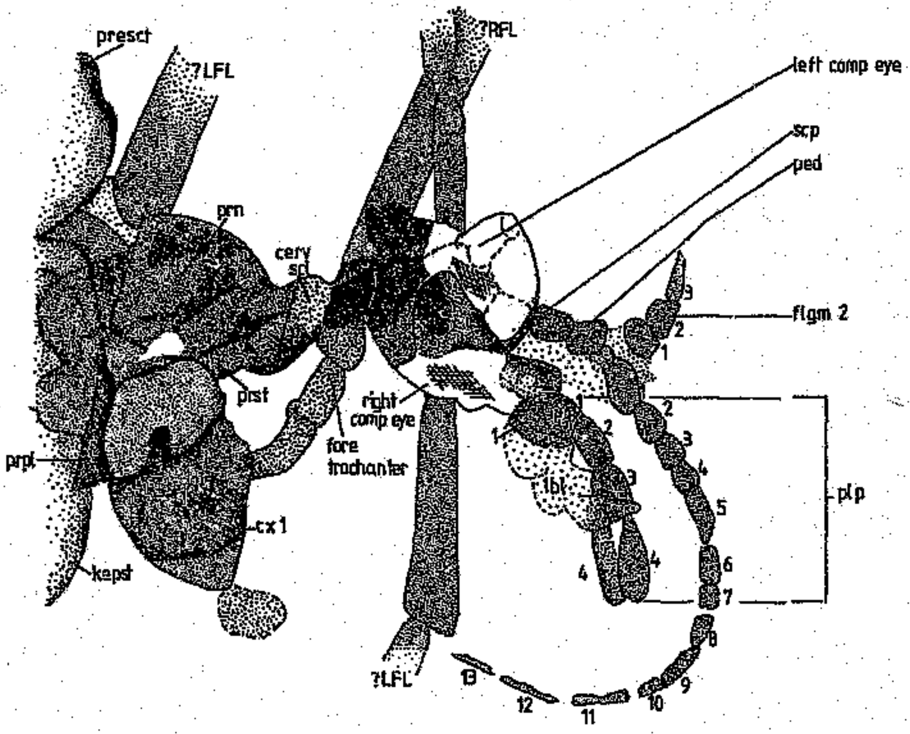

presct
?LFL
?RFL
left comp eye
scp
ped
prn
cerv
scl
flgm 2
3
2
1
prst
right
comp eye
fore
trochanter
1
2
3
4
5
6
7
plp
1
2
3
lbl
4
4
prpl
cx1
kepst
8
9
10
11
12
13
?LFL

FIGURE 32

FIGURE 33

Family TIPULIDAE

SPECIMEN 10: (BP/2/28228), whole specimen (x22.4).

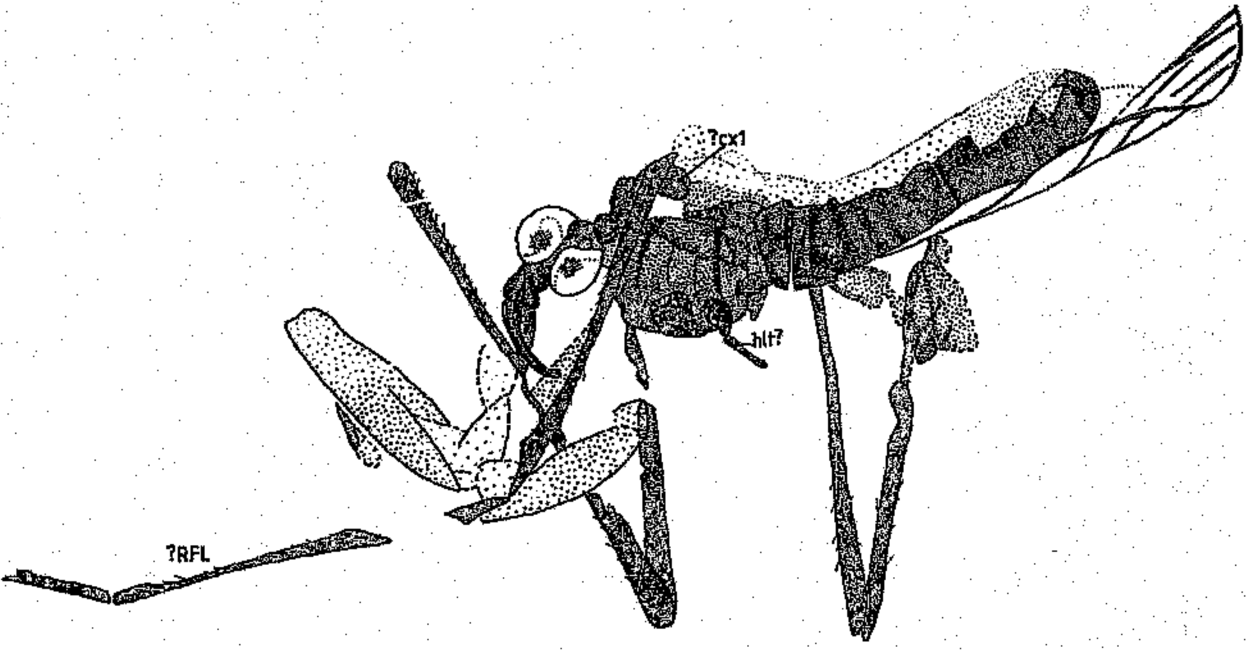


FIGURE 33

FIGURE 34

Family TIPULIDAE

SPECIMEN 10: (BP/2/28228), details of head (x88.9).

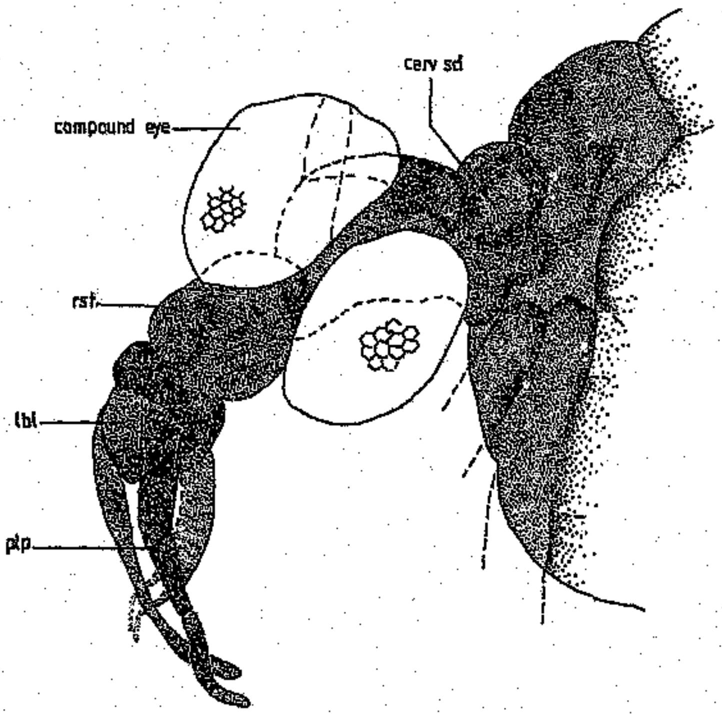


FIGURE 34

FIGURE 35

Family TIPULIDAE

SPECIMEN 11: (BP/2/28229), whole specimen (x19.6).

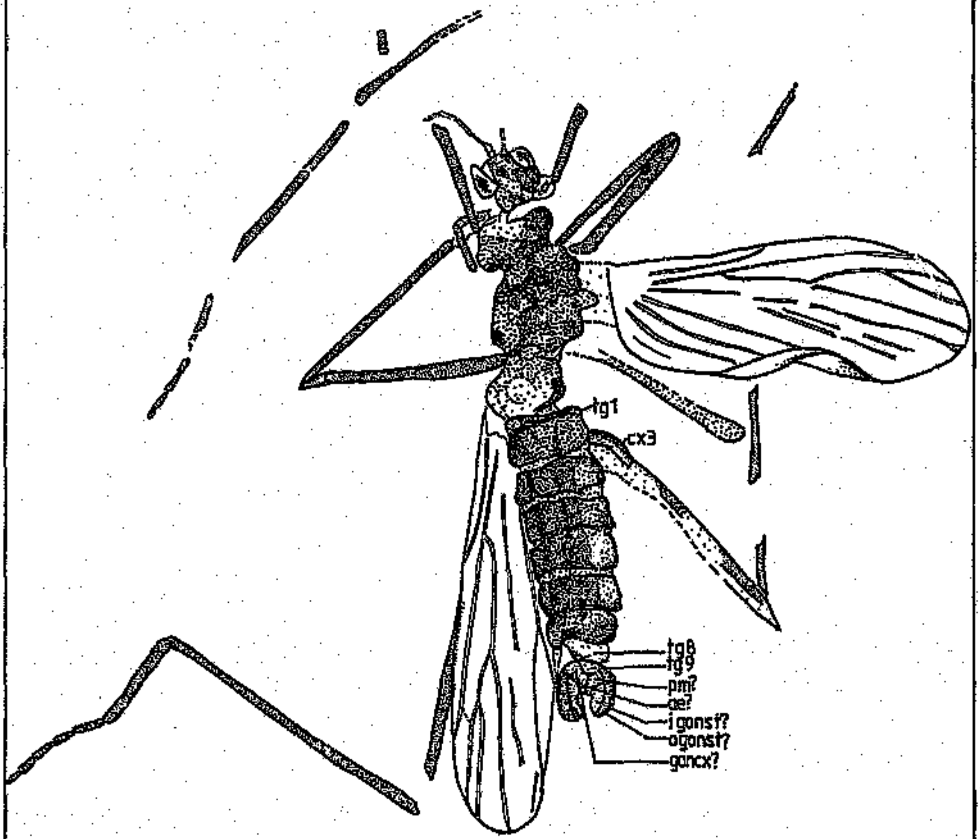
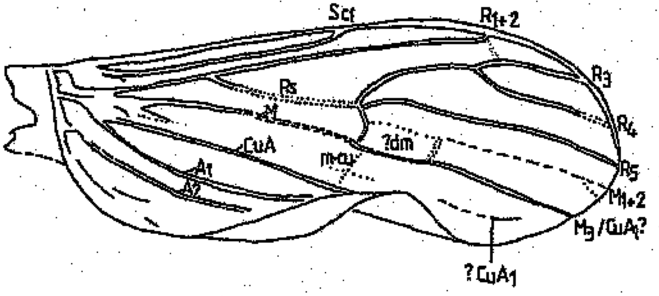


FIGURE 35

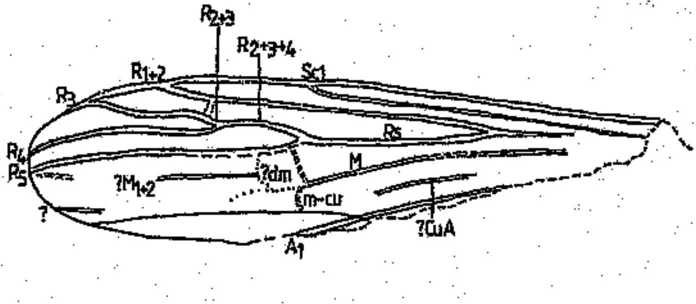
FIGURE 36

Family TIPULIDAE

SPECIMEN 11: (BP/2/28229), details of right wing (a) and left wing (b) (x30.8).



a: RIGHT WING



b: LEFT WING

FIGURE 36

FIGURE 37

Family EMPIDIDAE

Subfamily EMPIDINAE

Tribe EMPIDINI

Genus *Empis*

Subgenus *sensu stricto*

Empis (*sensu stricto*) *orapaensis* sp.n.

(BP/2/26943), whole specimen (x33.6); inset, the hypopygium, enlarged (x41.6).

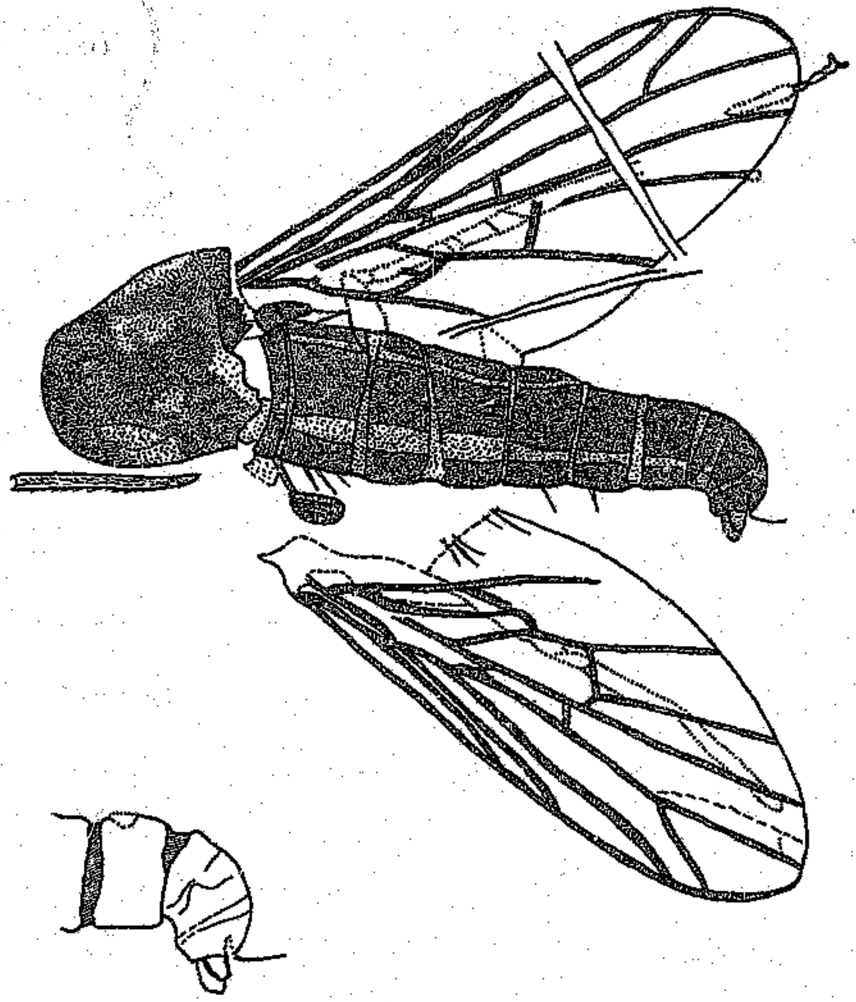


FIGURE 37

FIGURE 38

Empis (_sensu stricto_) _orapaensis_ sp.n. (BP/2/26943), composite drawing of left and right wings (x39.6).

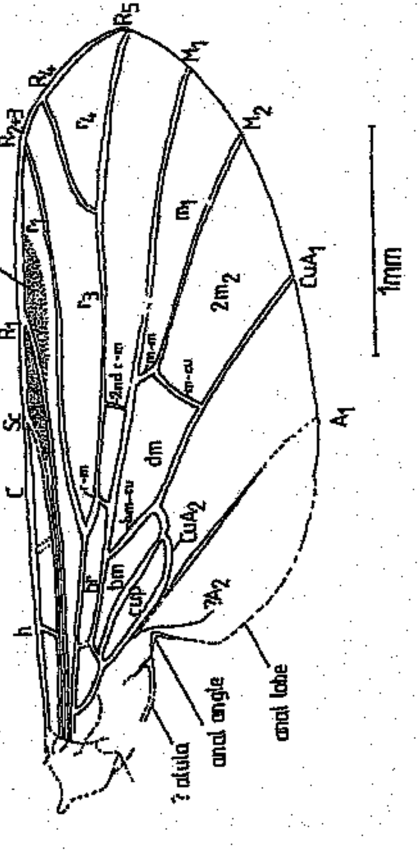

R5
M1
R4
R2+3
M2
r4
r1
m1
pt
CuA1
r3
2m2
1mm
R1
2nd r-m
m-m
m-cu
Sc
A1
r-m
dm
C
bm-cu
CuA2
br
bm
cup
?A2
h
anal lobe
anal angle
? alula

FIGURE 38

FIGURE 39

Presumed phylogeny of the Empidoidea: A-J, Fossil finds in support of the theory; A-H, after Chvala (1983); I-J, Fossils from Orapa, Botswana; Shaded areas represent relative numbers of extant species; Hatched areas represent the earlier origins predicted for the two Empidoidea families from Orapa; A, *Protempis* (Protempididae); B, *Trichinites*; C, *Cretoplatypalpus*; D, *Archiplatypalpus*; E, *Microphorites*; F, *Cretomicrophorus*; G, *Archichrysotus*; H, *Retinitus*; I, *Pseudoacarterus orapaensis*; J, *Empis* (*s.s.*) *orapaensis*.

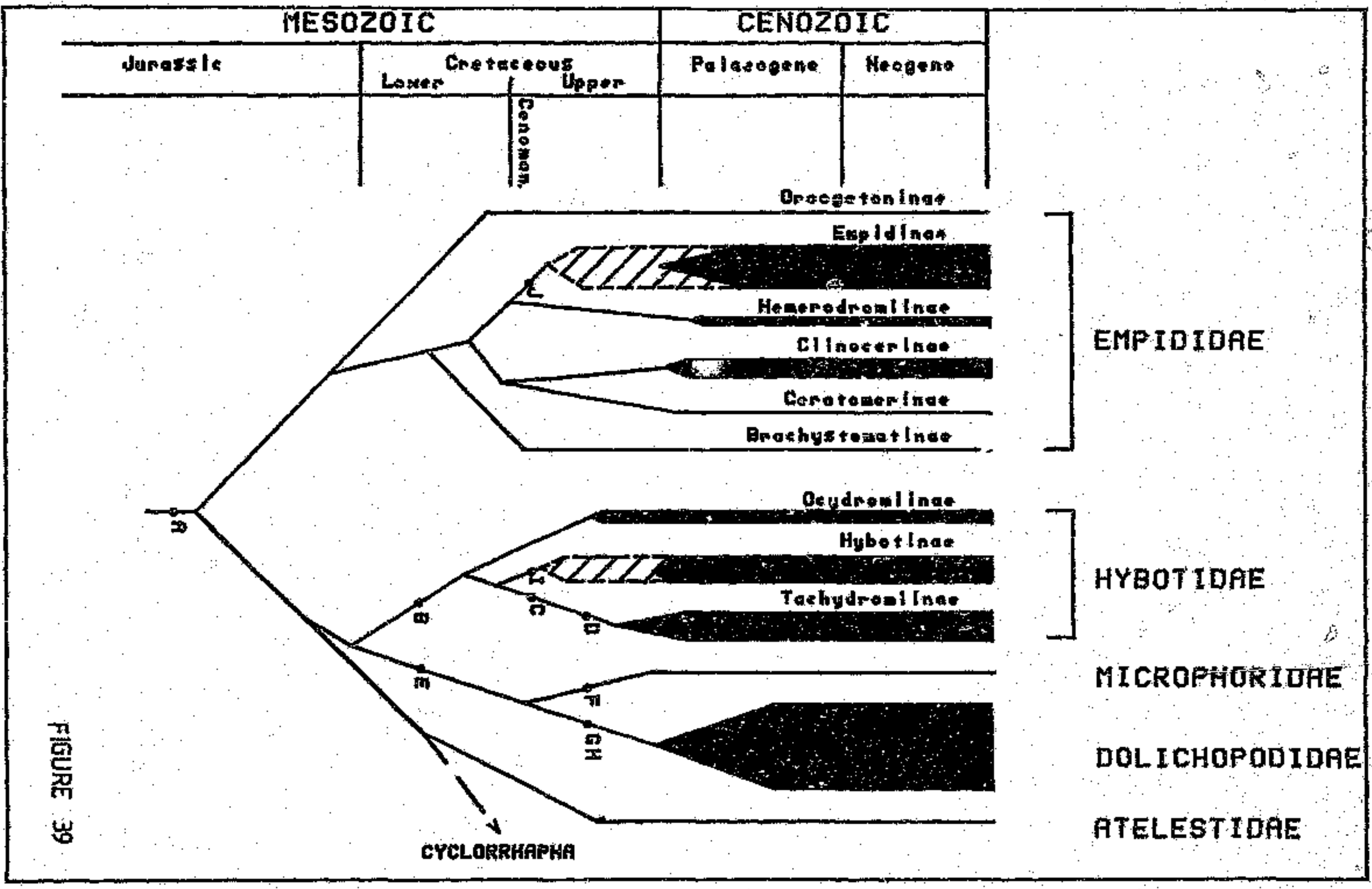

MESOZOIC
CENOZOIC
Jurassic
Cretaceous
Lower
Upper
Cenoman.
Palaeogene
Neogene
Oreogetoninae
Empidinae
L
Hemerodromiinae
Clinocerinae
Ceratomerinae
Brachystomatinae
EMPIDIDAE
Ocydromiinae
Hybotinae
I
Tachydromiinae
HYBOTIDAE
A
B
C
D
E
F
GH
MICROPHORIDAE
DOLICHOPODIDAE
ATELESTIDAE
CYCLORRHAPHA

FIGURE 39

FIGURE 40

Hunting and mating of <u>Rhamphomyia</u> <u>nigrita</u> (subfamily Empidinae) (after Downes, 1970).

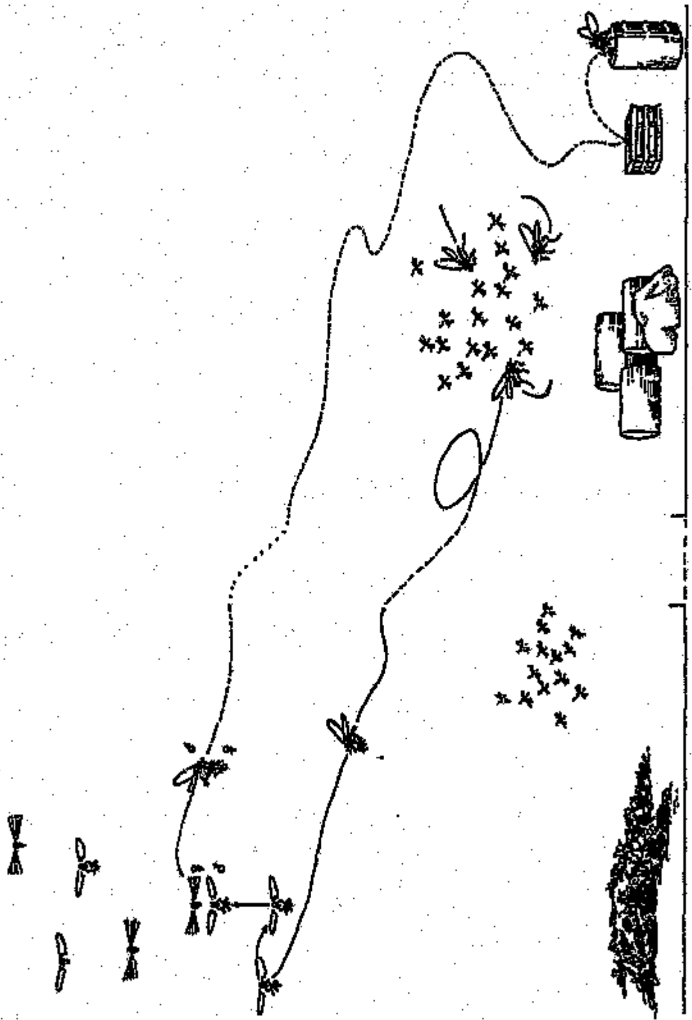


FIGURE 40

FIGURE 41

Distribution in southern Africa of Empis (subgenus Coptophlebia) (after Smith, 1969).

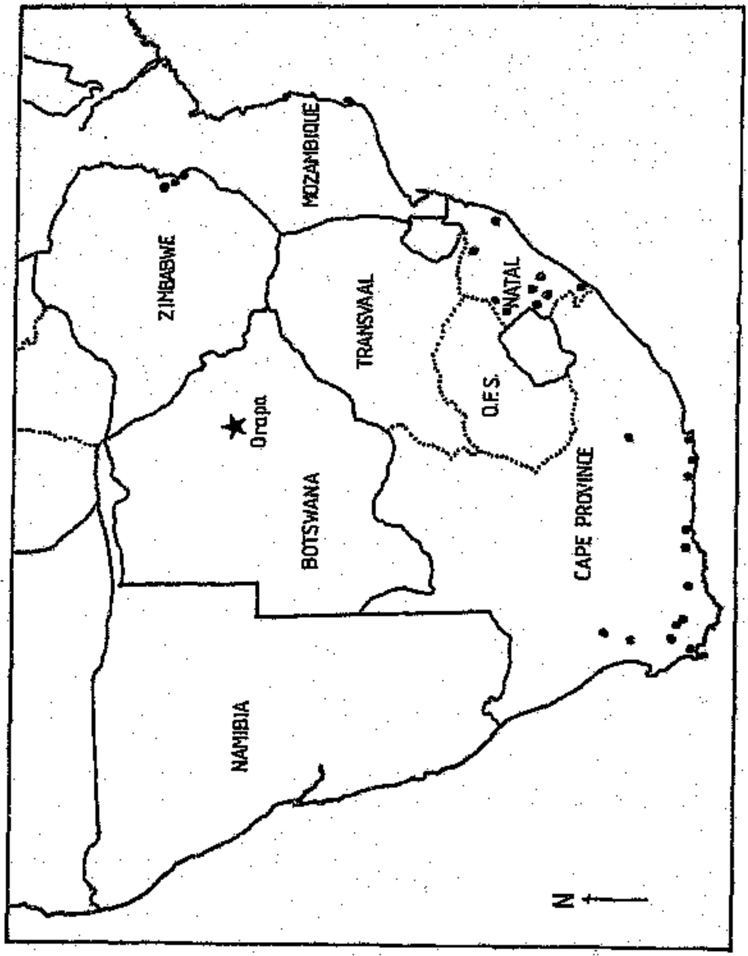

ZIMBABWE
MOZAMBIQUE
TRANSVAAL
NATAL
O.F.S.
Orapa
BOTSWANA
CAPE PROVINCE
NAMIBIA
N

FIGURE 41

FIGURE 42

Family HYBOTIDAE

Subfamily HYBOTINAE

Genus *Pseudoacarterus* gen. nov.

Pseudoacarterus orapaensis gen. et sp. nov.
(BP/2/25224a - part), whole specimen (x38.2).

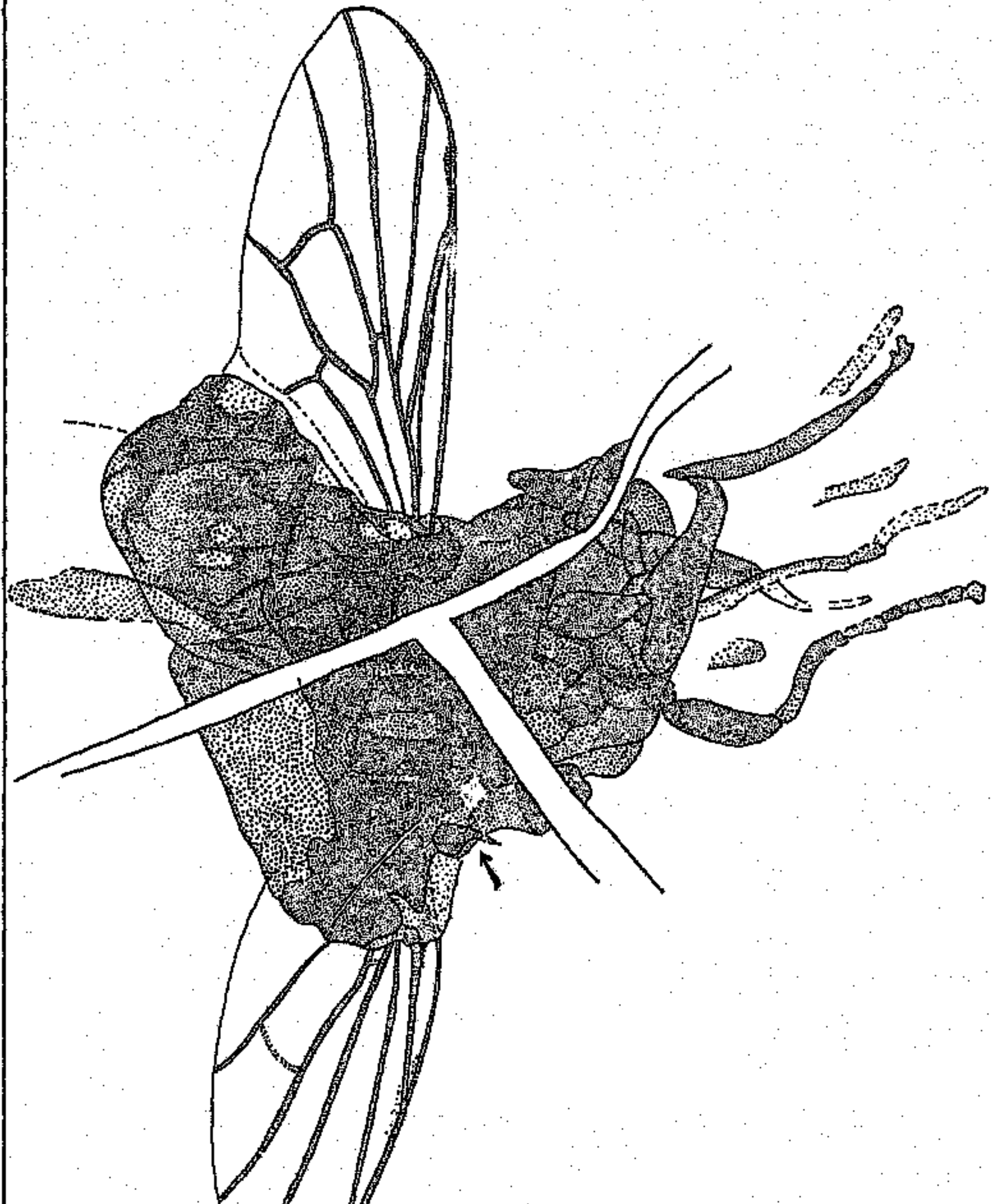


FIGURE 42

FIGURE 43

Pseudoacarterus _orapaensis_ gen. et sp. nov. (BP/2/25224b - counterpart), whole specimen (x32.5).

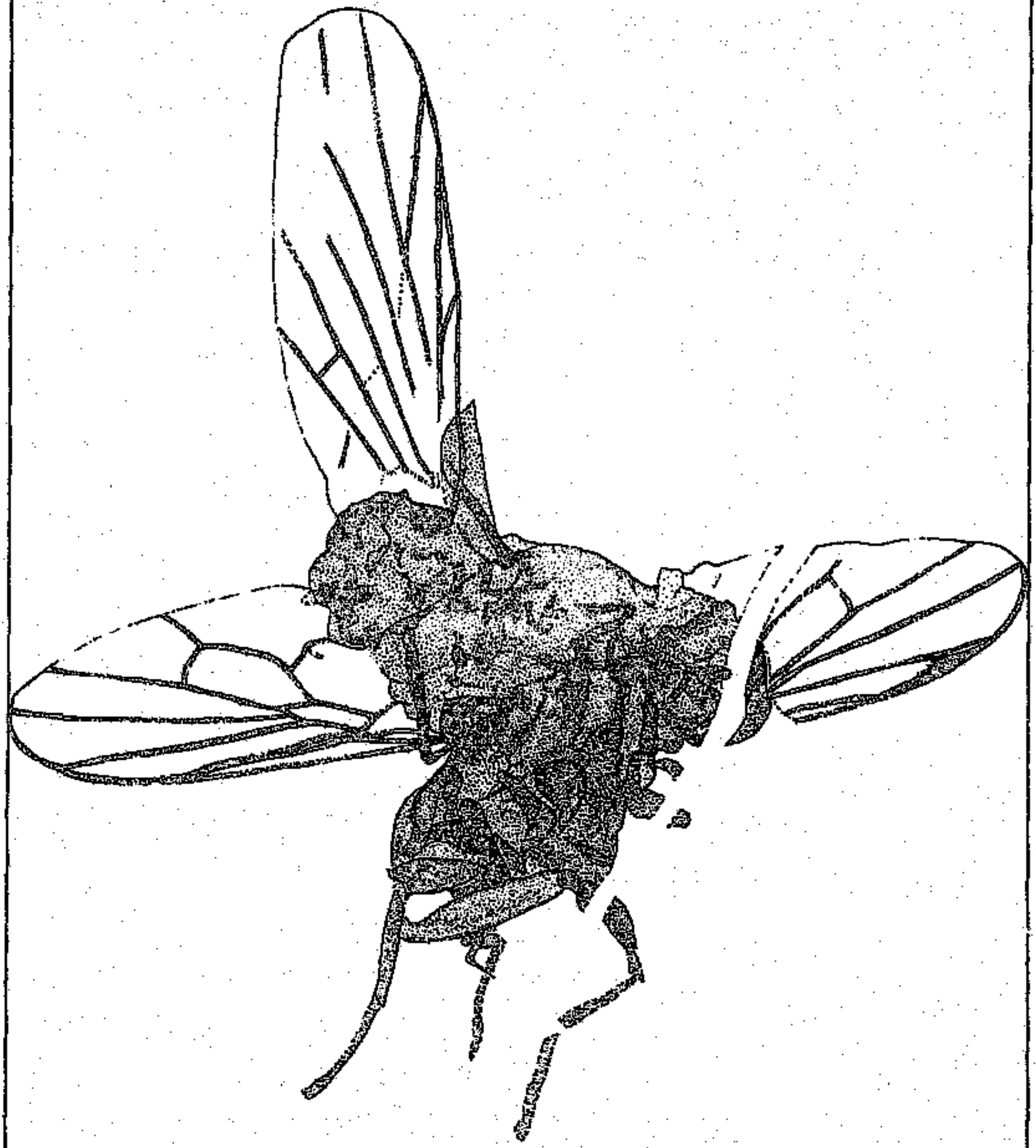


FIGURE 43

FIGURE 44

Pseudoacarterus orapaensis gen. et sp. nov. (BP/2/25224a and b), composite drawing of the wings (left and right wing of part and counterpart) (x44.1).

FIGURE 45

Wing of Trichinites cretaceus, (after Hennig, 1970).

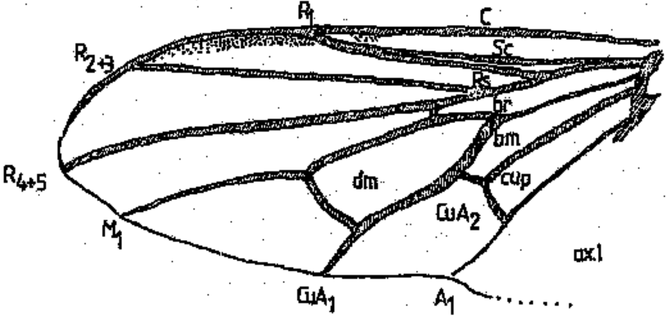


FIGURE 44

FIGURE 45