CRETACEOUS CARABIDAE (COLEOPTERA) FROM ORAPA, BOTSWANA

VOLUME ONE- TEXT

(Volume two- Figures)

Ian James McKay

Thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, for the degree of Doctor of Philosophy.

Johannesburg, January 1990.

ABSTRACT

A fauna of mid-Cretaceous Carabidae (Coleoptera), recovered from Orapa Diamond mine, Botswana is described. The carabids are similar to extant forms and include: the first record of a fossil of the subfamily Promecognathinae, Palaeoaxinidium orapensis (gen. et sp. nov.); the earliest record of a member of the Scaritinae; and ten specimens which are placed tentatively in the subfamilies Siagoninae (two specimens), Pterostichinae (three specimens), Anchomeninae (one specimen), and Harpalinae (four specimens); in addition two specimens cannot be placed in any particular subfamily.

The manner of preservation of the fossils is described, and a taphonomic analysis of the site is attempted. The exact age of the sediments is discussed, and a palaeoenvironment is inferred from a study of the carabids, the rest of the fossil fauna, and the sediments.

This fauna of carabids lived in a well-wooded crater formed by the eruption of a kimberlite. The climate of the time was seasonal, warm, and intermediate between tropical and temperate extremes.

The morphological conservatism of the promecognathine, and the apparent conservatism of the way of life of members of this group, provides support for the punctuated equilibrium pattern of evolution.

DECLARATION

I declare that this thesis is my own unaided work. It is being submitted for the degree of Doctor of Philosophy in 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 ---------------, 19--

ACKNOWLEDGEMENTS

This work was supported by a CSIR Bursary and a University of the Witwatersrand Senior Bursary. Additional funds were provided by the Friends of the Museum Society, Gaborone. Debswana Mining Co. provided accommodation and use of facilities at the mine while collecting. In particular, I would like to thank: Jim Gibson, Lorenz Shaw, Len Ellis, and Joe Joyce of Anglo American/DeBeers; and Alec Cambell and Jim Denbow of the National Museum, Gaborone.

The following helped in the collecting of the Orapa material, Prof. J. Kitching, Dr R. Rayner, Dr J. Maguire, Mrs J. Campbell, Dr C. Gow, Mrs M. Bamford, Dr J. Masters, Mr P. Forchammer, Mrs, R. Forchammer, Miss K. Goelst, Mrs A. Cadman, Mr A. Campbell, Mrs S. Waters, Miss C. Kleinjan, Mr P. Bender, and Mr B. Weissenbacher.

Special thanks go to Dr Richard Rayner, (BPI palaeontology) for his help and supervision. Dr Grenville Walters was extremely helpful in initially delimiting this project. The following provided useful and interesting discussions, Dr Rolf Oberprieler, Professor Robin Crewe, Garth James, Berndt Weissenbacher, Patrick Bender, Dr Martin Villet, Susan Risi, Marion Bamford, Saskia Waters, and Carien Kleinjan. Dr E. F. Riek made useful comments on the palaeoenvironment.

Prof. G. Ball and Dr D. Kavanaugh provided me with information about the American Promecognathinae and Dr D. Kavanaugh kindly provided me with specimens of Promecognathus. Dr P. Basilewsky examined photographs and drawings of the fossil promecognathine, and supplied many beneficial remarks. Dr S. Endrödy-Younga of the Transvaal Museum, Pretoria; Dr R. Oberprieler, of the National Insect Collection, Pretoria, and Dr. V. B. Whitehead of the South African Museum, Cape Town allowed me access to their collections. I also thank Dr Judith Masters for critically reading the manuscript and Desiree Pearce who helped with the photography.

CONTENTS

VOLUME ONE

CONTENTS

VOLUME TWO

LIST OF FIGURES

Figure

59. BP/2/27256b. Anchomeninae? Counterpart, line diagram.

60. BP/2/27256b. Anchomeninae? Counterpart, non-polarised light.

61. BP/2/18669a. Harpalinae? Part, polarised light.

62. BP/2/18669a. Harpalinae? Part, line diagram.

63. BP/2/18669a. Harpalinae? Part, non-polarised light.

64. BP/2/18669b. Harpalinae? Counterpart, polarised light.

65. BP/2/18669b. Harpalinae? Counterpart, line diagram.

66. BP/2/18669b. Harpalinae? Counterpart, non-polarised light.

67. BP/2/26255. Harpalinae? Polarised light.

68. BP/2/26255. Harpalinae? Line diagram.

69. BP/2/26255. Harpalinae? Non-polarised light.

70. BP/2/26260. Harpalinae? Polarised light.

71. BP/2/26260. Harpalinae? Line diagram.

72. BP/2/26260. Harpalinae? Non-polarised light.

73. BP/2/24006. Harpalinae? Polarised light.

74. BP/2/24006. Harpalinae? Line diagram.

75. BP/2/24006. Harpalinae? Non-polarised light.

76. BP/2/27585a. Carabidae, incertae sedis, part, polarised light.

77. BP/2/27585a. Carabidae, incertae sedis, part, line diagram.

LIST OF TABLES

LIST OF APPENDICES

CHAPTER ONE

INTRODUCTION

The Family Carabidae was erected by Latreille in 1802 and is today one of the largest families of Coleoptera having more than 21 000 described species (Kryzhanovskiy, 1976). It is a cosmopolitan group with members that are found in almost every conceivable environment including the Tundra regions (Erwin, 1979) although they are most common in moister microenvironments. However, contrary to most predictions that would be made from this great diversity of environments carabids are fairly homogeneous morphologically and the majority are ground dwelling, highly mobile, predacious beetles.

Carabids have been used extensively in studies on biogeography and speciation. Noonan (1979, 1985) and Erwin (1979, 1981, 1985) have modelled the distribution of the beetles through time, and Erwin (1979, 1981, 1985) has formulated the taxon pulse theory of carabid biogeography. In addition, attempts have been made to reconstruct the phylogeny of the Carabidae (Nichols, 1985; Erwin, 1985). Such historical studies are inevitably hampered because it is difficult to find evidence that will test them. One potential source of such evidence is the fossil record (Noonan, 1979), which unfortunately, in the case of carabids, is poor (Thiele, 1977).

This thesis describes a fauna of Upper Cretaceous carabids that has recently been recovered from central Botswana (Dobbs, 1978; McKay and Rayner, 1986; Rayner and McKay, 1986), and tries to obtain a coherent picture of the environment in which they lived.

First, the deposit in which the carabids were found is described with respect to geology, age of the deposits, the accompanying fossil flora and fauna, and taphonomy. Then the classification of the carabids, and their fossil history is reviewed. This is followed by a description of the methods and materials, terminology, etc. used to recover, describe and identify the fossils. Then a selection of fossil carabids is described and finally the fossils are discussed with respect to the age of the deposits, palaeoclimate, paleoenvironment, and general considerations of carabid evolution and palaeoecology.

CHAPTER TWO

LOCALITY, GEOGRAPHY AND GEOLOGY

2.1 Introduction

The Orapa diamond mine lies approximately 220km due west of Francistown, in the Republic of Botswana, at 21° 15'S and 25° 22'E (Fig. 1).

The mine and accompanying town are situated at an average elevation of 960m above sea level, within the Kalahari depression, about 35km south of the Makgadikgadi Pans. The climate is semi-arid, and receives an annual summer rainfall of 500mm (Allen, 1981). Temperatures range between a minimum of 0° in the winter and a maximum of 42° in the summer (Allen, 1981). The dominant vegetation is one of mopane trees (<u>Colophospermum mopane</u>) and grasslands.

The mine is situated on a kimberlite pipe, the Orapa pipe (DeBeers reference number 2125 A/k1). This is the largest of a cluster of 29 pipes in the area. It has an oval outline at the surface, with a long north-south axis of 1560m and a short east-west axis of 950m (Dobbs, 1978).

The kimberlite was discovered in 1967, and, in mid-1971, the Orapa diamond mine came into production (Allen, 1981). The mine, together with its sister mine at Lethlakane, and the mine at Jwaneng in southern Botswana, produces most of Botswana's diamonds. In 1982, according to the official report of the Orapa and Lethlekane mines, the Orapa mine produced 4 677 111 carats of diamonds. The same report stated that diamonds were the major source of foreign exchange for Botswana for the sixth consecutive year in 1982.

The Orapa kimberlite was intruded through rocks of the Karoo series, and is overlain by a few metres of Kalahari sands. A typical borehole log in the surrounding area would reveal the following: the top few metres would be sands and gravels of the Kalahari group, followed by 110m of Stormberg lavas which are, in turn, underlain by 91m of Cave sandstone; the latter are followed by 43m of the shales and marls of the Redbed stage, beneath which are 77m of Ecca shales and sandstones (Allen, 1981).

Drilling and mining operations have revealed the following geological sequence at Orapa: the top 60-90m of rock consist of sediments lying in a steeply dipping sedimentary basin (Hawthorne, 1975; Dobbs, 1978); underlying these sediments is true primary tuffaceous kimberlite, which becomes harder and darker with depth. The kimberlite is olive green in colour, with numerous basalt inclusions. It is highly altered but includes recognisable grains of garnet, ilmenite, clinopyroxene and mica (Hawthorne, 1975). The relationship of the primary kimberlite to the sediments is shown in Fig. 2. The kimberlite is complex and three distinct types of material may be recognised (Dobbs, 1978): the main body of kimberlite which occupies most of the Orapa pipe; a separate intrusion or feeder which occupies the north-east sector of the diatreme; and a third intrusion or feeder which occupies the south-west sector of the pipe and postdates at least part of the sedimentary sequence.

Dawson (1980) thoroughly reviewed literature concerning the emplacement of kimberlites. It seems the Orapa kimberlite consisted of fragmental material from the mantle transported in a calcite-rich fluid which included large amounts of gaseous carbon dioxide and water. The kimberlite was intruded rapidly through a system of deep seated fractures, as it approached the surface the carbon dioxide and water expanded, resulting in a flaring out of the kimberlite. The material cooled at this point, from an interaction with ground water and the expansion of the exsolving carbon dioxide. This accounts for the absence of thermal metamorphic effects on surrounding rocks. Dawson estimated that, as the kimberlite approached the surface, it was moving with a speed of 400m/s.

The kimberlite reached the surface, and formed an explosive vent, expressed as a crater, with a maximum depth of 140m. This was surrounded by a kimberlite tuff cone approximately 114m high (Dobbs, 1978). At some time after the eruption a crater lake formed. Slumping and erosion of the cone resulted in the crater filling with sediments. The filling of the crater was, however, not a continuous process; this is indicated by the presence of three unconformities (periods during which deposition of the sediments was halted and erosion occurred) within the sediments which were deposited prior to the crater lake sediments (Shaw, personal communication). The result of this sequence of events was a kimberlite pipe overlain by a sedimentary basin filled with fine-grained mudstones and interbedded conglomerates and sandstones (Hawthorne, 1975; Dobbs, 1978).

Sedimentary rocks which overlie primary kimberlite, and are derived wholly or partly from kimberlite, are termed epiclastic kimberlite. (Hawthorne, 1975). The presence of these sediments overlying the kimberlite, indicates that the Orapa pipe has been eroded relatively little when compared to many other southern African pipes of similar age [e.g. those in the Kimberly area (Hawthorne, 1975)]. Epiclastic sediments are known from Tanzania, Zambia, Botswana, Angola, Zaire, Mali and Bushmanland (South Africa) (Hawthorne, 1975). Epiclastic kimberlite which has been described in the literature, includes sediments from the Mwadui kimberlite of Tanzania (Edwards and Howkins, 1966), the Arnot pipe in the North-West Cape of South Africa (Reuning, 1931; 1934; Adamson, 1931; Haughton, 1931; Kirchheimer, 1934; Rennie, 1931; Estes, 1977; Scholtz, 1985), the Stompboor pipe also in the North-West Cape (van Dijk, 1985; Smith, 1986), and the Orapa pipe (Hawthorne, 1975; Dobbs, 1978; Allen, 1981; McKay and Rayner, 1986; Rayner and McKay, 1987; Rayner, 1987; Rayner and Waters, 1989a&b and Waters, 1989a&b).

Mining operations have resulted in the removal of some of the sediments overlying the Orapa pipe, producing a large oval pit (Fig. 3.), which was, in 1987, approximately 80m deep.

In the following section, I propose to describe the Orapa sediments and outline possible mechanisms for their formation. An understanding of the mode of formation of the sediments is essential for a palaeoenvironmental reconstruction, for taphonomic interpretation and an understanding of the limitations of the dating methods. Much of the data on the sediments is contained in Dobbs (1978), who conducted a sedimentological survey of the mine. Where possible, my own observations are included. These were restricted, mainly, to the fossilferous sediments and include exposures that were not available to Dobbs at the time of his study. Another useful reference, describing epiclastic sediments and the mechanism of their formation, is that of Smith (1986).

2.2 Sedimentary Facies and Sedimentation Process

The sediments around the periphery of the crater tend to be coarse, while those towards the centre of the crater are finer grained. Dobbs (1978) recognised four facies, coarse mass flows, granular mass flows, fine-grained sediments, and fluvial sediments. These he separated according to grain size, dip, nature of the matrix, sedimentary structures, sorting and genesis. I have departed from his scheme here by splitting his coarse mass flow facies into two separate facies that were formed through different sedimentary processes (i.e. volcanogenic and talus slope deposits and debris flow deposits).

2.2.1 Volcanogenic and Talus Slope Deposits

These deposits dip steeply (>20°) and contain dark brown basalt clasts. The latter range in size from 10m to minute particles, are angular to subrounded (many of the larger clasts are blocky in shape), and range in colour from dark grey to brown. Dobbs (1978) divided these deposits into massive boulder beds and segregated clast beds. A summary of Dobb's descriptions of these facies is given below.

> a) Massive boulder beds. These are clast supported poorly sorted units which may be more than 50m thick. Mean size of the 10 largest clasts is 40cm and they lack bedding and other sedimentary features.
>
> b) Segregated Clast Beds. These beds are in general thinner than massive boulder beds (up to 1.7m thick) and well sorted. They occur in

multiple layers; clasts vary in size from 2.8mm to 45mm, and are angular to subrounded. Dobbs described one sequence which was upward coarsening then fining. These beds tend to be clast supported. They dip at 30^{o}-40^{o} and are also found close to the perimeter of the crater.

Sedimentary Environment

According to Dobbs the lack of sedimentary structure in the massive boulder beds suggests a catastrophic mechanism of deposition. These beds are probably the remains of the shattered country rock and kimberlite extruded during the eruption. They may represent the extensions of the original cone into the crater (Dobbs, 1978) and are probably equivalent to the kimberlite-granite breccia of Edwards and Howkins (1966) and the volacanogenic suite of Smith (1986).

The well-sorted nature of the segregated clast beds suggests an avalanche type of deposition from the walls of the crater and cone (Dobbs, 1978). This sorting has been explained by Dobbs (1978) and Blatt et al., (1980) who cited Bagnold (1956). Such sorting may occur in sediments, when a mass of cohesionless grains are sheared. This produces dispersive forces normal to the direction of shear. Larger grain sizes are exposed to a greater force, and are thus forced into the regions of less shear, i.e. the outer surface and margins of the flow. Alternatively, a kinetic sieve mechanism may be responsible for the sorting. Here sorting occurs because "small grains work their way down in between the larger grains, as grain motion opens up cavities between the grains" (Blatt, et al., 1980). The segregated clast beds are analogous to talus or scree deposits which are formed by weathering of blocks from a cliff (Dobbs, 1978).

2.2.2 Debris Flow Deposits.

Dobbs distinguished these from the volcanogenic and talus slope deposits by their shallower dips (between 5° and 15°) and well defined flow boundaries which may be demarcated by shales or sandstones. They are situated closer to the centre of the crater than the volcanogenic and talus slope deposits and are often interbedded with finer sediments. According to Dobbs, demarcating layers may be destroyed by loading of boulders from overlying flows. Size sorting of the clasts is generally poor and grading absent. Clasts may show vertical orientation with their bases to the bottom of the flow. The bases of these flows are generally non-erosive, Dobbs did, however, mention one example of a debris flow occupying a channel cut into argillaceous sediments.

Sedimentary environment

Dobbs (1978) interpreted these sediments as debris flow deposits. The non-erosive flow boundaries (Smith, 1986), and random or poorly developed fabric (Blatt _et_ _al_., 1980) are diagnostic features of debris flows.

Debris flows occur when a mass of unconsolidated sediment loses shear strength and flows downslope (Blatt _et_ _al_., 1980). They are usually triggered by wetting of the sediments, perhaps from rainstorms (Curry, 1966; Vessel and Davies, 1981) or the rapid melting of snow (Sharpe and Nobles, 1963). Smith (1986) suggested that seismic events could be important. Johnson (1970 cited by Blatt _et_ _al_., 1980) described the mechanisms operating in a debris flow: normally only the base of the mass deforms, where shear stress produced by gravity is the greatest. The rest of the debris flow travels as a solid undeformed mass on this zone of shearing. Large boulders can be transported by the strength of the matrix (Rodine and Johnson, 1976), and the flow continues until the shear stress no longer overcomes the yield strength of the mass flow, and it freezes. Such debris flows can transport material over slopes as low as 1°, though slopes of 5° are more common (Blatt, _et_. _al_., 1980). This agrees with the dips of the debris flow deposits at Orapa. Dobbs (1978) suggested that the restricted size range of clasts found in some of the Orapa debris flow deposits may be due to them having had a source in pre-sorted talus slope material.

Debris flows have been reported most commonly in alluvial fan environments (Hooke, 1967; 1968; Beaty, 1970; Bull, 1977), but they also originate from unconsolidated material on talus slopes in mountain environments (Sharpe and Nobles, 1963; Curry, 1966) and on volcanic cones (Vessels and Davies, 1981). At Orapa they occurred on the inside of the volcanic crater and flowed towards the centre.

2.2.3 Granular Mass Flows.

Granular Mass flows (or mudflows) are finer grained than debris flows and occur, interbedded with the fine grained sediments (Figs 5 and 6), closer to the centre of the crater than the other facies. Individual flows vary in thickness from over a metre to under a centimetre; in colour from green, light brown through to yellow, and in form from matrix supported pebble conglomerates to poorly sorted sandstones. There is no strong correlation between the thickness of the massflow and largest clast size. The clasts may be composed of basalt, phlogopite, garnet and mudstone. Mudstone clasts are up to a metre in length and may be complexly folded and contorted. Other clasts seldom exceed 64mm and are subrounded to subangular. Basalt clasts may be blocky or spindle shaped. There are also rare blocks of kimberlite up to 2m across.

The massflows are poorly sorted. Many of the mass flows show upward fining sequences, and one example has been observed which shows reverse grading. A typical fining up sequence is shown at the base of the section in Fig. 4. The base of the mudflow consists of a granule to pebble conglomerate, which fines upwards to a poorly sorted, coarse sandstone. The sequence then grades into a fine non-laminated mudstone. In other cases, the contact between the mudflow and the conglomerate may be more sharply defined. Another feature which this mudflow demonstrates, which is typical of many others, is the way in which the clasts of mudstone are absent from the bottom half of the sequence.

Most granular mass flows lack sedimentary texture. In a few there is a rough texture, where the long axis of clasts are orientated parallel or subparallel to the bedding plane. A horizontal texture is also imparted by the mudclasts which, if they are not very deformed, prefer a parallel or subparallel orientation. Dobbs (1978) also reported that, in some mass flows, a texture is created by the vertical orientation of elongated rod shaped basalt fragments. The lower boundaries of the mudflows are non erosive. Where mudflows overlie mudstones, clasts often protrude into, and disrupt the mudstones below. According to Dobbs, soft sediment structures such as load and slump structures, are also common where mudflows overlie shales. Mudflows that overlie the conglomerate are draped conformably.

The mudflows may extend laterally for up to 100m. Dobbs reported one case where lateral thinning of a mudflow from 20cm thick to 1cm of poorly sorted medium mudstone was measured over a distance of approximately 50m. The mudflows generally dip at less than 5^{O}. Dobbs cautioned though that such low angles could easily have been caused by post-depositional movements in the underlying kimberlite.

Fossils in these layers are rare and we have only found occasional fragments of wood.

Sedimentary environment

The matrix supported nature of the granular mass flows, their non-erosive bases, reverse to normal grading, capping of structureless fine grained sandstone and frozen 'rip-up' clasts of shale are all evidence of a debris flow type of deposition (Smith, 1986). The clasts projecting from the matrix (Smith, 1986) and the kimberlite boulders are indicative of a high strength matrix. An alternative explanation for the presence of kimberlite boulders is that they are kimberlite bombs from renewed activity in the Orapa pipe, or from adjacent volcanoes (Dobbs, 1978).

The shale clasts could have originated from two sources. Firstly, momentary grounding of the mud flow as it moved over a mudstone layer could have resulted in the shale being incorporated in the mudflow as 'rip up' clasts (Dobbs, 1978; Smith, 1986). Movement of the mudflow with these shale inclusions would result in their deformation (Dobbs, 1978; Smith, 1986). Secondly, a shale layer could be deposited above a mudflow and movement over this layer, in a mudcracked condition, by a second mudflow would disrupt the shale (Dobbs, 1978).

The inverse grading and lateral thinning of some mudflows may be due to dilution of the mudflow matrix by water and the consequent deposition of larger clasts, resulting in the concentration of finer material at the base of the mudflow [Walker, in Harms et al. (1975) cited by Smith, (1986)]. Alternatively, Naylor (1980) suggested that, because clay that is sheared loses strength, the lower layers of a mud or debris flow which are most strongly sheared could only support smaller clasts. Therefore, inverse grading results. The lack of mudstone clasts at the bottom of the mudflows may also be a consequence of inverse grading. Dobbs (1978), however, suggested that shale clasts were found near the top of mudflows because they were "floated rather than truly incorporated". I think that this second explanation is unlikely if the shale clasts originated as 'rip up' clasts from the substrate.

Friction between a mudflow and water results in reverse shearing at the mudflow/water interface, with fine sediments taken into suspension and transported down slope as a turbidity current (Hampton, 1972). The eventual deposition of such fine sediments resulted in the formation of the massive fine-grained siltstone and mudstone layers which overlie many of the mudflows (Smith, 1986). The grading of the mudflows into the massive mudflows and siltstones may be due to reworking of the mudflows and siltstones at the water/mudflow interface (Smith, 1986).

The vertical [Lindsay (1968) cited by Dobbs (1978)] and the horizontal (Enos, 1977) fabric observed in some of the mudflows may be a consequence of laminar flow conditions in the mudflow, at least in the terminal stage of flow.

Deformation structures indicate standing water in the lake, and are usually formed when a dense sediment is deposited above an unconsolidated, less dense sediment, or when unconsolidated sediments are deposited on a slope (Blatt et al. 1980).

I suggest that the mudflows at Orapa are, equivalent to the type A and B beds of Smith (1986), and therefore that similar sedimentary environments operated at the Orapa and Stompboor pipes. The exact mode of formation of the mud flows is, however, uncertain. Sharpe and Nobles (1963) observed that debris flows were preceded and succeeded by muddy granular flows. Dobbs (1978) suggested that these may be represented at Orapa by the mud flows. Another possibility is that the mudflows were formed by caving from larger debris flows (Smith, 1986). A third possibility is that the mudflows could be the distal extensions of the debris flows, with the coarser materials being deposited due to dilution of the matrix with water (Smith, 1986), resulting in a decrease in its capacity to carry debris. As yet no transitions between debris flows and mud flows have been found.

2.2.4. Fine Grained Sediments.

These occupy an oval area, 500 X 750m, slightly to the east of the crater centre. They consist of fine mudstones, interbedded with the mud and debris flows and form a layer twenty metres thick. Calcite layers, both concordant and discordant with the bedding planes, are common.

The mudstone is made up of two types, laminated and unlaminated. The banding of the laminated sediments is imparted by numerously repeated sedimentary units. A typical sequence of repeating units is illustrated in Fig. 7. The base of a unit consists of a dark band usually varying in thickness from 0.02-0.05mm. Some of these bands, when split, reveal a layer rich in plant fragments and isolated beetle elytra. The layers can be extremely rich in organic matter and may contain almost complete plants, flowers and Coleoptera in such high densities that it is almost impossible to distinguish between them (Fig. 10). Overlying these laminae is a layer of poorly sorted fine to medium sandstone (largest clast size 0.4mm). Often sandstone layers interbedded in mudstone have been disrupted by soft sediment deformation to form lenses. The coarser laminae are covered by layers of mudstone, these frequently contain larger clasts (up to 0.2mm) which may decrease in frequency towards the top of the layers. Sometimes the mudstone units contain fragments of the dark basal band which is orientated parallel to the bedding plane, and has a rippled shape. The units vary in thickness from 2mm to 2cm. Often one or more of the components of the units are missing. Most frequently it is the basal lamina or the coarse component. Occasionally, only the basal lamina, overlain by a thin lighter (in colour) layer is preserved (Fig. 8).

The non-laminated mudstones correspond to those mudstones which overlie the mudflows. Some of these non-laminated mudstones are red or red-brown in colour. Some of the surfaces have a pitted pattern similar to those left by raindrops (Fig. 9). One of these pitted surfaces, when examined under the microscope, proved to be very rich in evaporite crystals. These mudstones have extremely high concentrations of insect remains which are often gathered together in groups. Many of the insects have their wings stretched out. Also of interest is that the sedimentary sequence in these areas is composed of interbedded mudflows, poorly sorted sandstones and massive mudstone. There is no trace of the laminations rich in organic material described above. In addition to the laminated and non-laminated mudstones, Dobbs also observed slightly coarser, buff-coloured sandstones on the outer edge of the shale area, which had lighter and darker laminae. He suggested that these may indicate ripple forms.

Structures reminiscent of mudcracks, often in association with evaporite layers, are visible at many localities. Dobbs also recorded the presence of these, but reported difficulties in differentiating between primary and secondary mud cracks.

It is within these fine grained sediments that most of the fossils are found.

Sedimentary environment

Formation of the non-laminated mudstones has already been discussed in the section on mudflows.

The sandstone and mudstone laminae are interpreted as having been deposited by turbidity currents, with the sandstone and mudstone having being deposited in progressively lower flow regimes. Supporting this interpretation is the decrease in frequency of the outsize clasts towards the top of some of the mudstone units. The fragments of basal lamina in some of the mudflows could have been torn up by the passage of the head of the turbidity current as it moved over them. The variation in the proportions of sand and clay may be explained as being due to distance of deposition from the origin of the current with the coarser sediments being deposited first.

The turbidity currents may have been triggered by mud or debris flows (Hampton, 1972; Smith, 1986), or formed by sediment laden cold stream water entering the lake (Allen and Collinson, 1986; Smith, 1986). There is some evidence for stream action in the Orapa crater as is discussed below.

The basal lamina appear to have been formed by deposition of organic matter on the lake bottom during periods of quiescence. The deposition must have occurred in deep water as formation of the lamina would be interfered with by water movement in shallow areas. O'Sullivan (1982) suggested that for a lake with an area of less than 20ha its maximum depth would have to exceed 7-20m for laminations to be preserved.

Where the turbidity current strata are missing, the organic layers are separated by thin lightly coloured layers to produce paired laminations usually under 0.5mm thick (Fig. 8) and similar in appearance to the type C beds of Smith (1986). Electron microprobe analysis of the type C beds revealed the light layers to be calcium rich and the dark layers to be calcium poor (Smith, 1986). Smith (1986) suggested that the laminations were of seasonal origin with the light layers representing increased calcite precipitation due to greater plant growth and evaporation during summer. It is possible, therefore, that the paired laminae at Orapa are also of seasonal origin. However, similar electron microprobe analysis did not revealed great concentrations of calcite in the light layers. This does not, however, rule out a seasonal explanation for the laminations; the lighter layers could still reflect some seasonal input of sediment into the lake. Such seasonal clastic laminations are known from Quaternary lakes (O'Sullivan, 1983). An alternative explanation for the lighter lamina is that they represent clastic material introduced into the lake by occasional storms or are perhaps the very distal ends of turbidity flows, and therefore have no seasonal significance. Further investigations on whether the laminations are seasonal would be worthwhile.

The coarse calcite layers are made up of fibrous calcite, which was perhaps precipitated at the sediment/water interface during fluctuations in the lake level (Smith, 1986). The calcite layers accompanied by mudcracks sometimes occur amongst deep water sediments which suggests that the lake may have dried up completely at times. However, some of the calcite layers were deposited after lithification as is indicated by the calcite layers which run across bedding planes. They were probably precipitated from ground waters in joints and cracks.

Dobbs suggested that the coarser sediments around the perimeter of the lake indicated wave action in shallow water. The red mudstone deposits were probably also formed in shallow water. Shallower conditions are suggested by the red colour of the mudstones indicating deposition in well oxygenated water, the lack of the dark laminations rich in organic material, and the presence of raindrop impressions. Further evidence for shallow water conditions is provided by the fossils, this is discussed in the section on taphonomy.

2.2.5 Fluvial Deposits.

These deposits were reported by Dobbs in two places on the south west side of the shale basin. He described the sediments as "cream coloured fine to coarse grained arenites". According to Dobbs, sorting of these sediments is moderate, bedding well developed, and some of the beds fine upwards. Trough crossbedding was visible at one of the sites.

Sedimentary processes

The fluvial sediments were deposited by streams on the inside of the crater.

2.3 Summary

The fossils are preserved in sediments which accumulated in a volcanic crater formed by the eruption of a kimberlite pipe. The coarse conglomerates around the periphery of the crater were formed as extensions of the volcanic cone into the crater. They were deposited as talus slope deposits or by debris flows. The matrix-supported conglomerates, sandstones, and laminated and unlaminated mudstones nearer the centre of the crater were formed by a combination of massflows, turbidity currents and gradual deposition in a crater lake. The fossils are found mainly in the mudstone deposits.

CHAPTER THREE

DATING

3.1 Introduction

An accurate date of deposition is essential if a fossil deposit is to be of use in palaeontological studies. In this section, the age of the fossil deposits at Orapa is discussed. Ages have been determined for both the kimberlite and the sediments overlying the kimberlite. In addition, attempts have been made to estimate the rate of deposition of the sediments as an indirect estimate of how much younger they are than the kimberlite.

3.2 Dating of the Kimberlite

Two independent methods have been used to determine the age of the Orapa kimberlite. Both are based on the decay of radioactive Uranium in zircon crystals. The first method, which has obtained widespread acceptance (Haggerty _et_ _al_., 1983), is the low-contamination hydrothermal U/Pb method. This method works on the principle that U^{238} and U^{235} decay at a known rate to Pb^{206} and Pb^{207}, respectively. By measuring the amount of the isotopes of U and Pb in a zircon crystal, it is possible to calculate the length of time that the Pb has been accumulating.

Lead is only likely to have started accumulating in the zircon crystal lattice when the temperature of the kimberlite had dropped sufficiently for the crystal lattice to stabilise. This would probably have been the time of intrusion of the kimberlite (Haggerty et al., 1983), or the time of its eruption (Davis, 1977). The intrusion and eruption times are likely to correspond closely, because kimberlites are extruded rapidly (Dawson, 1980). Using the low contamination hydrothermal U/Pb, method Davis (1977) obtained a date of 93.1 million years ago (mya) for the Orapa kimberlite.

The second method is the technique of fission track dating used by Haggerty et al., (1983). This method works on the principle that when U^{238} decays in a zircon crystal, recoil nuclei are released which damage the crystal lattice, resulting in a fission track which is detectable under an optical microscope. The age of the crystal is based on the ratio of the number of crystal tracks formed by spontaneous decay of the U^{238}, to the number of tracks formed by exposure of the zircon crystal to a known dosage of radiation. Again, the crystal lattice would only start recording fission tracks when the lattice had stabilised sufficiently at lower temperatures. Using this method Haggerty et al. (1983) obtained an age of between 87.4 (±4.7)mya and 92.4 (±6.1)mya for the Orapa kimberlite.

The available data, therefore, indicate that the Orapa kimberlite erupted between 87.4 and 93.1mya. How do these dates compare to those obtained for other kimberlites?

Dawson (1980) has summarised radiometric ages for southern African kimberlites, and has identified kimberlites of three ages. The Premier mine kimberlite in South Africa is of Precambrian age, the Dokolowayo kimberlite in Swaziland is of Permian age, and most of the remaining southern African kimberlites were extruded between ±140mya and ±40mya. The Orapa kimberlite thus erupted in the same period as most of the other kimberlites on the subcontinent.

How do the dates obtained for the kimberlite compare with the dates obtained for the sediments?

3.3 Dating of the Sediments

Sediments were dated indirectly, based on their fossil content. This was approached in two ways:

a) by using plant macrofossils from the sediments;

b) by using fossil pollen (palynomorphs) recovered from the sediments.

a) Plants

Two studies of the Orapa flora are pertinent to a discussion of the age of the Orapa sediments; the initial report on the plants by van Dijk (in Dobbs, 1978), and a recent and more complete study by Bamford (personal communication).

Van Dijk reported the presence of fossil plants belonging to the genera of Trimeria, Asplenium (a genus of fern), and Egolops (an early genus of grass in the Mediterranean). The grass is especially indicative of a Tertiary date as grasses did not become common in the fossil record until after the Cretaceous (Taylor, 1981). Van Dijk used the presence of these plant fragments as indicators of a Mid-Miocene age for the sediments. However, Bamford, has questioned these identifications (personal communication) because:

i) they were identified under the assumption that they could be compared with modern floras which assumes a young date for them;

ii) preliminary studies of better preserved material have revealed that the structures which van Dijk identified as grasses differs greatly in morphology from grasses;

iii) without fertile material it is impossible to identify the fern positively as Asplenium, also this genus is one which has existed over a large period of time and is therefore a poor indicater of age;

iv) the leaves which were placed in the genus Trimeria, although superfically similar to this genus, could belong to many other angiosperm families.

The fossil plants identified by van Dijk can, therefore, not be used as indicators of the age of the sediments, or as palaeonvironmental indicators, as has been done previously (Dobbs, 1978).

Bamford's, (personal communication) study of the flora, has obtained contradictory results as far as the age of the sediments is concerned. Her study of the angiosperm leaves revealed forms belonging to the form genus of Sapindopsis. This genus has only been found previously in Albian to Cenomanian (105-93mya) sediments from N. America and, therefore, suggests an age which is slightly older or similar to to the one suggested by the radiometric dating for the Orapa sediments. The general leaf flora also support a pre-Tertiary age for the sediments as Tertiary leaves can usually be placed among extant genera. It has proved impossible to do this with confidence for any of the Orapa leaves.

Some of the flowers from the Orapa sediments, however, suggest a Tertiary age. Friis and Crepet (1987) have suggested, from their studies of fossil and extant angiosperms, a sequence and time-table in which they would have expected the various levels of floral complexity to occur. Some of the flowers from the Orapa deposits are of a relatively complex tubular type. These Friis and Crepet predicted should only have appeared in the Tertiary.

Bamford suggests that the discrepancy between the age suggested for the sediments by the leaves and by Friis and Crepet's hypothesis can be explained by the poor fossil record of angiosperm flowers upon which their hypothesis was, in part, based. Therefore, the date indicated by the leaves for the deposition of the Orapa sediments should be taken as the correct one.

b) Palynology

Scholtz (personal communication) has examined palynomorphs from the Orapa sediments. He noted especially low concentrations of pollen compared to concentrations obtained from sediments covering other kimberlite pipes in the same area. However, he did obtain sufficient material to make a positive statement about the age of the Orapa sediments. Scholtz reported the presence of Ephredripites forms, a single tricolpate, and a Classopollis cf. jardinei type. He felt that these forms indicated a mid- to Late Cretaceous age i.e. not older than Albian or younger than mid-Senonian (100-75mya).

The mid to late Cretaceous age based on palynology is, therefore, close to the date obtained for the kimberlite using radiometric methods. An independent check on these dates could be obtained if the rate of sedimentation were estimated.

3.4 Rate of Sedimentation

Dobbs (1978, p21) described rates of sedimentation in the crater as follows, "Mud and debris flows are essentially instantaneous occurrences, taking only minutes from initiation to completion". Sedimentation rates would therefore have been extremely rapid in the crater, provided that the frequency of mud and debris flows was high.

Dobbs then proceeded to use the sedimentation rates in similar modern day alluvial fan environments, which had been recorded by Beaty (1970) and Hooke (1968), to estimate the sedimentation rate in the Orapa crater. Beaty obtained a sedimentation rate of 3" to 6" (7.6-15cm) per thousand years, and Hooke (1968), obtained a sedimentation rate of 0.8'-1.5'(24-45cm) per thousand years. Dobbs (1978) estimated further that there were, before erosion, approximately 140m of sediments covering the Orapa pipe. At the rate of deposition estimated by Beaty and Hooke, these sediments would have accumulated between 311 000 to 1 842 105 years.

Using these figures McKay and Rayner, (1986) and Rayner and McKay (1987) suggested that the Orapa sediments could have accumulated in less than half a million years. In addition Rayner and McKay cited Smith (1986) who calculated from the number of annual laminations or varves, in a 76m sequence of lacustrine epiclastic sediments overlying the Stompboor pipe, that the sequence accumulated in a time span of around 220 000 years. Again these figures indicated that the entire Orapa sedimentary sequence could have accumulated in around half a million years, and it seemed safe to say that the kimberlite and the entire sedimentary sequence were of similar ages.

However, recent evidence (Shaw, personal communication) for periods of erosion in the sediments which underlie the lacustrine sediments indicate that there were indeterminate periods of time when there was no deposition at all. This makes it impossible to estimate the time taken for the sequence of Orapa sediments to be deposited. Therefore, no independent check on the radiometric dates and the dates obtained from fossils in the sediments is possible.

It is, however safe to say that the lacustrine sediments were deposited fairly rapidly, perhaps at a rate comparable to that estimated by Smith (1986). Using Smith's figure, the highest and lowest localities at Orapa (which are 22m apart see, Table 2), from which fossils have been recovered, would have differed in age by approximately 64 000 years.

3.5 Summary

Radiometric dating indicates that the Orapa kimberlite erupted between 87.4 (±4.7)mya and 92.4 (±6.1)mya. Evidence from palynomorphs and plant macrofossils in the sediments supports this age determination. It is impossible to estimate the length of time taken for the Orapa sediments to have been deposited. However, an estimate for the rate of deposition of the lacustrine sediments reveals that the highest and lowest fossil localities are probably no more than 64 000 years apart in age.

The age of the Orapa deposits is considered again in the discussion with respect to evidence that the fossil insects can provide.

CHAPTER FOUR

OTHER FOSSIL FINDS AT ORAPA

4.1 Introduction

Early collections from the site formed the basis of preliminary work by van Dijk (in Dobbs, 1978), McKay and Rayner (1986) and Rayner and McKay (1987). However, new discoveries made in 1986, 1987, and 1988 surpass all previous collections in their variety and quality of preservation. In addition, there are now several people working on the Orapa material, which means that new identifications and discoveries are being made continuously. At present approximately 5 200 specimens (often with more than one plant or insect specimen per numbered block), have been recovered from Orapa. Of these 44.6% are plants [this includes only plant fragments which could readily be identified; undetermined plant fragments were ignored - Bamford (personal communication)], 51% are insects and 4.4% are unidentifiable fragments; in addition, two specimens of spiders have been found. In this section, the fossil fauna and flora from Orapa are reviewed and compared with assemblages from other epiclastic kimberlites.

4.2 Comparison with Fossil Assemblages from other Epiclastic Sediments

In contrast to faunas and floras reported from other epiclastic sediments, the Orapa fossil assemblage is mainly of a terrestrial nature (but see footnote to Table 1), has a large proportion of insects and there is a complete lack of vertebrate remains. Fossils have been recorded from epiclastic sediments overlying the, Mwadui, Mahenge and other pipes in Tanganyika, the Stompboor pipe in Bushmanland, South Africa, and the Arnot pipe in Namaqualand, South Africa. Fossils of aquatic organisms, which make up the largest proportion of remains recovered from these sites, include: frogs, fish, aquatic gastropods and bivalves, and ostracods. Terrestrial fossils include: isolated insect fragments (these could possibly be of an aquatic nature, as none have been positively identified), plant fragments (wood, leaves, and pollen) and remnants of birds and/or reptiles (only a tentative identification). A summary of these remains is given in Table 1 below.

Pipe	Fossil type	References
Arnot pipe	teeth of small reptiles	Reuning 1931
	Fish	" "
	Frogs	" "
	"	Haughton, 1931
	"	Estes, 1977
	a few beetles	Reuning, 1931
	leaves	Rennie, 1931
	petrified wood	Adamson, 1931
	pollen	Kircheimer, 1931
	"	Scholtz, 1985
Stompboor	bone of possible avian affinity	Smith, 1986
	frogs	" "
	"	van Dijk, 1985
	fish	Smith, 1986
	isolated insect wing fragment	" "
	non-marine bivalves	" "
	non-marine gastropods	" "
	ostracods	" "
	coalified wood	" "
	maple like leaf impression	" "
*Mahenge	fish	Edwards and Howkins, 1966
Mwadui	plant debris	" " " "

Table 1. Summary of fossil finds from epiclastic sediments.

---

*Edwards and Howkins reported that fish, frogs and plant debris are common in epiclastic kimberlite in Tanganyika. They stated specifically that fish have been collected from the Mahenge pipe and that plant fragments have been collected from Mwadui. They were not clear whether fish and frogs are also present at Mwadui. Therefore, it is possible that, as at Orapa, the fossils from the Mwadui sediment are mainly of a terrestrial nature.

4.3 Review of Fossil Finds from Orapa

In this section I review the fossil finds from Orapa in some detail. Plants are discussed first, and then insects.

4.3.1 Plants

The palaeoflora of Orapa has been mentioned several times in both published and unpublished work. Two of these studies, that of van Dijk (in Dobbs, 1978) on the macroflora and that of Scholtz (personal communication) on the microflora, have already been discussed in the section on dating. Plant remains have also been figured in McKay and Rayner (1986) and Rayner and McKay (1987). These include fern fragments (BP/2/18510 and BP/2/24459a), flowers (BP/2/18194, BP/2/18195, and BP/2/18047), angiosperm leaves (BP/2/27544a and BP/2/25700) and seeds (BP/2/24343a and BP/2/26889). However, the only detailed study of the macrofossils has been that of Bamford (personal communication), which has already been mentioned in the section on the dating.

Bamford found plant fragments in the following proportions, Pteridophyta (ferns) 9.4 %, angiosperm flowers 13.8%, angiosperm leaves 45%, angiosperm stems 14.9%, and angiosperm seeds 16.9%. She was able to identify 29 leaf types, 14 seed types, and four flower types belonging to five plant orders, the Magnoliales, the Laurales, the

Hamamelidales, the Violales and the Typhales. The first two orders are relatively "primitive" among the angiosperms and the representatives of the Hamamelidales and the Violales that she has identified are less derived members of these orders. The specimens which she placed in the Typhales are interesting because they resemble the extant genus Typha (without fertile material it would be impossible to be certain), which are the bullrushes.

Angiosperms first appear in the fossil record in the Early Cretaceous, becoming more common in the Upper Cretaceous (Taylor, 1981). Insects, in particular Coleoptera, were probably important in angiosperm evolution. Insects feeding on ovaries of ancestral forms may have provided a selection pressure for the development of ovaries protected by carpels - a characteristic feature of the angiosperms (Crowson, 1981).

Possible examples of early plant/insect interactions are to be found at Orapa. Many of the insects were feeding on the plants (McKay and Rayner, 1986; Rayner and Waters 1989a). Some of the Hymenoptera and Diptera may have pollinated the flowers (Rayner, 1987; Waters, 1989a&b). In any case, the discovery of a flora of early angiosperms along with an associated insect fauna in the mid-Cretaceous, may provide interesting insights into the evolution of this group of plants and plant/insect interactions.

4.3.2 Insects

Reports of southern African fossil insects are particularly sparse, and they are restricted to the Lower Permian (Upper Carboniferous?) (Pruvost, 1934; Zeuner, 1955; Riek, 1974a; 1976a and b), Upper Permian (Riek, 1973; 1976e Rayner and Coventry, 1985), Triassic (Haughton, 1924; Zeuner, 1939, 1961; Riek 1974b, 1976c and d; Anderson and Anderson, 1983), and a few isolated fragments from the Cretaceous (Reuning, 1931; Smith, 1986).

Cretaceous insect localities are rare, and most of these are in the Northern Hemisphere. In the southern Hemisphere, Cretaceous localities are known from Chile (Kuschel, 1959), Australia (Jell and Duncan, 1986) and Brazil (Wighton, 1987). The Orapa deposits will, therefore, contribute significantly to our knowledge of Southern Hemisphere fossil insects (McKay and Rayner, 1986).

Van Dijk (in Dobbs 1978) was the first to report on the insect fauna from Orapa. He found cockroaches, waterbugs, waterboatmen and "ladybird sized beetles". However, his finds were from the altered beige or yellow sediments mentioned in the section on geology and the following section and were consequently poorly preserved (van Dijk, personal communication).

Since then, Orapa insects have been described in McKay and

Rayner (1986), Rayner and McKay (1987), Rayner (1987), Rayner and Waters, (1989a&b), Waters, (1989a&b). Their findings, together with my own observations of the Orapa collection, are summarised below.

From the catalogue of Orapa fossils I have divided the insect fossils into the following categories: 40.4% of the insects could not be identifed; 9.9% were Blattodea; 1.5% were Orthoptera; 3.2% were Hemiptera; 38.7% were Coleoptera; 3.3% were Diptera; and 3.9% were Hymenoptera. In addition, one specimen of a zygopteran (Fig. 13) and four specimens belonging to the Dermaptera have been recovered. All of the insects found have been adults.

Orthoptera, an orthopteran jumping hind leg was illustrated by Rayner and McKay (1987) and a specimen (BP/2/18617a&b), tentatively placed among the gryllidae, was briefly described and illustrated by McKay and Rayner (1986) and McKay and Rayner (1987). A well-preserved cockroach (Blattidae) was illustrated by McKay and Rayner (1987).

Termites, which are today common in the Orapa area, are absent from the fossil fauna. Their reproductives are weak fliers and I predict they would have become trapped in the lacustrine deposits. However, only primitive termites have been previously described from the Cretaceous (Ruiz and Delclòs, 1986; Jarzembowski, 1981), so they presumably only diversified and became common in the Tertiary.

The forewing of an aphid has been described by Rayner and Waters (1989a) and tentatively placed in a new genus and species Siphonopteroides? orapensis, and McKay and Rayner (1986) and Rayner and McKay (1987) illustrated and briefly described a rather poorly preserved specimen of a heteropteran.

Coleoptera make up the largest proportion of the identified insect fossils. Three possible reasons are suggested for this below.

i) It is almost always possible to identify a beetle fragment because beetles have tough armored bodies and distinct elytra, whereas the wing fragments and soft bodies of most other insects are not so easy to classify.

ii) Coleoptera are the most species-rich of all insect groups, and would therefore be expected to be the most common.

iii) With their tough exoskeletons and elytra, Coleoptera are more likely to be preserved than their soft bodied relatives.

Families of Coleoptera which have been found include: Carabidae [described in detail in a later section; one specimen (BP/2/18669) was described briefly and figured in McKay and Rayner (1986) and Rayner and McKay, (1987)], Staphylinidae [BP/2/26888 was figured in Rayner and McKay (1987)], Scarabaeoidea [a specimen (BP/2/18564) was figured and described briefly in McKay and Rayner (1986)], Elateriodea [a specimen (BP/2/18625a and b) possibly belonging to the subfamily Cardiophorinae of the family Elateridae (Crowson, personal communication) was figured in McKay and Rayner (1986)], Cerambycidae, and Curculionoidea [one specimen (BP/2/18493), possibly belonging to the family Apionidae (Oberprieler personal communication) was described briefly and figured in McKay and Rayner (1986) and Rayner and McKay, (1987)].

The absence of Archostemata is notable, as these beetles made up the largest proportion of the earlier Mesozoic Coleoptera (Ponomarenko, 1977).

Another, interesting beetle which has been discovered is the specimen (BP/2/27354) illustrated in Figs 11 and 12. The specimen has two distinct pairs of eyes, which indicate that it belongs either to the Gyrinidae or the Mesozoic family of the Coptoclavidae. According to Ponomarenko (1977), the two families may be differentiated by the well developed meso- and meta-thoracic legs of the Coptoclavidae; these legs are reduced in the Gyrinidae. The specimen illustrated has well developed mesothoracic and metathoracic legs, which indicates that it may well be a coptoclavid. If this diagnosis is correct it is a most interesting occurence. Firstly because it supports a Mesozoic age for the Orapa deposits, and secondly because the Coptoclavidae (like the Gyrinidae) was an aquatic beetle family (Ponomarenko, 1977).

The families of Tipulidae (Rayners and Waters, 1989b), Bibionidae (Rayner, 1987), Empididae (Waters, 1989a), Hybotidae (Waters, 1989b), Mycetophilidae, Anisopodidae (a tentative identification) and Rhagionidae (Waters personal communication) have been identified among the Diptera. Diptera BP/2/18217 [possibly belonging to the family Tabanidae, Waters, (personal communication)] and BP/2/25963 were described briefly and figured in McKay and Rayner (1986) and Rayner and McKay (1987) respectively. The dipteran fauna is apparently very modern, two specimens <u>Empis</u> <u>orapaensis</u> (Empididae) (Waters, 1989a) and a <u>Helius</u> sp. (Tupilidae) (Rayners and Waters, 1989b) were placed in modern genera. A third specimen, <u>Pseudocarterus</u> <u>orapaensis</u> (Hybotidae) (Waters, 1989b) is closely related to extant genera. The Diptera are at present being studied by S. Waters.

The Hymenoptera are represented by the families of Ichneumonidae, and Braconidae, and by the superfamily Proctotrupoidea (Wiessenbacher, personal communication). There are also many unidentified hymenopteran specimens. An unidentified specimen (BP/2/22898b) is described briefly and figured in McKay and Rayner (1987). Ants and Bees are interesting in their absence from the Orapa hymenopteran fauna. However, I am not confident that I would neccessarily have identified specimens if I had come across them; particularily those fragments represented by wings only, or primitive bees which resemble wasps (Connel, personal communication). Ants have already been described from the Cretaceous but only diversified during the Tertiary (Wilson, 1987). The evolution of the Apoidea was well underway by the end of the Cretaceous. Michener and Grimaldi (1988) have described a stingless honey bee (Trigona prisca) from deposits of a similar age to those at Orapa.

The absence of Lepidoptera from the Orapa fauna is also notable. Rain in the Orapa pit, while we were collecting in April 1986, resulted in the formation of numerous mud puddles in which many insects became trapped. Lepidoptera were the most common of these. If Lepidoptera were as common in the Cretaceous, it seems reasonable to expect that they would have been represented in the fauna at Orapa. Lepidoptera first appeared in the Triassic of Australia (Tindale, 1980), but possibly only became common when the angiosperms had risen to dominance.

With the exception of the coptoclavid, all the fossil insects from Orapa which have been studied in sufficient detail and are well enough preserved, have been placed in extant families or even genera (Waters, 1989a; Rayners and Waters, 1989b). There are, however, three other forms which seem to be exceptions. The first (Form 1, Fig. 14), which is represented by at least ten specimens (a search of the entire Orapa collection will almost certainly produce more), is a fairly large soft bodied insect with long filamentous antennae, small slender legs, full length elytra with no trace of venation, hind wings with many longitudinal and cross veins, and a pair of cerci. The second (Form 2, Fig. 15), which is represented by 25 specimens, has antennae with at least twenty segments; fore wings which are reduced to short 'knobbly' elytra which, like those of a staphylinid, do not cover the abdomen; a pair of hind wings with complex venation reminiscent of primitive Mecoptera, Megaloptera, and Neuroptera (as illustrated by Riek, 1970); a pair of short hairy cerci, and an ovipositor. One of these specimens (BP/2/18419) was initially described as a staphylinid beetle by McKay and Rayner (1986). The third (Form 3, Fig. 16), which is represented by only one specimen (BP/2/27302), is soft bodied. Its distinguishing characters are a pair of cerci, an ovipositor, and wings with many cross veins and intercalated longitudinal veins.

Carpenter (personal communication), who has examined photographs of these specimens, suggested that forms 2 and 3 may belong to the cockroach genus of Articoblatta Handlirch, which is known from the Upper Jurrasic of England and the USSR. According to Carpenter, Articoblatta, along with other female cockroaches of the Palaeozoic and

Mesozoic, may be distiguished from extant cockroaches because they had external ovipositors. Carpenter further reported that similar insects have also recently been recovered from Brazil. In addition, Chen and Chuan-Chien (1973) described a fossil from the lower Cretaceous of Yumen, which has full length elytra with distinct venation, membranous non folded hind wings with complex venation, and antennae with 15-16 visible segments. They suggested that the specimen is an intermediate between Coleoptera and Megaloptera and place it in a new family the Umencoleidae (Coleoptera).

The small number of fossils of these archaic insects recovered from the the Cretaceous suggests, either that they were rare, or had a low fossilisation potential.

The Orapa specimens still need to be systematically described in order to test Carpenter's diagnosis. However, the discovery of these archaic forms from Botswana, Brazil and China in the Cretaceous does reveal that, during this time period, unique Mesozoic insect forms and modern forms [sometimes closely related or belonging to extant genera (Jell and Duncan, 1986; Waters, 1989a, Rayners and Waters, 1989b)] could be found together. The discovery of such a mixed fauna suggests that the archaic fauna of the early Mesozoic was gradually replaced by a modern insect fauna. This change over probably occurred largely in the Upper Jurassic (judging from the mainly modern faunas reported from Orapa and other Cretaceous insect sites), throughout the Cretaceous and perhaps even as late as the Palaeocene. Fossils from Eocene ambers are modern in form although Crowson (1981) pointed out that different forms were dominant during the Eocene than are dominant today. This gradual change over indicates that insects were little affected, at least at the higher taxonomic levels, by the terminal- Cretaceous event which apparently had such a dramatic effect on the vertebrate and marine invertebrate fauna.

4.4 Summary

The Orapa fossil assemblage consists mainly of terrestrial plants and insects. No vertebrates have been recorded. In contrast other epiclastic deposits have fossils assemblages with a high proportion of aquatic forms, some vertebrates and with few insects. The plant macroflora includes ferns and both primitive and advanced angiosperms. Few palynomorphs have been recovered from the Orapa deposits. The insect fauna is diverse but represented only by adults. The fauna seems, superfically, to belong mainly to extant families or even genera, although there are a few archaic forms. The Isoptera, Formicidae, Apidoidea and Lepidoptera, which are common in modern insect faunas, are made conspicuous by their absence.

CHAPTER FIVE

TAPHONOMY

In this section, I propose to discuss the manner in which the insects and plants at Orapa were buried, became fossilised, and were altered after deposition.

The fact that fossils are limited almost exclusively to the laminated and unlaminated shales in the center of the sedimentary basin, suggests that they were not transported into the lake by mud or debris flows. They either lived in the lake, or somehow walked, flew, or were blown into the waters. They then became trapped in the muddy bottom, where they were buried and eventually fossilised.

This raises the question of whether or not animals were living in the lake. There is some evidence for both alternative hypotheses. Evidence for life in the lake is given below.

i) There are aquatic insects in the collections. These are the fossil waterbugs and waterboatmen, reported by Dobbs (1978), and the zygopteran (damsel fly) (Fig. 13) and waterbeetle (Figs 11 & 12).

ii) The presence of almost complete plants, including flowers alongside numerous Coleoptera (which have yet to be identified) (Fig. 10). This assemblage suggests that the plants were perhaps growing in shallow waters in the lake, when they became buried by a mudflow. The Coleoptera may have been feeding on the flowers at the time of burial. Such an assemblage could only have grown in the lake waters if the waters were not poisonous to the plants.

iii) Specimens have been tentatively ascribed to the genus Typha (bullrushes).

Evidence against life in the lake is now given.

i) No fish, frogs, aquatic gastropods, aquatic insect larvae, or ostracods have been recorded from the Orapa sediments. As mentioned in the review of the fossil fauna and flora from Orapa, these are a common component of faunas from other epiclastic deposits. The Australian Koonwarra fauna (Jell and Duncan, 1986) is also from lacustrine sediments and has all the above components (except for the frogs) in abundance.

ii) Most of the insect remains are complete. This indicates a lack of scavenging.

iii) There is no sign of animal activity such as burrowing or tracks (bioturbation) in the sediments.

iv) The terrestrial nature of the insect fauna recovered from Orapa.

How can these opposing groups of evidence be reconciled? McKay and Rayner (1986) suggested that conditions at the bottom of the lake may have been inhospitable to animal life. They suggest further that frogs and fish may have lived in the oxic layer at the surface of the lake, but were not preserved because of acidic conditions at the lake bottom. I now think that this is unlikely because anoxic, acidic conditions apparently existed at the lake bottom which overlay the Stompboor pipe (Smith, 1986), yet fish and frogs are still preserved there.

It is more likely that the water was inhospitable to animal and plant life, and that the aquatic insects flew in from elsewhere. An analogous situation is found today at Soutpan, a saline lake in an extinct volcano (Trusswell, 1977) about 40km north-west of Pretoria. The crater-lake water is inhospitable to most aquatic life, yet I have observed dead aquatic insect adults such as nepids (Nepidae: Heteroptera) and dytiscids (Dytiscidae: Coleoptera) at the waters edge. Also the plants could have been blown or washed into the lake and concentrated together with the Coleoptera; perhaps by wave action. The identification of the genus Typha is, in any case, tentative (see section reviewing the fossil flora).

McKay and Rayner (1986) also suggested that waters in the lake may have been poisoned, either by volcanic residues, or perhaps by excessive salinity. It is interesting that beetles from the famous lacustrine Kara Tau series in Soviet Central Asia belong mainly to terrestrial groups, and are also frequently in a complete condition suggesting a lack of scavangers. It has been suggested that here also the water was poisoned or heated by volcanic activity at the time of deposition Crowson (1981).

I suggest that most of the plants and insects preserved in the sediments came from outside the lake. Plant matter and insects landed on the water, and, in most cases floated, to become concentrated round the lakes edge and in the shallows by wave action. Soutpan again provides an analogous situation. Here the water is rich in insect remains, which mostly float on the surface of the water and become concentrated in a ring round the lake's edge. Evidence for a shallow water depositional environment for many of the insects is:

i) most of the well preserved insects and many of the well preserved plants come from shales that are red or brown in colour, indicating deposition in an oxidising environment;

ii) some of the red shales in which insects are preserved have a pitted pattern at their surface rather like rain drop impressions, indicating that the muds at the lake bottom were at some stage exposed to the atmosphere;

iii) many of the insects were deposited with their wings outstretched; I think that insects settling through the water column in deeper water would tend to have their wings folded over;

iv) insects are often aggregated into clumps indicating concentration through wave action (concentration through wave action around a lake edge, or on a mud flat would also explain the extremely rich deposit of fossil insects at locality 14);

v) there are no organic rich laminations which could only form in undisturbed deeper waters.

In contrast to the shallow water sediments, deep water environments are indicated by green or grey mudstone (which probably represent anoxic conditions), and laminated shales that are rich in plant fragments and isolated beetle elytra.

Once the plants and insects were trapped in muddy lake sediments, they were buried, perhaps gradually by lacustrine deposition, or more rapidly by turbidity currents and mud flows.

Plant and insect remains were placed under high pressures, and perhaps moderately high temperatures as the sedimentary sequence grew thicker. This drove all the volatiles from the organic matter, resulting in the formation of coalified compressions (sensu Schopf, 1975). Coalified compressions (eg. Fig. 13) are usually very well preserved, with fine details such as hairs and spurs visible. Sediments containing coalified compressions tend to be grey, olive-green or dark brown in colour and rich in carbonaceous material.

After deposition, many of these sediments were subject to oxidisation by ground waters. This resulted in the formation of cream or buff coloured sediments. Oxidisation also removed, all or most, of the organic matter from the coalified compressions leaving behind only impressions (sensu Schopf, 1975). An example of an impression is illustrated in Figs 18 and 20. Such impressions are often stained brown or red by iron oxide or hydroxide. Fine details may be visible, especially under oblique non polarised light. However, structures such as hairs or spurs are seldom preserved.

Evidence that oxidisation of the sediments occurred after deposition was visible in April 1986 at locality 11. Here, the shales were observed grading from green, grey and brown to a cream or buff colour across the strike of the sediments in the space of three meters.

Summary

The terrestrial nature of the Orapa fossil fauna and flora suggests that the waters of the palaeolake were poisoned, perhaps by volcanic residues or excess salinity. Insects and plants flew, walked or were washed into the lake. They then either sank to become deposited in the deeper parts of the lake, or they floated on the waters surface to become concentrated around the lakes edge by wind and wave action. They were buried by mudflows, turbidity currents or gradual lacustrine deposition and became fossilised. Post-depositional oxidisation, perhaps by ground waters, resulted in the formation of the cream or buff coloured sediments and altered coalified compression fossils to impressions.

CHAPTER SIX

CLASSIFICATION AND FOSSIL RECORD OF THE CARABIDAE

6.1 Classification of the Carabidae

The family Carabidae is included in the Adephaga, which is one of the four suborders of the Coleoptera. Adult adephagans are distinguished from other Coleoptera by the following characters:

i) the metacoxae are enlarged, more or less immobile, and lie in the same plane as the metathorax and the abdomen (Crowson, 1955; Ponomarenko, 1977; Lawrence and Newton, 1982);

ii) six sternal plates, representing segments two to seven, are usually visible (Crowson, 1955);

iii) the first visible abdominal sternite is sclerotised (Lawrence and Newton, 1982), and divided completely in two by the hind coxae (Crowson, 1955);

iv) the presence of pygidial defence glands (Schildknecht, 1970; cited by Crowson, 1981).

Adephagan larvae are characterised by:

i) mandibles without a mola (Crowson, 1955; Lawrence and Newton, 1982);

ii) labrum fused to head capsule (Crowson, 1955; Lawrence and Newton, 1982);

iii) hypopharynx without a sclerome (Crowson, 1955);

iv) narrowing of the buccal opening (Lawrence and Newton, 1982).

The classification of the Adephaga is controversial, and a variety of schemes have been proposed (e.g. Crowson, 1955; 1960; Bell, 1967; Lawrence and Newton, 1982). For convenience of discussion, the classification of Lawrence and Newton (1982) is used here. These authors divide the Adephaga into the following groups:

i) the aquatic, Haliplidae, Amphizoidae, Hygrobiidae, Noteridae, Dytiscidae, and Gyrinidae;

ii) the terrestrial, Trachypachidae, Rhysodidae, Paussidae, Cicindelidae and Carabidae.

Traditionally, these two groups have been termed the Hydradephaga and the Geadephaga.

However, the Trachypachidae have many of the hydradephagan characters (other than the various aquatic adaptations), making this division artificial (Crowson, 1960; Roughley, 1981; Evans, 1985; Kavanaugh, 1986). The classification of the Carabidae itself is also a matter of dispute. This subject has been reviewed thoroughly by Ball (1979). At one time or another, all the Geadephaga have been included among the Carabidae. In one of the most recent classifications (Kryzhanovskiy, 1976), all the geadephagans, except the Rhysodidae, were included in the Carabidae. However, Bell and Bell (1962; cited by Kryzhanovskiy, 1976) and Erwin (1985) classified the Rhysodidae among the carabids. Nichols (1985) questioned whether the Cicindelidae should be included among the carabids, and even whether the carabids themselves should be considered a monophyletic group. Most authorities seem to agree now that the trachypachids should be excluded from the Carabidae (Crowson, 1955; 1960; Ponomarenko, 1977; Roughly, 1981; Evans, 1985; Erwin, 1985; Kavanaugh 1986), and that the paussids be included among the carabids (Kryzhanovskiy, 1976; Erwin, 1985).

In the following section I propose to discuss the fossil record of the Carabidae and early Adephaga.

6.2 The fossil record of the Carabidae

It is convenient to divide the the fossil history of the Carabidae into three phases, 6.2.1 the pre-adephagan Coleoptera, 6.2.2 the Mesozoic Carabidae, and 6.2.3 the post-Mesozoic Carabidae.

6.2.1 The Pre-adephagan Coleoptera

The Coleoptera probably arose from a neuropteroid ancestor in the late Carboniferous or early Permian periods (Crowson, 1981; Lawrence and Newton, 1982). Further, Erwin (1979) has hypothesised that the Adephaga arose from an aquatic neuropteroid ancestor in the Permian.

The first coleopterans which appear in the fossil record, however, are members of the Lower Permian Tschercardocoleidae from Czechoslovakia and the USSR. They differ radically from extant Coleoptera (Crowson, 1981; Lawrence and Newton, 1982). There are no reports of adephagan-like beetles from this period, and the Lower Permian Protcoleoptera (sensu, Crowson 1981), if they resemble any extant beetle group, are most similar to the Archostemata.

The first Coleoptera which are truly modern in appearance have been found in the Triassic (Crowson, 1981). During this period, in fact during most of the Mesozoic, the Archostemata was the dominant beetle group (Ponomarenko, 1977). Of particular importance to adephagan phylogeny is the archostematan family Schizophoridae. This group, which was common in the Triassic, was very similar to the Adephaga and could only be distinguished reliably from it by the structure of the hind coxae (Ponomarenko, 1977). Ponomarenko (1977) suggested that it was from these Schizophoridae that the Adephaga were derived.

6.2.2 The Mesozoic Adephaga

The oldest described carabid, <u>Umkoomasia depressa</u>, was described by Zeuner (1961) from middle Triassic deposits in Natal, South Africa. This identification is, however, only tentative and based on a single elytron. In view of the difficulty experienced by Ponomarenko (1977) in differentiating between archostematan schizophorids and Adephaga, that identification should be considered suspect.

Almost our entire knowledge of Mesozoic Adephaga comes from beautifully preserved fossils from localities in the Asian part of the USSR. Recent references pertaining to these fossils include Ponomarenko (1977, 1980 *, 1985, 1986*, 1987). In addition there have also been discoveries in China; recent publications include Hong (1982*; 1983*) and Lin (1983*; 1986*).

---

* I have not had the opportunity of examining these references, but was able to ascertain what taxa were described from the Zoological record (1982, 1984, 1985, 1987, 1987/88). No new families of Adephaga, other than those described by Ponomarenko (1977, 1985) have been described. There were, however several new genera which were placed <u>Incertae Sedis</u> among the Caraboidea (considered here to include all the families of Adephaga) (Hong 1982; 1983; Ponomarenko, 1986) or Adephaga (Ponomarenko, 1986).

These early Adephaga differ from extant forms in several respects. Firstly, most of them had the metepisterna forming part of the wall of the mesocoxal cavities. This character is today found in the Amphizoidae, some Dytiscidae and Spanglerogyrus of the Gyrinidae (Kavanaugh, 1986). A second character is that of enlarged metacoxae which extend to the elytral epipleura. This type of metacoxa is today found in the Hydradephaga and the Trachypachidae. The third character is the posterior metacoxal plates of many of them (e.g. Triaplidae, Eodromiinae, Jurodidae, Protorabinae and some Coptoclavidae). In extant Adephaga, this character is found in the Noteridae (Kavanaugh, 1986), and in an enlarged state among the Haplidae where it functions as a posterior air store for exhaled air (Evans, 1985). Ponomarenko (1977) and Kavanaugh (1986) agreed that the first two characters are pleisiomorphic for the Adephaga. Ponomarenko considered character three to also be pleisiomorphic. However, Kavanaugh disagreed, he considered enlarged metacoxal plates to be apomorphic in the groups where they occur. The subsequent discovery (Ponomarenko, 1985) of this character in the Jurodidae suggests that it was even more widespread than Kavanaugh suspected and, therefore, that it could, indeed, be pleisiomorphic. Thus, the ancestral Adephagan possibly had the three above characters with a semi-aquatic (Erwin, 1979; Kavanaugh, 1986) way of life.

For alternative views to the above hypothesis see Evans (1977; 1980; 1982; 1985), Roughly (1981) and Nichols (1985). These authors assumed that the enlarged metacoxae which extend to the elytral epipleura are a derived character (from the state in most carabids where they do not reach the elytral epipleura), that the first carabids were terrestrial, and, therefore, that they have not been found as fossils yet. For a critical review of these hypotheses, see Kavanaugh (1986).

The earliest Adephaga are from the Upper Triassic Madigen series of Central Asia. Three groups have been described: the terrestrial Trachypachidae (subfamily Eodromeinae) represented by the genus Sogdodromus, the aquatic Triaplidae (very similar to modern Haliplidae) represented by the genus Triaplus and the aquatic genus Triadogyrus, which Ponomarenko (1977) suggested is ancestral to the gyrinids. This radiation of the Adephaga indicates that the first adephagans appeared early in the Triassic- perhaps even in the late Permian (Ponomarenko,1977; Erwin, 1979; Kavanaugh, 1986) and that by the Upper Triassic both terrestrial and fully aquatic forms already existed.

However, the most suitable fossil ancestor (Ponomarenko, 1977; Kavanaugh, 1986) to the terrestrial and aquatic groups [excluding the Haliplidae (Ponomarenko, 1977; Kavanaugh, 1986) and possibly even the Gyrinidae (Evans, 1985) which may have arisen as earlier separate lineages] only appeared in the early Jurassic. This is the genus

Necronectulus which was erected by Ponomarenko (1977) and is apparently very similar to _Amphizoa_ (Kavanaugh, 1986). The first true carabids also appear in the Jurassic and have been described by Ponomarenko* (1977). These are the Protorabinae and the Conjunctini. Members of the Protorabinae have been recorded from sediments ranging throughout the Jurassic, and also in the Lower Cretaceous (Ponomarenko, 1977; 1980; 1986). They differed from the eodromines, which they resembled in general morphology, because they lacked the laterally extended metacoxae and differed from extant forms because the metepisterna formed part of the boundary of the mid-coxal cavities and the presence of metacoxal plates. The protorabines were possibly derived from an eodromine ancestor as the latter group does not appear to have any apomorphic characters. The Conjunctini were rather unusual because they had the combination of the primitive feature of an isochaete protibia together with the more derived feature of disjunct coxal cavities. Ponomarenko considered them an aberrant group which are an early analogue of modern

---

* Hong (1982; cited by Zoological Record, 1985) has described the genus _Sinocarabus_ with one species _S. longicornutus_ from the Upper-Jurassic of China. It is apparently a true carabid but I am unable to find where exactly it was placed within the family.

carabids. Specimens identified as belonging to the Conjunctini have been reported from both the Upper Jurrasic and the Lower Cretaceous (Ponomarenko, 1977).

Another anomalous, probably terrestrial group from the lower central Jurassic, is the Jurodidae (Ponomarenko, 1985). Its members were characterised by the following combination of characters:

i) enlarged metacoxal plates;

ii) metepisterna which formed the boundary of the mid-coxal cavities;

iii) metacoxae which reached the elytral epipleura;

iv) a non streamlined body with a mobile head;

v) antennae with the last segment dilated;

vi) a small transverse thorax.

Ponomarenko (1985) speculated that they may have been ancestral to the Rhysodidae because of the similar shape of the head. However, I think that this would be unlikely if Erwin (1985) is correct in placing the rhysodids amongst the Carabidae.

These peculiar Mesozoic Adephaga disappeared from the fossil record towards the end of the lower Cretaceous.

6.2.3 The Post-Mesozoic Carabidae

The Carabidae which replaced the Mesozoic forms described above are entirely modern in character. The first of these, which appeared in the Lower Cretaceous, are Carabites vitimensis (Ponomarenko, 1977) and C? nigriventris (Ponomarenko, 1986 cited by the Zoological record 1987). A third species, C. creta, from the Upper Cretaceous (Turonian), is similar to modern mollusc eating forms (Ponomarenko, 1977). However, none of these species was placed formally by Ponomarenko in any carabid tribe or subfamily (I presume this is so for the second species). Ponomarenko (1977) also described a protibia of the harpaline (sensu, Crowson 1955) type from the Turonian. In addition to the Asian fossils, Fujuyama (1978) tentatively placed a pair of elytra, from the lower Cretaceous Tedori Group of Japan, among the Harpalinae. However, Fujiyama did not mention whose definition of the Harpalinae he used.

Carabid fossils of Eocene and Oligocene age are known from the Baltic, Dominican and Mexican ambers (Spahr, 1981a; 1981b). The excellent preservation of insects in amber has made it possible to classify most of them to generic level and a few even to specific level. Spahr (1981a, 1981b) has provided a full bibliography of amber Coleoptera. She listed 34 genera of Carabidae (excluding the Cicindelidae and Paussidae and Rhysodidae), of which seven are extinct.

In these 34 genera, 21 carabids have been identified to species level, 13 of them are extinct and eight are very close to extant species, but cannot positively be placed among them. Therefore, it seems that Tertiary carabids are essentially modern. It is interesting that Spahr listed six genera of Paussidae, of which five are now extinct. Furthermore, 20 species in these six genera have been identified, and all are now extinct. This disparity in extinction between carabids and paussids (which was also noted by Thiele, 1977) indicates that paussids have undergone a far higher speciation rate since the Tertiary than have the carabids. It can perhaps be explained by the close relationship of paussids with ants, which first appear in the fossil record in the Cretaceous and have diversified since then (Wilson, 1987). In addition to paussids and carabids, Spahr listed a species of Rhysodidae and three genera of Cicindelidae, two of which are extant, Megacephala (Tetracha) carolina and Pogonostoma chalybeam. Lindroth (1957, cited by Thiele 1977) has questioned the identification of Megacephala carolina. Matthews (1979) has recorded carabids from alluvial sediments of the Alaska and Canadian archipelago of Miocene age. These remains are very well-preserved and have been placed with confidence in extant genera, but probably belong to extinct species which occupied different habitats from those of their extant relatives.

In comparison with earlier fossils, Quaternary carabids are well known. This is due to their excellent preservation, often in tarpits and peatbogs, which makes it possible to identify them with confidence to the level of species. Indeed, it has been possible to demonstrate that most of them belong to extant species (e.g. Coope, 1979; Ashworth, 1979). Coope (1978; 1979) has traced climatic changes during the Pleistocene glaciations in Britain using changes in carabid faunas as indicators. However, Kavanaugh (1979) has inferred speciation in the genus Lebia in North America during the Pleistocene glaciation.

6.3 Summary

The adephagans probably arose from an aquatic or semi-aquatic schizophoroid ancestor in the early Triassic. The carabidae possibly arose from an ancestor resembling the Eodromeinae (Trachypachidae) with metepisterna which reached the mesocoxal cavities, metacoxal plates, and metacoxae which reached the elytral epipleura. The first true carabids appear in the Jurassic and are members of the Protorabinae and the tribe Conjunctini (Incertae sedis). The Protorabinae had metepisterna which reached the mesocoxal cavities and metacoxal plates, while the Conjunctini were distinguished by the combination of conjunct mesocoxal cavities and isochaete protibia. In the Cretaceous, carabids which are modern in appearance appeared. Tertiary carabids can usually be placed in extant genera but belong to extinct species. Quaternary carabids can generally be placed in extant species.

CHAPTER SEVEN

MATERIALS AND METHODS

7.1 Sites within the Mine

Fossil material was collected from eighteen sites in the mine, between 1983 and 1988. Dates when the collections were made, co-ordinates of the localities, and their approximate elevations above sea level are given in Table 2. The position of the localities within the mine are also shown in Fig. 17.

Date Collected	Site	E-W co-ordinate	N-S co-ordinate	Elevation (m
August 1983	1	49.00	45.50-46.00	927.45
	2	50.50	43.50-44.90	932.44-932.26
October 1983	As Above			
February 1985	3	48.00	45.50-46.00	927.52
	4	48.75	46.00-46.75	928.12-929.75
	5	48.00	47.00	929.15-930.00
	6	49-50-50.00	46.50-47.00	934.22
	7	50.50-51.00	47.00-47.50	934.65
	8	51.50-51.75	46.80-47.00	928.09
September 1985	9	51.50	46.50-47.00	928.09
	10	49.40	44.00-44.80	925.11-925.48
	11	49.40-50.00	44.75-45.00	925.11
	12	48.00	43.75-44.00	921.45
	13	50.50-51.25	44.80-45.75	924.52-925.65
April 1986	as in September 1985			
	14	51.00-51.50	44.70-45.30	919.51-920.31
	15	50.00-50.50	43.75-44.10	920.82
October 1987	revisited 13			
	16	49.50-50.00	44.50-44.75	921.52
September 1988	17	48.00-49.00	45.75	912.04
	18	49.25-49.80	47.50	930.00
	Spoil Heap			

Table 2. Elevations, and grid co-ordinates of the various sites in th mine (see Fig. 17) and dates when the collections were made.

7.2 Collecting Methods

The most efficient and reliable method of collecting fossils from the mine was only achieved after a certain amount of trial and error. At Orapa, fossils are found in the bedding planes of the shales, some of which proved to be more productive than others. When a productive bedding plane was found, every attempt was made to follow it laterally. Bedding planes were split with a hammer and a chisel. A chisel 2.5cm in width and a geologists pick were found to be most suitable for the task, though smaller implements were useful for uncovering small, delicate specimens, and a larger hammer was useful for splitting large rocks. A crowbar was used to free large blocks of rock from the rock face.

Rock that was exposed by mining activities began to weather rapidly. Partially weathered rock surfaces proved the easiest to work with. Unweathered rock was often too hard to split, and very weathered rock yielded delicate specimens that crumbled easily. Most specimens were, therefore, collected from the talus slopes at the base of the rock face. This means that, in general, it was impossible to determine the exact origin of any specimen in a rock face. Locality 14 had already been dynamited and bulldozed before we collected there. In addition, specimens were collected from the spoil heap which is the dumping ground for fine grained sediments collected from within the Orapa pit.

7.3 Storage

It proved a difficult task to preserve many of the the delicate plant and insect specimens during transportation back to the Bernard Price Institute in Johannesburg. Freshly collected specimens were slightly damp, and were wrapped in newspaper to stop them from drying too rapidly and, therefore, cracking. Glyptal varnish (a laquer cement produced by General Electric) was used in some cases to bind cracked specimens, but, it generally proved more suitable to wrap the specimens immediately in newspaper, and glue them together back in the laboratory. In early collecting trips specimens were coated in glyptal to prevent them from rapid dehydration. This has proved to be a most undesirable practice for four reasons:

i) dust always becomes trapped in the glyptal, obscuring surface details of the specimen;

ii) it becomes impossible to uncover a specimen further if necessary;

iii) glyptal creates reflections in non-polarised light, making it extremely difficult to examine a specimen under the microscope;

iv) a specimen treated with glyptal cannot be examined under the electron microscope.

After, specimens were wrapped with newspaper, they were packed tightly in tin trunks or cardboard boxes between layers of foam, to prevent damage during transportation-particularly on the calcrete roads of Botswana.

Once the fossils had arrived in the laboratory they were unwrapped, sorted, and numbered. Where a specimen was not fully exposed, it was uncovered with fine needles (*dégagement* of Leclerq, 1960). This proved to be a delicate task, and in many cases the specimen came away with the rock covering it, or the needle slipped and damaged the specimen irreparably. An attempt to uncover a fossil should, therefore, only be made if most of it is covered, or if some structure crucial to its identification is obscured by sediment.

Specimens were stored on foam covered metal trays. At present there are 5200 (excluding the majority of material collected in 1989) specimens from Orapa, many with more than one fossil visible on its surface, and more collecting trips are planned. The sediments will be completely removed in the process of mining diamonds, and it is hoped that further collections will be made until then. In the future, half of the specimens, including those figured in this thesis and other publications, will be housed in the National Museum, Botswana, in Gabarone, and the other half in Johannesburg.

7.4 Techniques.

Interpretation of the fossils was often difficult with many structures only becoming visible under light from certain angles. Specimens were observed under stereo microscopes (Zeiss SV8 and Wild M5) and light from a fibre optic light source.

Non-polarised light proved best for examining relief in a specimen, but excess reflection made it difficult to view the outline and fine details. Polarised light (obtained by attaching a polarising filter to both the light source and the objective lens of the microscope, and rotating one of the filters until the polars are crossed) was very effective for this. The way in which the filters work is described below.

Light passing through the polarising lens, covering the light source, is polarised. This is then reflected from the specimen, without having its plane of polarisation affected, and is thus eliminated when it passes through the polarising filter covering the objective lens of the microscope. Polarised light reflected from the matrix has its plane of polarisation changed by the anisotropic minerals in the matrix, and thus may be passed through the polarising filter covering the objective without extinction. The result of the above principles is that the specimen appears very dark against a much lighter matrix. Unfortunately, however, polarised light removes all relief from the specimen and the polarising filters decrease the resolution of the microscope.

Drawings were made with the aid of a Wild camera lucida and a Zeiss camera lucida attached to a Wild M5 and a Zeiss SV8 stereo microscope respectively. Photography involved the use of a Zeiss M35 camera attached to a Zeiss SV8 stereo microscope, and Ilford PanF 50 ASA film. The negatives were printed on Tura grade three paper.

7.5 Selection of the Specimens.

Unfortunately more specimens of Carabidae were collected than was possible to identify or describe in the time available. Therefore, the specimens presented in this thesis are the best preserved. With the experience gained from describing these it may be possible to describe some of the others, or possibly to assign them to the same species/types described here. The numbers of the 34 specimens not described here are given in Appendix 3. Preliminary examination of these indicates that it is unlikely that any of them will substantially alter the conclusions drawn in this thesis.

7.6 Method of Identification, Terminology and Measurements.

7.6.1 System of Classification Used.

The arrangement of the genera into higher taxa, for convenience, follows that of Basilewsky (1950, 1951, 1958,

1963) and Straneo (1958), who have been responsible for most of the recent work on Southern African carabids. This arrangement differs from that of other authors (e.g. Jeannel 1941, 1942; Kryzhanovskiy, 1976; Erwin, 1985) mainly in that their convention has no hierarchical arrangement of taxa above the level of tribe, which Basilewsky terms subfamilies.

7.6.2 Method of Identification.

Fossils were examined, drawn, described, and photographed. Attempts were made to identify them by comparing them with extant Southern African species, and, as far as possible, to diagrams and descriptions of tribes and subfamilies not represented in the subregion. A list of the genera of African carabids with which the fossils were compared is given in Appendix 1.

This comparative approach was necessary because the features used in the identification of extant carabids, such as setae, genitalia and the position of tibial spurs and ventral sclerites are in most cases either not preserved or difficult to interpret on fossils, making it impossible to identify them using a key.

Unfortunately many of the tribes and genera of Carabidae are very similar in morphology. This does not make them amenable to identification using general shape and size. In addition it is possible that convergence produced forms in the Mesozoic, which although superficially similar in morphology to extant taxa, if they existed today would be placed in completely different taxa because they possessed unique combinations of characters which are not preserved on the fossils. An example of such forms are the Conjunctini of Ponamerenko (1977) which, although they are superficially modern in form have the unique combination of both conjunct mesocoxae and isochaete protibia.

Therefore, Darlington (1967) is followed in naming many of the specimens. Where a specimen cannot definitely be placed in a subfamily because it lacks the relevant taxonomic characters, it is placed in the subfamily to which it is the most similar in general morphology. The uncertainty of this assignation is indicated by a question mark after the subfamilies name. In addition, the genus or genera which the fossil most resembles is also mentioned.

I do not think it impossible, in view of the conservative evolution displayed by the fossil diptera from Orapa, and the intercontinental distribution of some of the extant carabid genera (indicating that it is possible that they might have been in existence before the splitting of the continents), that the specimens might belong to extant genera. A taxonomist with a knowledge of extant carabids from elsewhere in the world may be able to assign some of the specimens with ease. In addition, it may be possible, with future technology and techniques (e.g. image analysis), to identify some of the characters on the fossils that are, at present, not immediately visible.

7.6.3 Terminology.

Conventional terminology used for describing extant carabids is used in the descriptions here. A list of terms used, and a diagram illustrating the various structures of a carabid are given in Fig. 85.

Fossils are often preserved in two parts, one on either side of the bedding plane in which the fossil was preserved. One of these images usually has the same relief (a positive image) as the original specimen. The other has the reverse relief (a negative image) of the original. These two images are termed the part and the counterpart, respectively. Therefore, a groove on the part (e.g. a stria) will be preserved as a ridge on the counterpart. Where a specimen is not preserved in part and counterpart, I use the terms positive and negative image to describe its relief relative to the original.

Where a specimen is represented in part and counterpart, and a term is used which indicates relief (e.g. groove or ridge), the term refers to the part of the specimen. The terms left and right refer to the specimens left and right and, again, if the specimen is represented in part and counterpart, the term refers to the part unless unless otherwise stated.

7.6.4 Measurements.

Measurements were made from the camera lucida drawings, and compared well with those made with a micrometer. They were made in such a way as to enable comparison, as closely as possible, with extant species. For example, if a specimen was not totally straight, I attempted to compensate for it, when measuring length, by measuring the head, the prothorax and the abdomen separately and then deriving the length of the specimen from the sum of these measurements. Where only half of the beetle was preserved, and width was being measured, the position of the midline was estimated, and the measurement was doubled. Measurements of the specimens are presented in the descriptions and summarised in Appendix 2. A diagram showing the parameters measured is presented in Fig. 86. The measurements referred to in each description under the title of "Dimensions" are total body length and width at the widest portion of the prothorax.

7.6.5 Diagrams.

No attempt was made to reconstruct the fossils in the diagrams, as this would require too much interpretation. Diagrams are the only way of representing a fossil faithfully. It would be almost impossible to produce one photograph, or even a series of photographs, which show all the features visible in the actual specimen. In these drawings, dotted lines indicate incomplete structures, and solid lines complete structures. The scale line indicates 1mm.

7.7 Distortion of the fossils during fossilisation.

Fossils cannot be interpreted correctly without a knowledge of the ways in which they may be distorted during fossilisation and decomposition.

The first possible source of distortion may occur before fossilisation, while an organism is undergoing decomposition. I have not come across any examples of this type of distortion during my study of fossil beetles. However, Ponomarenko (1977) reported difficulties in interpreting the hind coxae of fossil Archostemata, and Adephaga because of distortion during decomposition. Adephaga may be separated from the Archostemata because their coxae lie in the same plane as the sternal plates, whereas in the Archostemata the metacoxae are in a higher plane than the sternal plates (Ponomarenko, 1977). According to Ponomarenko (1977), during decomposition the abdomen fills with gas, lifting the sternal plates to the same level as the metacoxae, and making it very difficult to distinguish between fossil Archostemata and Adephaga.

A second source of distortion occurs during fossilisation, when the beetle is compressed by the weight of the overlying sediments. The body of the beetle collapses in upon itself, becoming effectively transparent. This results in several unusual effects listed below.

i) It becomes possible to view structures on both the dorsal and ventral surface of the beetle simultaneously (e.g. the stria and the coxae), making it difficult, in many cases, to differentiate between structures that are dorsal and those that are ventral (e.g. it is difficult to differentiate between the dorsal and ventral, anterior and posterior margins of the prothorax; or to differentiate between the prothoracic lateral borders and the proepipleura.)

ii) Internal structures become visible [e.g. the longitudinal median depression or ridge on the prothorax of several fossil carabids is possibly the invagination crease of the internal carina on the notothorax of Hlavac (1975); or in some cases the flanges on the anterior margin of the mesothorax, which function to attach it to the prothorax become visible].

iii) The pressure on the beetle gives it the appearance of having distinct lateral margins, whereas in the living organism, these may be absent (Darlington, 1967). However, in beetles where there are distinct lateral margins, the beetle will collapse along the line of maximum weakness under pressure, which will presumably be the lateral margin.

It is unlikely that major overall changes in shape or general proportions of an organism occur when it is exposed to high pressure. This is because pressure from overlying sediments is equal to pressure from the sides as well as the bottom (Walton, 1936). Evidence in support of this is that the promecognathine, the scaratine, and the harpalines have similar shapes to their extant relatives. However, if a beetle is not lying with its horizontal plane normal to the direction of vertical pressure, it will not collapse symmetrically about its longitudinal axis, and thus may have its shape and proportions changed (e.g. the distortion of the prothorax of BP/2/27356).

CHAPTER EIGHT

TAXONOMY

8.1 Subfamily Promecognathinae

The Promecognathinae is a small subfamily. It is represented on the North West coast of North America by the genus *Promecognathus* Chaudoir with two species (Lindroth, 1961), and in Southern Africa by six species, placed in four genera: *Axinidium* Sturm, *Paraxinidium* Basilewsky, *Metaxinidium* Basilewsky and *Holaxinidium* Basilewsky (Basilewky, 1963). Basilewsky (1963) placed the American promecognathines in the tribe Promecognathiini, and the African species in the tribe Axiniidiini. The species described below is the first ever fossil promecognathine.

Palaeoaxinidium gen. nov.

Diagnosis: The elongate, pedunculate, convex body; mouth parts; and narrow legs with the protibiae only expanded slightly distally, are typical of the subfamily Promecognathinae (Basilewsky, 1958).

The elytra of the fossil differ from those of extant genera as they are unfused terminally, and have distinct stria.

It resembles Promecognathus with respect to the terminal segment of its maxillary palps which are unexpanded or only slightly expanded (the Axinidiini have the terminal segment distinctly expanded) and the frontal grooves which are well developed (the Axinidiini have frontal grooves which are reduced). Palaeoaxinidium has no characters in common with the Axinidiini that it does not share with Promecognathus.

Remarks: In all the extant forms, the elytra are fused along their whole length. It is possible (Basilewsky, personal communication) that the parting of the elytra in the fossil is a product of crushing during the fossilization process. I think that this is unlikely as the elytra have a distinct sutural border distal to the elytral parting which becomes indistinct, or perhaps disappears proximal to the parting. Also, an organism buried in mud will experience equal pressure from the top, bottom and sides and, will therefore be unlikely to undergo any major changes in shape during fossilisation (Walton, 1936).

The specimen may be distinguished from the extant genera by two additional characters. These are the lack of a notch on the labrum, and the maxillary palps which are the same length as the mandibles. However, the notch may not be visible simply because of poor preservation, and, although most promecognathines have maxillary palps which are much shorter than than the mandibles (Kavanaugh personal communication and my own observation), I have observed one specimen where they are almost the same length. Therefore, the length of the maxillary palps relative to the mandibles is variable and is not a good taxonomic character.

Type Species: *Palaeoaxinidium orapensis* sp. nov.

Etymology: Generic name derived from *palaios* which is Greek for ancient, and *Axinidium* the type genus of the Axiniidini (*sensu* Basilewsky, 1963).

Palaeoaxinidium orapensis sp. nov.
(Figs. 18-20)

Holotype: BP/2/18302. Locality 2. An impression fossil, with some dark staining which is probably coalified organic material. The fossil is preserved in a buff coloured mudstone, and shows reverse relief to the original beetle. Parts of the whole body and its associated appendages are preserved.

Dimensions: length 8.56 mm, width 1.72mm.

Description: Body is elongate, pedunculate and convex.

Head: elongate and wide in relation to the prothorax; antennae not preserved; mandibles elongate, as long as the head, curved along their entire length but curved more sharply distally; left mandible with a short longitudinal groove at its base, both mandibles show traces of a central, longitudinal, slightly oblique ridge; maxillae elongated, lacinias long and curved, almost as long as mandibles; maxillary palp with terminal segment incomplete, that portion which is visible is expanded only slightly with at least one prominent seta, penultimate segment small and triangular, second segment long, about four times as long as penultimate segment, and basal segment indistinct; sutures separating labrum and clypeus, and fronto-clypeal suture are poorly preserved; frontal grooves are elongate, extending from just anterior of posterior of head to fronto-clypeal suture; compound eye is small, convex and protruding.

Prothorax: wider than long (ratio of width of the prothorax at its widest point to the estimated length of the prothorax = 1.10), as wide as or slightly wider than head at anterior end; anterior and posterior angles and margins are not visible; prothorax narrows regularly towards its base; lateral grooves are parallel to the lateral margin widening posteriorly, legs are represented by a pair of elongated femora and tibiae, tibiae are slightly expanded distally.

Mesothorax: mesothorax with a long scutellum and a pair of elytra which are fused along their entire length except for their distal portion; elytra have distinct striae, which are not well enough preserved to determine their exact number or pattern; lateral margins of elytra are incomplete, and curve gradually and evenly until the last fifth of their length, from where they curve more sharply towards the apex; left coxal cavity is visible, it is indistinct, small and oval; legs are represented by a pair of elongated femora and tibiae.

Metathorax: legs represented by an oval trochanter (about twice as long as wide), a pair of elongated femora (ratio of length of trochanter to length of femur is 0.31), and a pair of elongated tibiae.

Abdomen: with a pair of sternal sutures.

Etymology: orapensis, latinised form of Orapa, the site where the specimen was recovered.

Remarks: The longitudinal ridges on the mandibles may represent similarly positioned ventral seteated grooves on extant promecognathines. Such grooves may be involved with some form of pre-oral digestion as described by Evans and Forsythe (1985).

Phylogeny: Basilewsky (1958, 1963) noted that the Axinidiini and the Promecognathini are very similar, despite their great geographical separation. However, he was able to separate them on several characters. Taking those characters of Basilewsky and those on the fossil, whose polarity can be determined, the following list is obtained. A (0) implies an ancestral character and a (1) a derived character.

A) Marginal groove of the elytra is well developed and reaches as far as the peduncle (0), or the marginal groove of the elytra stops well before the peduncle from which it is separated by tubercle (1).

B) Dorsal surface of the elytra with setae (0) or glabrous (1).

C) Parameres with terminal bristles (0) or without terminal bristles (1).

D) Apical orifice of median lobe with a ligule (0) or without a ligule (1).

E) Terminal segment of maxillary palp unexpanded (0) or expanded (1).

F) Frontal sutures well developed (0) or poorly developed (1).

G) Elytra unfused distally (0) or fused along their whole length (1).

H) Elytra with well developed stria (0) or with reduced stria (1).

Characters A(1),B(1),C(1),D(1), F(1) and H(1) all represent losses or reductions of structures, hence their probable derived state. Character E(1), the expanded state of the terminal maxillary segment, is derived because most carabids do not have their terminal maxillary segments expanded in this manner. The two states of character G are possibly stages in a sequence leading from unfused elytra to fully fused elytra. The former state presumably correlates with fully developed hind wings which is the primitive condition in carabids (Kavanaugh, 1985). A summary of the polarities of the characters in the various taxa is presented in Table 3.

Table 3. Character state matrix for cladistic analysis of fossil and recent Promecognathinae. 0=ancestral state, 1=derived state, ?= not preserved.

Taxon	Character							
	A	B	C	D	E	F	G	H
Promecognathini	1	1	1	0	0	0	1	1
Axinidiini	0	0	0	1	1	1	1	1
Palaeoaxinidium	?	?	?	?	0	0	0	0

The cladogram representing the shortest tree with the least convergence and parallelism is shown in Fig. 21. The Promecognathini and the Axinidiini are monophyletic sister groups which, together, form a sister group to Palaeoaxinidium.

Palaeoenvironment: Little is known about the biology of the living Promecognathinae. *Promecognathus*, is found under rocks and in leaf litter, in mixed hardwood and oak-woodland forests (Kavanaugh, personal communication). Bousquet and Smetana (1986) have described the first instar larva of *Promecognathus laevissimus*. Macswain and Garner (1956) reported that *P. laevissimus* adults feed almost exclusively on the millipede *Xystocheir francisca*. There is also one report of them feeding on tipulid larvae (Macswain and Garner, 1956).

Even less is known about the Axinidiini, of which only one specimen has been collected in the last 25 years. They have been collected from under rocks and plant litter in temperate coastal and riverine forests (Basilewsky, 1963). However, nothing is known of the habitat of *Axinidium angulatum* Basilewsky which has been collected in arid areas. Presumably, this species is found in thick bush along water courses, as is *Paraxinidium andraei* Basilewsky (Endrödy-Younga personal communication). I tried to collect the axinidines from their type localities in 1988 but was unsucessful.

The presence of a promecognathine from the Orapa crater suggests that the crater was probably thickly vegetated in the Upper Cretaceous.

Zoogeography: Basilewsky (1958) remarked that the geographical distribution of the Promecognathinae indicates a former widespread distribution for the group, and suggested that the Axinidiini and the Promecognathini have been separated since, at least, the Tertiary (Basilewsky, 1963). Erwin (1985) labelled the distribution of the Promecognathinae as an 'old amphitropical' pattern (i.e., where a group of carabids has no representatives at the tropics and is not replaced by its sister group there either).

(Erwin, 1979, 1981) suggested a zoogeographic hypothesis (Figs. 22-24) explaining the distribution of the extant Promecognathinae. He hypothesised that during the Jurassic the promecognathines originated in tropical-central Pangea. Then, after an initial period of dispersion, they were split into two lineages by the separation of Gondwanaland and Laurasia. These lineages are today represented by the Axinidiini and Promecognathini. If the position of Orapa is plotted onto Erwin's map (Fig. 23) of the Cretaceous, it falls within the distribution of the Promecognathinae, which he predicted, for that period.

The distribution of the Promecognathinae can, however, also be explained by other hypotheses; three are discussed below. The first, and the one which I think is the most likely, is an adaptation of Erwin's hypothesis. It is based on three critisicms of his model; these concern the time of origin of the Promecognathinae, the rather limited distribution which Erwin allows the promecognathines during the

Mesozoic and the place of origin of the promecognathines.

In order to achieve their present day distribution the promecognathines must have arisen at a time when a dispersal route existed between Africa and North America. Galton (1981) reviewed the evidence for such a dispersal route. Upper Jurassic dinosaur faunas of the Morrison formation in North America and the Tendaguru formation in Tanzania are very similar suggesting that free interchange of the dinosaur faunas between these continents was possible at that time (Galton, 1977, 1981). Such dispersal could have taken place via South America or Europe. According to Schweickert (1981) a land bridge may have existed between North and South America until the end of the Jurassic. However, Galton (1981) also cited evidence for an intermittent land bridge between North America and Africa via Europe as late as the Lower Cretaceous. Therefore, the latest possible time that the promecognathines could have originated would have been the Lower Cretaceous (but see the next hypothesis).

If it is accepted that the promecognathines appeared at some time during the Jurassic then, it is possible or even probable, given the uniform temperature distribution between the poles and the equator (Hallam, 1985), vegetation (Barnard, 1973; White, 1986) and lack of physical obstacles to dispersal between and within the continents during this period, that the promecognathines may have achieved an almost cosmopolitan distribution before the final split between Gondwanaland and Laurasia. This is in contrast to Erwin's rather restricted distribution for the promecognathine stock during that period.

Evidence that Mesozoic caraboids may have had cosmopolitan distributions comes from the Trachypachidae. Erwin (1979, 1981, 1985) has constructed a biogeographic model explaining the distribution of this amphitropical group which is similar to his hypothesis for the promecognathines. One genus of trachypachid Trachypachus has an holarctic distribution, the other genus Systolosoma is located in the temperate zone of South America. According to his model (1979, 1981), the trachypachids, in the Triassic were divided into two vicarient populations; the Systolosoma lineage with a restricted distribution in South America and the Trachypachus lineage, also with a restricted distribution, in North America. The Eurasian trachypachids, according, to Erwin, only dispersed from North America in the Eocene. However, recent fossil finds (Ponomarenko, 1977) indicate that trachypachids occurred in central Asia throughout the Mesozoic. Erwin, (1985), therefore suggested that they had achieved a cosmopolitan distribution in this era. This first alternative hypothesis to Erwin's, therefore, predicts that the Trachypachidae and perhaps even the Promecognathinae might well be found in Australia, either as fossils or as living forms. It is also predicts that promecognathines could be found in Eurasia.

According to Erwin, it was probable that the promecognathines originated around the intersection of pre-S. America, pre-N. America and pre-Africa. However, as already mentioned, temperature distribution in the Mesozoic era was more far more equable than today. According to Hallam (1985), temperatures characteristic of the tropics extended into the mid-latitudes and the distribution of ferns in the mid-Jurassic suggest that climate within the belt 40°N and 50°S was of a tropical to sub-tropical type (Barnard, 1973). Thus, it is possible that the promecognathines could have originated anywhere within this belt. It is also possible that the promecognathines did not originate in the tropics, or that the distinction which we make today between tropics and temperate regions did not exist in the Mesozoic. Extant promecognathines are only found in temperate forests. It seems reasonable, especially considering the morphological consvervatism of this group, that the ancestral promecognathine lived in similar conditions. According, to White (1986), world wide Jurassic floras had a uniform composition and were equivalent to present day warm temperate rainforests. Therefore, the promecognathines could have arisen almost anywhere on the continent of Pangea. Perhaps this similarity between Jurassic vegetation and present day temperate forests also explains the ditribution of other temperate fossil amphitropical groups such as the Trachypachidae. By the above I mean that it is probable that fewer evolutionary change would have been required for promecognathines and trachypachids to adapt to Tertiary and modern day temperate forests than to adapt to the Tertiary and the modern day tropics.

The second alternative hypothesis to that of Erwin's is that the promecognathines could have originated on Gondwanaland after this continent had separated from Laurasia. They could then have dispersed into North America from South America (which had by this time split off from Africa) after the two continents became rejoined during the Tertiary (Hallam, 1981). If this hypothesis is correct the Promecognathinae could have originated almost as late as Orapa times, when South America and Africa had finally separated (Reyment and Dingle, 1987; Owen, 1983).

A third, less conservative alternative model, is that of Humphries and Parenti (1986). They suggested this model in order to explain the amphitropical distributions of the Fagaceae (beeches) and chironomid midges (Diptera), which, like the Promecognathinae and Trachypachidae, have sister taxa represented in the Austral and Boreal regions. They hypothesized that the Austral and Boreal regions were at one time adjacent to each other and adjacent to the tropical zone on a hypothetical continent: Pre-Pangea (this hypothesis of Pre-Pangea is based upon the Pacifica hypothesis of Nur and Ben-Avraham, 1981). Movement of the Austral zone to the other side of the tropical zone would have resulted in the formation of Pangea. Then the break up of Pangea, following conventional models of continental drift, would give the Amphitropical patterns we see today.

This hypothesis suggests a Triassic or even earlier origin for the promecognathines. This is not in accord with the fossil record of the carabids, where modern taxa first appear in the Cretaceous (Ponomarenko, 1977). However, neither is the zoogeographic data in general. Nor does Humphries and Parenti's hypothesis agree with the fossil record of the Coleoptera where only the suborders (with the exception of the Myxophaga) represented by a few archaic families (including the trachypachids) had appeared in the Triassic (Crowson, 1981; Lawrence and Newton, 1982). It is possible, though, that if the trachypachids were already widely distributed in the Triassic they may have originated early during this period [or even in the Permian (Erwin, 1979, 1981, 1985)], and it is thus not beyond the realms of possibility that the promecognathines already existed during the Triassic.

An additional argument against the Pre-Pangea hypothesis is that there is no convincing geological evidence for the existence of a continent of Pre-Pangea (Hallam, 1981; Batten and Schweickert, 1981; Tedford, 1981). Humphries and Parentis (1986) however, argued that there are several hypotheses of earth history and that by formulating biogeographical hypotheses independently of any geological theory, it is possible to test them and, if necessary, construct new hypotheses.

Higher Classification of the Promecognathinae: Modern classifications of the Carabidae (Lindroth, 1961; Kryzhanoviskiy, 1976; and Erwin, 1985) do not follow Basilewsky (1958, 1963) in considering the Promecognathinae as a subfamily. Lindroth (1961) and Kryzhanoviskiy (1976) considered them a tribe while Erwin (1985) considered them a supertribe. In the following discussion I assume that the promecognathines have a rank higher than tribe.

I suggest that the promecognathines may be classified in the following manner in order to be compatible with the cladogram in Fig. 21. The 'subfamily' can be divided into two tribes. The Palaeoaxinidini, represented only by the fossil, and the Promecognathini, the sister group of the Palaeoaxinidini. The Promecognathini can be further subdivided into two sister subtribes the Promecognathina and the Axinidiina, which are equivalent to the Promecognathini and Axinidiini of Basilewsky (1963).

8.2 Subfamily Scaritinae

Specimen number: BP/2/26253 a&b. Locality 14; Figs 25-30.

Dimensions: Part BP/2/26253a: length 14.67mm, width 3.80mm; counterpart BP/2/26253b: length 14.50mm, width 3.80mm.

This specimen is a coalified compression imbedded in micaceous red mudstone along with a dipteran or perhaps a hymenopteran. It is an elongated beetle with a convex, pedunculate and parallel sided body. The whole body with portions of the associated appendages are preserved.

Head: large and wide, as wide as, or perhaps slightly narrower than the prothorax in the neck region; antennae represented by about six segments of the right antenna; antennal segments similar in size and shape; are small, about twice as long as wide, and closely packed together; mandibles are large and comprise about 2/3 of the size of the head; maxillary palps and labial palps project beyond the mandibles; distal two segments of the maxillary palps (visible on the counterpart) and the terminal segment of the left labial palp are easily distinguishable; right compound eye is convex, and protrudes slightly on the counterpart.

Prothorax: anterior and posterior angles and margins not apparent; lateral margins are straight and parallel; lateral border is narrow and together with the epipleura, is parallel to the lateral margin; coxal cavities visible; right leg is represented by an indistinct femur, and tibia (visible on counterpart); left leg is represented by a poorly preserved tibia with an apical spine on its inner surface, an elongated lobe on its outer surface, and a five segmented tarsus.

Mesothorax: elytra elongate, oval, do not cover the terminal abdominal segment; with seven pairs of parallel impunctate striae and a pair of scutellary striae in interval one; right coxal cavity, and portions of the outlines of the left coxal cavity are visible on the part; left leg is represented only by fragments of the tibia and the right leg by an impression of a femur, a tibia and a basal tarsal segment.

Metathorax: legs represented by a right leg with a coxa, an oval trochanter, an indistinct femur, an indistinct tibia with an apical spine, and a five-segmented tarsus, and a left leg with a coxa, an oval trochanter, and an indistinct tarsus with three segments.

Abdomen: four of the sternal sutures are visible on the counterpart, and two on the part.

Identification: The parallel sided pedunculate body, large, dilated protarsi produced into "fingers" are all typical of the Scaritinae. Without any distinguishing features it is impossible to place it positively in a lower taxonomic category. If the southern African Clivinini are typical of the fauna of the rest of the world, they may be excluded from the list of possibilities, because of their small size and narrow width.

Comment: This is the earliest record of a scaritine. The Scaritinae is a large subfamily having approximately 15 000 species (Kryzhanovskiy, 1976). The world-wide distribution of this subfamily (Kryzhanovskiy, 1976) suggests to me an even earlier origin than the mid-Cretaceous, at least as early as the Jurassic, when the continents were joined to form the supercontinent Pangea (Fig. 22). Scaratines are found in almost every conceivable climate (Erwin, 1979). The majority are burrowers (Erwin, 1979), a lifestyle reflected in their elongate bodies and expanded protibiae.

8.3 Subfamily Siagoninae?

The Siagoninae as defined by Erwin (1985), who refers to them as the Siagonini, has two genera; the genus Siagona which is distributed in the south Palaeartic region, southern Asia, the Malay archipelago, and Africa; and the genus Luperca which occurs in India and Africa (Erwin, 1978). According to Erwin (1979) Siagona is found on the ground in damp areas with decaying vegetation or under bark, while Luperca have been found associated with termitaria.

The two specimens referred to this subfamily are very similar, and in my opinion, probably represent the same species. The fossils are described separately, and followed by a description combining the features visible on both specimens.

Specimen number: BP/2/27356. Locality 14; Figs 31-33.

Measurements: length 8.45mm, width 2.5mm

A well preserved coalified compression imbedded in red mudstone, and comprises a negative image of a beetle with a flat pedunculate body and stout legs.

Head: elongated and broader at the neck than between the antennae (ratio of width of the head between the antennae to the width of the neck = 0.56); antennae stout and filiform; right antenna represented by eight proximal segments; the left antenna, except for the terminal segment, is complete; scape at least twice the length of segment two, which is slightly shorter than segment three, segments three to ten approximately the same length; mandibles large and curved, with the left mandible larger than the right; two distal segments of each maxillary palp visible, the terminal segments elongated, with square tips (visible on right palp); anterior margin of mentum and portions of gular sutures visible; compound eyes indistinct; posterior part of the head raised to form a prominent ridge.

Prothorax: prothorax transverse (ratio of maximum width of the prothorax to its length = 1.27); anterior margin straight; anterior angles prominent and acute; the posterior angles and margin not visible; lateral margins difficult to interpret, because the left of the prothorax was tilted into the sediment at the time of fossilisation; left margin straight from the anterior angle to about half the length of the prothorax, then curves strongly towards the base; right margin curved more evenly from the anterior to the posterior of the prothorax, the right margin probably represents the actual state on the living beetle; the lateral borders are apparently narrow, parallel to the margin suddenly becoming much broader at the anterior angles; prothorax far narrower at its posterior end than the elytra between the humeral angles; greatest width of prothorax narrower than the elytra at their greatest width (ratio of maximum width of the prothorax to the maximum width of the elytra is 0.86); a median longitudinal depression runs down the length of the prothorax; epipleura parallel to the lateral margins, though slightly broader at the anterior angles; coxal cavities closed posteriorly; legs present, each consists of a stout femur and a tibia; right tibia has a distinct median longitudinal groove.

Mesothorax: scutellum situated at the base of the elytra; elytra with rounded obtuse humeral angles, sides that curve gently for 2/3 of the elytral length, then curve strongly towards the apices of the elytra which are not preserved, seven distinct non-punctate striae, stria seven is curved around at the apex, and is joined by striae three to six, it is not clear whether striae one and two also intersect stria seven; mesepimera apparently do not form part of the boundary of the mesocoxae, which are therefore conjunct;

legs consist of a tibia and stout femur; the left tibia has a distinct groove and is slightly expanded distally.

Metathorax: with a pair of metepisterna and a pair of legs; it is not possible to decide whether or not the metepisterna have metepimera at their bases; legs consist of a pair of contiguous coxae which do not reach the elytral epipleura, elongated-oval trochanters (three times as long as wide), stout femora (ratio of length of the trochanter to the femur = 0.49), tibiae (the left tibia has a median longitudinal groove and the right tibia is expanded distally), and four indistinct tarsi.

Abdomen: with three sternal sutures.

Specimen number: BP/2/24004 a&b. Locality 12; Figs. 34-39.

Measurements: Part BP/2/24004a: length 7.70mm, width 2.4mm; Counterpart BP/2/24004b: length 7.86mm, width 2.51mm.

A carbon stained impression, represented by a part and a counterpart. It is imbedded in a buff-coloured mudstone, along with numerous plant fragments, and in the close vicinity of a curculionoid. The specimen is almost complete, but not well preserved, and represents a beetle of medium proportions, with a flat, pedunculate body and stout legs.

Head: triangular in outline, broader at neck than between antennae (ratio of width of the neck to width of the head between the antennae = 0.77); antennae incomplete; only three segments of the left antenna, and two of the right, are preserved, scape twice as long as segment two, which is slightly shorter than segment three; mandibles large; maxillary palps indistinct; right compound eye visible but indistinct; gular sutures poorly preserved, only visible on part; posterior part of head with a transverse depression, and, on the counterpart, possesses a number of punctures.

Prothorax: transverse (ratio of maximum width of the prothorax to its length = 1.26); anterior margins incomplete; anterior angles acute and prominent; posterior angles and margins not preserved; lateral margins curve out from anterior angles, and then, from about half way down the length of the prothorax, curve in towards base; prothorax far narrower at its posterior corners than elytra between humeral angles; elytra at widest point wider than the prothorax at its widest point (ratio of maximum width of the prothorax to the maximum width of the elytra = 0.88); median longitudinal ridge visible; proepipleura broad and parallel to the lateral margins becoming slightly broader at the anterior angles; coxal cavities closed posteriorly; each of prothoracic legs includes a stout femur and a tibia.

Mesothorax: scutellum indistinct, situated at base of the elytra; elytra with rounded and obtuse humeral angles, sides that curve very gently, and are almost parallel, for 2/3 of their length, after which they start curving more sharply towards the apex, seven distinct striae, stria seven curves around the apex and joins with stria three, four, five and six; mesoxal cavities poorly preserved; legs include a pair of stout femora and tibiae.

Metathorax: each leg consists of a coxa, an elongated-oval trochanter (three times as long as wide), a stout femora (ratio of length of the trochanter to the length of the femur = 0.49); and a tibia; left tibia of counterpart with a distinct median longitudinal groove; coxae contiguous, and do not reach elytral epipleura.

Abdomen. The abdomen has four (on the part) or three (on the counterpart) sternal segments.

Composite description

Beetles with flat, pedunculate, parallel-sided bodies, ranging in length from 8.45 to 7.70mm.

Head: head elongated; broader at neck than between antennae; antennae filiform, scape at least twice the length of segment two; segment two slightly shorter than segment three; segments three to ten of similar proportions; mandibles large; terminal segment of maxillary palps with square tips; compound eyes not prominent; posterior part of the head with a number of distinct punctures.

Prothorax: prothorax wider than long; anterior angles prominent and acute; anterior margin straight; sides of prothorax curve out from anterior angles until about halfway down its length, then curve evenly towards the base; lateral border narrow, parallel to lateral margin suddenly becoming dilated at the anterior angles; pro-epipleura broad parallel to the lateral margin only slightly dilated at the anterior angles; median longitudinal ridge runs down the length of the prothorax; coxal cavities are closed behind; femora and tibiae are stout.

Mesothorax: scutellum at base of elytra; elytra with rounded, obtuse humeral angles; sides which curve gently along 2/3 of length of elytra, at which point they curve strongly towards the apices; elytra with seven pairs of striae; striae seven curved around the apex of the elytra and joined by striae three to six; striae one and two parallel and may or may not intersect with stria seven; coxal cavities disjunct; femora broad, as broad as or slightly narrower than prothoracic femora; tibiae dilated slightly anteriorly.

Metathorax: coxae contiguous, do not reach the epipleura; trochanters elongate, ovate; femora stout, stouter than either the pro-or mesothoracic femora; tibiae are elongated, slender with median longitudinal grooves and dilated anteriorly; metepisterna are present.

Identification: Numerous carabids have pedunculate bodies, however, of the genera I have examined, the fossil is most similar to Melaenus and Siagona. The elongated head and size of the fossil is more reminiscent of Siagona than of Meleanus and so the fossil is referred to the Siagonini for the present. Two structures of the fossil that appear to contradict this diagnosis are the conjunct mesocoxal cavities and the scape. The apparent conjunct mesocoxal cavities of the fossil, may simply be due to poor preservation. Even the configuration of the mesocoxal cavities of museum specimens of Siagona can be difficult to determine. According to Erwin (1985), an elongated narrow scape is a synapomorphy of the siagonines and related taxa. The fossils do have elongated scapes but not nearly as elongated as in the Siagoninae, however, this may only be a matter of degree.

Unfortunately I have not had the opportunity to examine all the genera related or similar in form to Siagona (Cymbionotum, Luperca, and Enceladus). Examination of these genera is necessary before any final conclusion concerning the relationship of the fossil can be made.

Remark: The occurrence of Enceladus, which is closely related to the Siagonini (Erwin, 1978, 1985) in South America, suggests that these taxa were in existence before the split between S. America and Africa (Erwin, 1978) and therefore, that the discovery of a closely related fossil in the middle of the Cretaceous period is perfectly possible.

8.4 Subfamily Pterostichinae?

This is a large cosmpolitan subfamily with at least 2 500 species (Krizhanovskiy, 1976). Its world-wide distribution, as with the Scaritinae, suggests a Jurassic origin for the group. According to Erwin (1979), this subfamily (which he calls a tribe) and its near relatives are found in a wide variety of habitats.

Specimen number: BP/2/27583 a&b. Locality 21; Figs 40-45.

Dimensions: Part BP/2/27583a: length 6.47mm, width 1.89mm; Counterpart BP/2/275835b: length 6.57mm, width, 1.86mm.

A well-preserved coalified compression, represented in both part and counterpart, imbedded in olive-green mudstone. The body is more or less parallel sided and has portions of all its associated appendages preserved.

Head: roughly triangular in shape, lacks a post-orbital constriction (ratio of width of the head between the antennae to the width of the neck = 0.66), antennae filiform, incomplete, with segments which are broad in comparison to the head, each antenna is (except for the left antenna on the counterpart which has a poorly preserved seventh segment) represented by six segments, scape twice as long as the second segment which is 0.8 times as long as segment three, segments three to six are of equal length; mouthparts represented by a pair of mandibles, a pair of maxillary palps (the best preserved maxillary palp is visible on the right side of the part) with the terminal segments slightly expanded, a lacinia (visible on the right side of the part), and a pair of labial palps, with the terminal segment expanded (visible on the left side of the part); anterior margin of the mentum is visible; compound eyes convex; counterpart with a pair of supraorbital ridges (however, as these are preserved as ridges on the counterpart which usually has structures in reverse relief this interpretation may be incorrect); posterior of the head is depressed to form a distinct transverse depression.

Prothorax: slightly transverse (ratio of maximum width of the prothorax to its length = 1.1); anterior margin (dorsal or ventral) slightly concave; anterior angles prominent and acute; posterior angles obtuse; the lateral margins are subparallel and curve slightly back from the anterior angles in the anterior half of the prothorax, then they curve inward more sharply towards the posterior angles; width between the posterior angles is less than the width of the elytra between the humeral angles (ratio of width of the prothorax between the posterior angles to the width of the elytra between the humeral angles = 0.71); width at the widest point is slightly less than the maximum width of the elytra (ratio of maximum width of the prothorax to the maximum width of the elytra = 0.85); epipleura are parallel to the lateral border except at the posterior and anterior angles where they are broader; a median longitudinal depression runs from just posterior of the anterior margin to the coxal cavities; the coxal cavities have a postcoxal bar and are, therefore, closed; legs are represented by a femur and a tibia, right tibia (on the part only) has a distinct indentation near its tip which suggest a comb organ.

<u>Mesothorax</u>: with an oval scutellum; elytra unfused with rounded humeral angles, sides that curve slightly and evenly towards the apices, and seven impunctate stria; stria one to three are parallel, stria four to six are also parallel except they curve slightly towards one another at the apex where they intersect with stria seven that curves round at the apex (stria one to three may also intersect with stria seven but it is not possible to see because of the incomplete elytral apices); conjunct coxal cavities (most clearly visible on the right side of the part); and legs represented by a femur and an incomplete tibia with a longitudinal groove (or two parallel ridges).

<u>Metathorax</u>: with a pair of metepisterna (not possible to see whether there are metepimeral lobes attached to their bases) and a pair of legs represented by a pair of contiguous coxae and a pair of elongated trochanters (three times as long as wide); the right leg is also represented by a femur and a tibia; this leg has been twisted so that the

the femur is below the trochanter.

Abdomen: with five sternites, sternite one is divided by the metacoxa, sternite two is almost as long as sternites three, four and five, and as with many extant carabids probably actually represents two fused sternites; sternites three, four and five are distinct and separate. This type of abdomen is apparently common to all the fossils described on the following pages.

Identification: The specimen, although it is most similar in general morphology to the pterostichines, does not closely resemble any of the pterostichine genera which I have examined. The shape of the elytra is similar to that of Cophsomorpha arnoldi Straneo and Wahlbergia undulatorugosa Tschitscherine.

Specimen number: BP/2/27584. Locality 17; Figs 46-48.

Measurements: length 7.43mm, width 2.23mm

A well preserved positive, coalified compression imbedded in micaceous red-brown mudstone along with fragments of organic matter. A beetle of medium proportions with a prothorax that is large in proportion to the elytra, the whole body with portions of its associated appendages is preserved.

Head: roughly triangular in shape, lacks a post-orbital constriction; antennae filiform, incomplete, with segments that are broad in proportion to the head; left antenna is represented by six segments and the right by five, scape is 1.8 times as long as segment two which is in turn 2/3 as long as the remaining visible segments; mouthparts are represented by a pair of mandibles, a three segmented maxillary palp (visible on the right side), and what is probably a lacinia (also visible on the right side); compound eyes protrude, left eye is bordered by a portion of the supraorbital ridge; posterior of the head is depressed to form a transverse depression.

<u>Prothorax</u>: transverse (ratio of width of the prothorax at its widest point to the length of the prothorax = 0.43); anterior margin (dorsal or ventral) is sinuate; posterior margin slightly sinuate or concave; anterior angles acute; posterior angles oblique, left and right posterior angles differ due to poor preservation, right posterior angle probably represents the original condition; lateral margins curve evenly from the anterior to the posterior angles; width between the anterior angles is greater than the width between the posterior angles (ratio of width of the prothorax between the anterior angles to the width of the prothorax between the posterior angles = 1.65); width between the posterior angles is less than elytral width between the humeral angles (ratio of width of the prothorax between the posterior angles to the width of the elytra between the humeral angles is = 0.58); width at its widest

point is narrower than the elytra at their widest point (ratio of width of the prothorax at its widest point to the width of the elytra at their widest point is = 0.98); the lateral border, where visible, is parallel to the lateral margin; proepipleura are also parallel to the lateral margin except at the anterior angles where they broaden considerably; proepimera visible; coxal cavities closed posteriorly and separated by a prosternal process; legs represented by a pair of femora, a pair of incomplete tibiae and the remnants of some tarsal segments.

Mesothorax: with a rounded scutellum at the base of the elytra; elytra unfused and with a pair of rounded oblique humeral angles, lateral margins that curve evenly around to the apices, and no trace of any stria; numerous ridges run longitudinally down the lateral portions of the elytra, their interpretation is uncertain, but they must, in part, represent the elytral epipleura; mesepimera do not form part of the boundaries of the coxal cavities which are, therefore, conjunct; legs represented by a femur and a tibia, each tibia has a pair of parallel longitudinal ridges.

Metathorax: with a pair of metepisterna, a pair of metepimeral lobes (visible as lobe shaped posterior margin of the left metepisternum) an antecoxal suture and a pair of legs which are represented by a pair of contiguous coxae, a pair of trochanters almost three times as long as wide, a pair of femora (ratio of length of the trochanter to the length of the femur = 0.41), and a pair of incomplete, broad, grooved tibiae.

Abdomen: with five visible sternites. Sternite one is divided in two by the metacoxae, sternite two is broad and again, actually probably represents two fused sternites; sternites three to five are distinct and separate.

Identification: This specimen is similar in form to many extant carabids, especially some of the harpalines, however, it is most similar to the pterostichines especially some members of the genus Abacetus (A. crenulatus Dejean, A. majorinus Peringuey, A. perplexus Peringuey).

Specimen number: BP/2/27586 a&b. Locality 20; Figs 49-54

Measurements: Part BP/2/27586a: length 8.74mm, width 2.50mm; Counterpart BP/2/27586b: length 8.61mm, width, 2.55mm.

A well preserved beetle of medium proportions, which is represented by a part and a counterpart, and is imbedded in a layer of micaceous red mudstone. On this block there are also a staphylinid beetle, an unidentified beetle and an unidentified heteropteran. The specimen consists of a whole body with portions of its associated appendages.

Head: is narrow when compared to the width of the prothorax between the anterior angles, is roughly triangular in shape, and is tilted to one side, this, together with poor preservation, makes the neck invisible; antennae are filiform and the segments are elongated, more so than those of the other fossils described here, except, perhaps, for BP/2/2655; left antenna is represented by six segments, the right by portions of all eleven; scape is twice as long as segment two, which is only slightly shorter than segments three and four, segments five to ten are in turn marginally shorter than the scape and approximately four times as long as wide; mouthparts are represented by a labrum which is small compared to the mandibles and has a concave anterior margin, a pair of mandibles, a pair of maxillary palps (with an elongated basal segment, a reduced penultimate segment, and a slightly expanded terminal segment), and a pair of labial palps, of which only the bases are visible; compound eyes protrude slightly and are bordered by supraorbital ridges; remnants of the gular sutures and anterior margin of the mentum are visible; the posterior of the head is depressed to form a trough.

Prothorax: transverse (ratio of width of the prothorax at its widest point to its length = 0.84) and wider between the anterior angles than between the posterior angles (ratio of width of the prothorax between the anterior angles to its width between the posterior angles = 1.44); its base is narrower than the width of the elytra between the humeral

humeral angles (ratio of width of the prothorax between the posterior angles to the width of the elytra between the humeral angles = 0.62); its maximum width is equal to the width of the elytra between the humeral angles but less than the maximum width of the elytra (ratio of maximum width of the prothorax to the maximum width of the elytra = 0.84); anterior angles are acute; posterior angles obtuse; ventral anterior margin is concave and the dorsal posterior margin is straight; lateral margins are parallel to one another or slightly curved in the anterior half of the prothorax, they then curve inwards too the posterior angles; epipleura are parallel to the lateral margins, except at the anterior and posterior margins where they become broader; the lateral borders are, where visible, parallel to the lateral margin; the epimera are poorly preserved; the coxal cavities are closed posteriorly, and the legs are represented by portions of a thick femur and a tibia.

<u>Mesothorax</u>: anterior margin of the mesothorax has a number of complex structures which are probably flanges for the attachment of the prothorax; base of the elytra with a scutellum; elytra are unfused, have rounded obtuse humeral angles, sides which are semi-parallel and only curve slightly until just before the apices where they curve more sharply, apices which are rounded and not truncated, and eight non-punctate stria; stria one to three are parallel and curve towards stria four to seven near the apex, stria seven and eight curve towards one another and are parallel to the

margins of the elytra until near the apex where they are separated by only a narrow ridge; the apex of the right elytron (visible only on the part) has a distinct puncture which may have been the site of a seta; coxal cavities are conjunct*; left leg represented by a femur and the right leg by a femur, a tibia and poorly preserved tarsal segments.

<u>Metathorax</u>: metepisterna have metepimeral lobes attached to their posterior ends; the legs are represented by a pair of contiguous coxae which do not reach the elytral epipleura, a pair of oblong trochanters, (approximately four times as long as wide), a pair of broad femora (ratio of femoral length to trochanteral length = 0.57), and a pair of incomplete tibiae, the right tibia has a pair of parallel ridges.

---

*There are a number of structures which could represent the mesepimeron making contact with the coxal cavities. One such structure which is particularly prominent is visible on the right side of the counterpart, however, it is not visible on the part which is better preserved and would, therefore, be expected to show the structure more clearly. It is more probably the impression of the femur. Therefore, it is more likely, that the coxal cavities are conjunct.

Abdomen: sutures between sternal plates two and three, three and four, and four and five are visible.

Identification: The specimen is most similar in general appearance to the genus *Abacetus*, in particular to the species *A. congruens* Peringuey.

8.5 Subfamily Anchomeninae

According to Kryzhanovskiy (1976), this subfamily (Kryzhanovskiy considered it a tribe) is cosmopolitan with approximately 2 000 species. Some authors (Erwin, 1979; 1985; Moore, 1965) have placed this taxon among to the pterostichines. Again, the cosmopolitan nature of this group suggests a Mesozoic origin.

Specimen number: BP/2/26256 a&b. Locality 14; Figs 55-60.

Dimensions: Part (BP/2/26256a): length 7.4mm, width 2.2mm: counterpart (BP/2/26256b), length 6.88mm, width 2.08mm.

A coalified compression imbedded in micaceous red mudstone along with an unidentified insect and fragments of organic matter. The specimen represents a beetle of medium proportions preserved in part and counterpart. The whole body with portions of the associated appendages is apparent.

Head: slightly narrower between the antennae than at the neck (ratio of width of the head between the antennae to the width of neck = 0.70), without a post-orbital constriction; antennae filiform and complete, scape twice as long as segment two, and approximately the same length as segments three to ten, segment eleven is 1.2 times as long as the scape; mouthparts represented by a pair of incomplete curved mandibles, a pair of maxillary palps, of which three segments are visible, and the tips of the labial palps; compound eyes are small and convex; there are a pair of gular sutures.

Prothorax: transverse (ratio of maximum width of the prothorax to its length = 1.28); anterior angles not prominent, oblique and rounded; anterior margin (dorsal or ventral) slightly concave; posterior angles obtuse and rounded; dorsal posterior margin straight; lateral margins gently and evenly rounded; width between posterior angles less than width of the elytra between humeral angles (ratio of width of prothorax between the posterior margins to the width of the elytra between the humeral angles = 0.73); maximum width the same as maximum width of the elytra; a median longitudinal depression runs down the length of the prothorax; lateral borders and epipleura are thin and parallel to the lateral margin; proepisterna are visible; procoxal cavities closed; each leg is represented by a femur and a tibia; each tibia has a comb organ and median longitudinal ridge.

Mesothorax: scutellum, circular, lies at the base of the elytra; elytra with obtuse shoulders, subparallel sides that curve gently until the last third of their length, where they start to curve more sharply towards the apex and at least six stria, the right elytron of the counterpart has longitudinal ridges running parallel to and between the stria; coxal cavities are indistinct, but from their position relative to the metepisterna and mesepisterna, are probably conjunct; legs represented by a tibia with a longitudinal groove, and a femur.

Metathorax: with a pair of metepisterna, an antecoxal suture, and legs represented by a coxa, an oval trochanter (twice as long as wide), and a femur (ratio of length of the trochanter to the length of the femur = 0.43); counterpart also has a pair of indistinct tarsi; coxae are contiguous, and do not reach the elytral epipleura.

Abdomen: with three sternal sutures.

Identification: This fossil is similar to the genus *Agonum* in morphology.

8.6 Subfamily Harpalinae

The Harpalinae is, according to Kryzhanovskiy (1976), a cosmopolitan group comprising approximately 2 600 species (if the Amblystomini are included). Again, its world wide distribution suggests a Jurassic origin. These beetles are found in most climates (Erwin, 1979) where they are ground dwellers (Basilewsky, 1950; 1951). Many are phytophagous, and in particular granivorous (Basilewsky, 1950; 1951).

Specimen number: BP/2/18669 a&b. Locality 2; Figs. 61-66.

Measurements: Counterpart BP/2/18669b: length 9.98mm, width 3.49mm; part BP/2/18669a: length 6.16mm.

A well-preserved coalified compression imbedded in micaceous olive-green fine sandstone. It is represented in both part and counterpart. However, the part consists only of the mesothorax, metathorax and abdomen. Also the counterpart is missing the anterior portion of the head and the right portion of the prothorax. Fig. 65 shows the specimen before the right portion of the prothorax broke off; a dotted line represents the break. Therefore, the terms left and right as used in this description refer to the counterpart. It is a short squat beetle with legs that are long in proportion to its body.

Head: short, broad, triangular in outline (ratio of width of the head between the antennae to the width of the neck = 0.67) with no post-orbital constriction; antennae represented by a pair of incomplete scapes; two poorly preserved segments of the left maxillary palp are distinguishable, right maxillary palp not preserved; mandibles incomplete; compound eyes small, convex, and only protrude slightly; there are a pair of supra-orbital pits on either side of the head; posterior portion of the head is raised in a prominent half dome.

Prothorax: transverse (ratio of maximum width of the prothorax to its length = 1.45), narrower between the posterior angles than the elytra between the humeral angles; width at the widest point is far narrower than the elytra at the widest point (ratio of maximum width of the prothorax to the maximum width of the elytra = 0.60); anterior margin, posterior angles and posterior margin are not preserved; anterior angles are prominent and acute; lateral margins curve gradually outwards from anterior angles, until about a third of the way down the length of the prothorax, where they straighten out, become subparallel and curve gently until the posterior of the prothorax; lateral border, which is visible only on the left posterior side of the prothorax, is narrow and parallel to the lateral margin, as are the epipleura; a longitudinal ridge runs down length of the prothorax; epipleura are parallel to the lateral margin; coxae not visible; right leg is represented by a poorly preserved femur and tibia; left leg by the remnants of a femur.

Mesothorax: with a scutellum at the base of the elytra; elytra with gently rounded humeral angles, parallel sides, that curve gradually towards the apex in the last third of their length and just before the apex turn sharply inwards so that the apex of the elytra is almost flat (this effect may be compounded by the fact that the tips of the elytra are incomplete), and nine pairs of non-punctate striae; stria one is intersected basally by a scutellary stria; striae one and two are parallel; striae three and four and striae five and six are connected to form two U's, the U formed by three and four being longer than the U formed by five and six; striae seven and eight are parallel; and stria nine is very close to, and converges with, the edge of the elytron near its apex, stria eight has a number of expansions along its length, three are visible at its distal end on the right elytron of the counterpart, and two are visible at its proximal end on the left elytron of the counterpart, these could have been the sites of setae; mesepimera do not form part of the border of the coxal cavities (visible on left side of part), which are, therefore, conjunct; right leg not preserved; left leg consists of portions of a femur, a tibia with a distinct longitudinal ridge and setae on its anterior margin, and a five-segmented tarsus; tarsal segments are triangular and unexpanded, with setae at their basal corners, tarsal segments one and two are one and a half times as long as segments three and four, which are in turn a third of the length of segment five; segment five has a pair of claws, between which is a third appendage, which may be a long seta.

Metathorax: with a pair of metepimera, and a pair of legs; right leg with a trochanter, a femur, an elongated tibia with a pair of apical spurs (only one is visible on the part), and a poorly preserved tarsus; left leg with a coxa, trochanter, femur, tibia, and a poorly preserved tarsus; the tarsal segments have some hairs and spines (the number of segments cannot be distinguished), and the terminal segment has a pair of diverging claws; trochanters are elongated, three times as long as wide, (ratio of the length of the trochanter to the length of femur = 0.56); the tibiae have a prominent longitudinal groove.

Abdomen: with three sternal sutures.

Identification: The general shape of the body, the elytral pattern with an elongated scutellum, and the mesotibia which is spiny on the outer edge, are all typical of the Harpalinae. The specimen is similar to members of the genera *Harpalus*, *Cratognathus*, *Dichaetochilus* and *Egadroma*, and in fact to many other genera.

In contrast, the two supra-orbital pits above each eye are not typical of the harpalines, which only have one supraorbital seta above each eye. However, in other Carabidae, which have two supra-orbital setae above each eye (e.g. the Pterostichinae), the setae are usually situated further back and closer to the eye than the pits in the specimen. Similarly situated pits which are not the sites of supra-orbital setae, are found in the species Systolocranius ampliolatus Peringuey (subfamily Oodinae). None of the harpalines I examined had similar punctures. Even if the character of the supra-orbital pits is excluded, none of the harpalines examined had the same combination of characters as the specimen: i.e. the thorax narrow relative to the elytra; the head without a postorbital constriction; the strial pattern with the elongated scutellary stria intersecting stria one, giving it the appearance of a Y; and the elongated tarsal segments.

However, without a thorough knowledge of the world harpaline fauna, it is not possible to erect a new taxon with confidence.

Specimen number: BP/2/26255. Locality 14; Figs 67-69.

Measurements: length 7.7mm, width 2.64mm.

This is well-preserved coalified compression, imbedded in micaceous red mudstone. It is a positive image with portions of the head, thorax and abdomen and their associated appendages preserved.

Head: without any obvious post-orbital constriction, slightly narrower between the antennae than at the neck (ratio of width of the head between the antennae to the width of the neck = 0.72); antennae slender, filiform with portions of all eleven segments visible, scape twice as long as segment two, which is just over half the length of segment three; segment three same length as segments four to ten; and segment eleven is 1.4 times the length of the scape; maxillary palps represented by three elongated segments (visible on left side) that protrude beyond the mandibles; only distal portions of the labial palps are preserved; labial and gular sutures are visible.

Prothorax: transverse (ratio of maximum width of the prothorax to its length = 1.48); anterior angles gently curved, oblique; anterior margin (dorsal or ventral) straight; posterior margin (dorsal or ventral) slightly concave and gently curved; posterior angles obtuse; lateral margins curved evenly from anterior to posterior angles; width between the posterior angles is less than the width of the elytra between the humeral angles; width at widest point less than that of the elytra at the widest point (ratio of maximum width of the prothorax to the maximum width of the elytra at the widest point = 0.92); a median longitudinal depression runs from just posterior to the coxal cavities to the anterior angles; where visible, the epipleura are parallel to the lateral margin except at the anterior angles where they become broader; coxal cavities poorly preserved; each leg represented by portions of a femur and tibia.

Mesothorax: scutellum rounded and situated at the base of the elytra; elytra with a pair of oblique humeral angles, sides which are subparallel, and curved gently and evenly until the last quarter of their length, where they curve more sharply towards the apex, and indistinct stria; the left elytron with three, the right with five; elytral epipleura visible; coxal cavities, poorly preserved, probably conjunct because the mesepimera (visible on the right side) do not appear to form part of their boundary; mesepisternal sutures present, legs are represented by a pair of femora; left leg also has a tibia with a longitudinal groove.

Metathorax: with a pair of metepisterna, an antecoxal suture, and legs represented by a pair of contiguous coxae which do not reach as far as the elytral epipleura, a pair of oblong trochanters, which are twice as long as wide, and a pair of femora (ratio of the length of the trochanter to the length of the femur = 0.48); left leg also has a tibia with a longitudinal groove, and a tarsus with three square tarsal segments.

Abdomen: with at least four sternal sutures, probably representing six sternites as in many carabids.

Identification: The genera which I think the specimen resembles the most are Harpalus, Heterohyparpalus, Aulocoryssus, Acupalpus, and Egadroma. It is not, however, identical, and cannot be placed in any one of them.

Specimen number: BP/2/26260. Locality 14; Figs 70-72.

Measurements: length 7.04mm, 2.4mm wide

This is a well preserved coalified compression imbedded, together with a fragment of an insect wing, in micaceous red mudstone. It is a positive image, with the whole body and portions of its associated appendages preserved.

Head: with a slight post-orbital constriction, broader at the neck than between the antennae (ratio of width of head between the antennae to the width at the neck = 0.72), left antenna represented by portions of all eleven segments, the right by portions of seven; the part of the scape which is projecting is almost the same size as segment two; segments three to ten are of equal size, and the same size as the scape, segment eleven is about one and a quarter times longer than the scape; mandibles are large and curved; left maxillary palp with three distinct segments, terminal segment is three times as long as wide, and the penultimate segment is 2/3 as wide as long; right maxillary palp is indistinct and represented by one segment; compound eyes are small, convex and protruding; portions of the gular sutures are visible.

Prothorax: prothorax transverse (ratio of maximum width of the prothorax to its length = 1.32), anterior angles prominent and acute, anterior margin (dorsal or ventral) concave, shaped like a wide V; posterior angles oblique, posterior margin not distinct; lateral margins of the prothorax curved evenly from the anterior to the posterior angle; a median, longitudinal depression runs down the length of the prothorax; coxal cavities closed behind by the post-coxal bar; legs represented by a pair of femora, and a pair of tibiae; right tibia with a comb organ, a longitudinal groove, and four spines or setae on its anterior outer surface; right leg has a tarsus with four square segments of similar proportions, and the left leg, the remnants of a poorly preserved tarsus.

Mesothorax: elytra with poorly preserved sides; sides subparallel, gently rounded for 2/3 of their length when they start curving more sharply towards the apex; striae indistinct; right elytron with two visible striae, the left elytron with five; coxae indistinct, probably conjunct, right leg consists of what is possibly a trochanter, a femur, a tibia with a longitudinal groove, and a four-segmented tarsus; left leg consists of a poorly preserved femur, and a tibia.

Metathorax: metathorax represented by a pair of legs, a pair of metepisterna, and an antecoxal suture; each leg consists of a coxa, an elongated oblong trochanter (about twice as long as wide), a slender tibia with a tibial spur (visible on the left side), and a tarsus with five segments; coxae are contiguous and do not reach the elytral epipleura; first four tarsal segments are of similar size, and shape, and the terminal segment is three times as long as segment four.

Abdomen: with four sternal sutures, probably representing six sternal plates.

Identification: This specimen is very similar in shape to BP/2/26255. The chief differences between the specimens are: the post orbital constriction of BP/2/26260, the difference in the shape of the eyes, the elongated palps of BP/2/26255, the difference in shape of the anterior margins of the two specimens and the more slender antennal segments of BP/2/26255.

Specimen number: BP/2/24006. Locality 12; Figs 73-75.

Measurements: length 4.85mm, width 1.6mm

The specimen is an impression which has been stained brown, perhaps by the remains of organic material, and is imbedded in micaceous buff-coloured mudstone along with fragments of organic matter. The whole body with the associated appendages is preserved. It is a negative image of a small beetle with a pedunculate body.

Head: wider at the neck than at the antennae (ratio of width of the head between the antennae to the width of the neck = 0.51), with no post-orbital constriction;

antennae slender and filiform; scape 1.6 times as long segment two, which is, in turn, half the length of segment three, segment three is slightly longer than segments four to nine, and shorter than the terminal segment which is incomplete; mandibles curved, with the left mandible being longer than the right; portions of both the maxillary and labial palps are visible; compound eyes indistinct, and the remnants of the gular sutures distinguishable.

Prothorax: prothorax transverse (ratio of maximum width of the prothorax to its length = 1.36); anterior angles acute; anterior margin (dorsal or ventral) is concave and rounded gently; posterior margin (probably the ventral) is convex and curved evenly; lateral margins are curved slightly from the anterior to the posterior angles; prothorax narrower at the posterior angles than the elytra between the humeral angles (ratio of width of the prothorax between the posterior angles to the width of the elytra between the humeral angles = 0.8); maximum width is equal to width of the elytra between the humeral angles, and narrower than the maximum width of the elytra (the ratio of the maximum width of the prothorax to the maximum width of the elytra = 0.85); a median longitudinal ridge runs down the length of the prothorax; epipleura are narrow and parallel to the lateral border, except at the anterior angles where they widen slightly; coxal cavities are indistinct; legs are represented by a pair of femora and tibiae.

Mesothorax: scutellum oval; elytra, unfused, with a pair of obtuse humeral angles, sides which curve gently and evenly towards the apex, and poorly preserved non-punctate stria; the left elytron has two parallel stria and the right has four; legs represented by a pair of poorly preserved coxal cavities (conjunct?) femora and tibiae; right leg also has an indistinct tarsus.

Metathorax: legs represented by a pair of coxae, a pair of oblong trochanters (twice as long as wide), a pair of femora (ratio of length of the trochanter to the length of the femur is 0.53), a pair of slender tibiae with median longitudinal ridges, and a pair of indistinct tarsi; five segments of the left tarsus and two or perhaps three of the right tarsus, are visible; terminal segment of the left tarsus has a pair of tarsal claws.

8.7 Carabidae Incertae Sedis

The carabids described in this section are too incomplete to be referred to any subfamily. They do, however, have conjunct mesocoxae which indicates that they belong to the division Psydriformes of Erwin (1986). Their general morphology supports this conclusion.

Specimen number: BP/2/27585 a&b. Locality spoilheap; Figs 76-81.

Measurements: Part BP/2/27585a: length 8.32mm, width not possible to measure; Counterpart BP/2/275845b: length 6.57mm, width, 2.14mm.

A very well preserved coalified compression imbedded in micaceous red-brown mudstone along with a few fragments of organic material. The specimen is represented by a part and counterpart. It consists of the whole body of a slender beetle with portions of its associated appendages. Unfortunately the rock in which the specimen is imbedded had been partially weathered resulting in large portions of the specimen flaking off.

Head: lacks a post-orbital constriction and narrower between the antennae than at the neck; antennae are slender and filiform, left antenna represented by nine segments, the right antenna (visible only on the counterpart) by four, scape 3/2 times as long as segment two which is only slightly shorter or the same length as segments three to eight; mouthparts represented by the remnants of a labrum and an incomplete pair of mandibles; compound eyes indistinct (only visible on the counterpart); remnants of the supraorbital ridges are visible, particularly on the right side of the part; posterior of head depressed to form a transverse depression.

Prothorax: wider than long (the poor preservation of the prothorax makes it impossible to give any accurate ratio of maximum width to length), anterior and posterior angles and margins not preserved; lateral margins, where visible, curve evenly and gradually towards one another in the anterior 2/3 of the prothorax, I infer (from the position of remnants of the proepipleura and lateral borders) that they then start curving more sharply towards the posterior; maximum width is equal to the width of the elytra between the humeral angles and narrower than the maximum width of the elytra (ratio of maximum width of the prothorax to the maximum width of the elytra = 0.81); lateral borders, where preserved, are parallel to the lateral margins; proepipleura converge towards the lateral margins posteriorly; epimera visible; coxal cavities closed posteriorly; legs represented by a pair of coxae and a femur.

Mesothorax: with a scutellum at the base of the elytra; unfused elytra with rounded humeral angles that approach 90°, sides that curve gradually and gently toward the apices which are not preserved, and at least six parallel non punctate stria; conjunct coxal cavities; and legs which are represented by a trochanter and a femur (visible on the left side of the counterpart).

Metathorax: metepisterna are visible, apparently without metepimeral lobes attached to their posterior ends (this could just be poor preservation); legs are represented by a pair of contiguous coxae which do not extend to the elytral epipleura, a pair of elongated trochanters which are

3/2 times as long as wide (the hinge between the coxa and trochanter is visible on the left side of the part), a pair of femora (ratio of femoral length to trochanteral length = 0.53) and a pair of grooved tibiae.

Abdomen: probably had six sternites, though the boundary between sternite two and three is not visible.

Identification: Abacetus confinis Boheman (Pterostichinae), Stenolophidius pallidus Boheman (Harpalinae) and Enoicus fallax Peringuey (Anchomeninae) are of a similar shape.

Specimen number: BP/2/27587. Locality 20; Figs 82-84.

Measurements: length 6.23mm.

A well preserved positive specimen imbedded in a layer of micaceous red-brown mudstone along with a portion of the abdomen and metathoracic tibia of a hemipteran(?) and an unidentified coleopteran. The complete body of the beetle with portions of its associated appendages is apparent.

Head: large relative to the pronotum, roughly triangular and lacks a post-orbital constriction (ratio of width of the head between the antennae to the width of the neck = 0.57); both antennae are preserved and represented by eleven segments, they are filiform and taper towards the tip, scape is least twice as long as the second segment which is 3/4 of the length of the third segment, segments three to ten are of similar length, segment eleven is incomplete; mouthparts represented by a labrum, a pair of large mandibles, a pair of maxillary palps, and a pair of labial palps; the anterior margin of the mentum and a portion of the lateral margins of the lobes of the mentum (situated near the base of the antennae) are visible; the portion of the head between the posterior of the eyes is raised to form a transverse ridge; the posterior part of the head has a pair of parallel gular sutures.

Prothorax: wider than long; small in proportion to the rest of the thorax and abdomen; dorsal anterior margin straight, anterior angles acute and prominent; lateral margins incomplete but were apparently curved outward from the anterior angles until about halfway down the length of the prothorax and then inward towards the posterior angles giving the body a pedunculate or semi-pedunculate shape; posterior angles and margin not preserved; it is, however, probable that at its widest point the prothorax was of similar width to the width of the elytra between the humeral angles and narrower than the elytra at their greatest width; it is also likely that the width between the posterior angles was narrower than the width of the elytra between the humeral angles; proepipleura incomplete and parallel to the lateral margin except at the anterior angles where they widen; lateral border is incomplete and apparently broader than the proepipleura; proepimeron is visible on the right side; a narrow central longitudinal depression runs down the length of the prosternum; coxal cavities are poorly preserved and distorted; legs are represented by a pair of femora and a portion of a tibia on the left side.

Mesothorax: with a scutellum and flanges for the attachment of the prothorax at its anterior margin; elytra that have humeral angles that are not preserved, subparallel sides which are curved slightly until just near their apexes where they curve inwards more sharply and at least six non-punctate parallel stria; conjunct coxal cavities (several structures could be interpreted as the mesepimera making contact with the coxae but none are clearly enough defined to be convincing, especially on the right side where the coxal cavity is well preserved); and legs that are represented, only on the left side by a portion of a femur and a tibia with a longitudinal ridge.

Metathorax: with a pair of metepisterna that apparently do not have metepimeral lobes attached to their rear ends (again this could just be due to preservation of the fossil); a distinct antecoxal piece; and legs represented by a pair of contiguous coxae that do not reach the sides of the body, a pair of oblong trochanters (three times as long as wide), and a pair of femora (ratio of femoral length to trochanteral length = 0.55) and tibiae (almost entirely complete on the right side and only fragmentary on the left side).

Abdomen: with six sternal plates.

Identification: The fossil appears to have been similar in form to the genus *Amblystomus* (Amblystomini: Harpalinae).

CHAPTER NINE

DISCUSSION

9.1 Palaeoclimate at Orapa.

9.1.1 Introduction

What type of climate and environment did the carabids live in? In the following section an attempt is made to reconstruct the palaeoenvironment at Orapa. In addition to concentrating on data from Orapa, knowledge of global climates in the Cretaceous is reviewed, and an attempt is made to reconstruct the Cretaceous climate and environment in the entire southern African subregion.

9.1.2 Palaeolatitude of Orapa

One of the most important factors which affect the climate of an area is its latitude (Frakes, 1979). Therefore, in order to infer the palaeoclimate at Orapa, it is first necessary to estimate its palaeolatitude.

If the reconstructions of continental movement through time (where the earth is considered as being of a constant size) of Owen (1983) are used, Orapa would have been approximately 14° south of its present position at the co-ordinates 0^{o} 40'E and 35^{o} 30' S at about 90mya (Turonian). This would place it slightly to the south and east of where Cape Town is today.

9.1.3 Global Temperatures

Cretaceous global temperatures were apparently more equable than today. This conclusion is derived from work reviewed by Frakes (1979) and Hallam (1985). Further, a good critical review, which concentrated only on the mid-Cretaceous between Albian and Cenomanian times, is that of Barron (1983). According, to Barron evidence that temperatures (mean annual surface temperatures) during the mid-Cretaceous were more equable includes the following.

i) Oxygen isotope analysis of planktonic Foraminifera from Cretaceous tropical waters indicate surface temperatures in the range of 27^{o}C-32^{o}C which is similar, or warmer than the present day.

ii) Extensive carbonate deposition and coral reef formation, which can only occur where water temperature exceeds 21^{o}C, was at a maximum during the mid-Cretaceous. Corals and carbonates during this time period were found between 5-15^{o} latitude further north and south than at present.

iii) Midlatitude temperatures obtained from oxygen isotope analysis of belemnites are contradictory, probably because this technique is subject to considerable error. In the Northern Hemisphere, a reduced midlatitude temperature gradient (when compared with the present) is implied. The data also indicated that midlatitude temperatures were similar to those of today. However, these data conflict with those suggested by coral reef formation and carbonate deposition, which suggest a higher temperature at the same latitudes. In the Southern Hemisphere, isotopic data suggest that sea temperatures actually increased towards the poles, however, all the temperatures indicated are higher than those at the same latitude today.

iv) Palaeobotanical data provided evidence that the boundary between seasonal and nonseasonal floras was displaced as much as 15° towards the poles compared to today. In addition, floras from high latitude positions (as high as 80°N and S) indicate warm to cool temperate conditions (see also Donn, 1982; Douglas and Williams, 1982). Also, there is no evidence for permanent ice in the polar regions during the Cretaceous. The evidence for continents at high latitudes is good (Donn, 1982; Douglas and Williams, 1982), and the lack of glaciation during the Cretaceous (and probably the rest of the Mesozoic) cannot be explained as being due to the relatively low latitude position of the continents, as was suggested by Kavanaugh (1986).

v) The distribution of terrestrial tetrapod faunas (including ectothermic crocodiles and alligators) above 60° palaeolatitude provides evidence that midlatitude isotherms were displaced at least 20° towards the poles when compared with the present situation.

vi) Oxygen isotope measurements from benthic Foraminifera suggest that bottom temperatures in the polar oceans may have been as high as 15°C in the mid-Cretaceous (they subsequently declined to present day levels of 2-3°C during the Tertiary).

All the above data suggest that, during the mid-Cretaceous, temperatures at the tropics were higher than, or similar to today's, while temperatures in the mid-latitudes and polar regions were above those of today. Frakes (1979), Hallam (1985), and Barron (1983) suggested that similar conditions persisted throughout the Mesozoic.

What about the temperature regime experienced at Orapa? Despite its position some 14° latitude to the South of its present position, Orapa probably experienced similar, or even warmer temperatures than at present (see below).

9.1.4 Rainfall

Hallam (1984), presented a review of palaeorainfall indicators. Evaporites and aeolian sandstones indicate arid or semi-arid conditions. Coals, bauxites, laterites, and kaolinite are some of the more important indicators of humid climates. A combination of arid and humid palaeorainfall indicators suggests seasonal rainfall. Of course, plant fossils, and sometimes animals, may also give a good indication of palaeohumidity.

Various authors (Frakes, 1979; Hallam, 1984) have plotted the position of palaoehumidity indicators on Mesozoic maps in an attempt to determine the distribution of arid and humid zones during this era. Hallam (1984) suggested that, the Late Jurassic was a time of global aridity; then in the Early Cretaceous, conditions began to ameliorate, and, by the Late Cretaceous the extent of arid areas had reached a Mesozoic minimum. Hallam ascribed this amelioration of climate to the breakup of Pangea and the extensive epicontinental seas in the Cretaceous, which would have introduced humid marine conditions to areas which were previously continental.

How would the humidity of Cretaceous climates compare with that of today? According to Hallam (1981), sea level in the mid-Cretaceous was approximately 100m higher than today with 30% of the present continental area under water. This suggests that humid marine conditions were far more extensive than today and, therefore, that the global climate was moister.

What type of rainfall can be inferred for Orapa? A major reason for the arid or semi-arid conditions experienced over large portions of the southern African subregion at Orapa today is its position within the subtropical high pressure belt (Jackson and Tyson, 1971). This is a region of cool descending air which consequently does not release moisture easily. Today the subtropical high pressure belt is situated at an average latitude of 30° north and south (Lloyd, 1982). Therefore, crucial to answering the question of the palaeorainfall at Orapa is the position of the high pressure belt during the mid-Cretaceous.

Various authors have tried to address this question, unfortunately with differing results. Frakes (1979) suggested, because of the weaker temperature gradient in the Cretaceous, that the high pressure belt would have been closer to the poles than at present. The modelling exercise of Barron and Washington (1982) suggested that the high pressure belt would have been in a similar position in the Cretaceous to its position today. However, attempts by Lloyd (1982) to model the mid-Cretaceous climate suggested that the high pressure belt would have been situated closer to the equator, around about 25°S. Evaporites, in the mid-Cretaceous are not found further poleward of about 30° latitude (Barron and Washington, 1982; Lloyd, 1982; Parrish, et al., 1982). This suggests that Frakes's hypothesis is wrong but makes it impossible to distinguish between Lloyd's and Barron's hypotheses. However, both theories suggest that Orapa would have been situated in the high pressure belt during the Cretaceous, and therefore, possibly could have had a dryish climate.

What does this imply in terms of actual rainfall? Barron and Washington (1982) modelled mid-Cretaceous climates in two cases; (i) with modern day climatic parameters, but mid-Cretaceous geography, and (ii) with minimum ocean temperatures of 10^{o}C (i.e. decreased pole to equator temperature gradient) and mid-Cretaceous geography. In both cases they suggested that western southern Africa would have had a relatively moist climate in the mid-Cretaceous. However, Barron's control model for the present day also indicated a moist climate for the western part of southern Africa, which is incorrect. Parrish et al. (1982) attempted to map the distribution of rainfall patterns throughout the Mesozoic. They compared cases (i) where the only factor affecting rainfall was assumed to be latitudinal changes in air pressure parallel to the equator (zonal model) with more realistic cases, where (ii) other factors, for example, orographic effects and continentality, were taken into account (circulation-rainfall model). For the Cenomanian, the distribution of evaporites was better predicted by the zonal model than by the circulation-rainfall model, suggesting that during this time continentality and orographic factors were not so important. According to their reconstruction, taking into consideration the west to east decrease in precipitation which occurs on most continents today, Orapa would have had a relatively low rainfall in the mid-Cretaceous.

It is difficult to determine exactly what a relatively low rainfall means, as this prediction of Parrish et al., is not directly comparable to modern rainfall figures. It is probable that the rainfall at Orapa in the Cretaceous would have been higher than today. The reasons for this are described below.

Firstly, the cooling of the Antarctica at the Eocene/-Oligocene boundary resulted in a cooling of the world's oceans. Estimates of the drop in tropical Pacific sea-surface temperatures at this time vary from 1°C (Keigwin, 1980) to 5°C (Savin, 1977). A similar cooling probably occurred in the waters surrounding southern Africa (Martin, 1981 discussed this with regard to the the Aghulas current). Cooler sea-surface temperatures, imply less evaporation, which implies less moisture in the air moving over the continent and, therefore, lower precipitation. According to Frakes (1979 cited by Martin, 1981), a decrease in 5°C of sea surface temperatures would result in a 20-30% reduction in evaporation. This implies that before the oceanic cooling at the Eocene/Oligocene boundary the southern African subregion would have recieved a higher rainfall.

Secondly, today the northward flowing cold Benguela current, which does not yield moisture to the atmosphere easily, accentuates the difference in climate between the east and west coasts (Jackson and Tyson, 1971). According to Siesser (1980) major cooling of the Benguela current only occurred in the Miocene. Therefore, prior to this cooling event the difference in precipitation between the east and west coasts would not have been so extreme.

Thirdly, Nicholson and Flohn (1980; cited by Martin 1981) suggested, on theoretical grounds, that the cooling of the Antarctic, would have resulted in an increase in the pole to equator temperature gradient and a strengthening of the subtropical high pressure belt, which would result in a decrease in precipitation. The models of Barron and Washington (1982) for mid-Cretaceous climates support this result, but both with and without a decrease in the pole to equator temperature gradient.

All of the above suggest that during the mid-Cretaceous Orapa (and the southern Afican subregion in general) would have received a higher rainfall than today. However, two factors could affect this conclusion. (i) Higher temperatures during the Cretaceous imply higher evaporation rates which would offset the increase in precipitation. (ii) Modeling exercises by Barron (1982) and Lloyd (1982), which assume a lower pole to equator temperature gradient suggested that continentality would have been increased in the mid-Cretaceous, resulting in cold winters and hot summers. According to Barron, this is because a lower pole to equator temperature gradient in the Cretaceous would have limited the atmosphere's ability to advect warm, moist oceanic air into the interior of continents at times of low solar radiation. If these models are correct, a strong seasonal component to the rainfall is implied.

In the following sections the hypothesis of a warmer, wetter, Orapa in the mid-Cretaceous is tested using geomorphological, geological and palaontological data pertaining to southern Africa during that time period.

9.1.5 Position of Africa with respect to the Neighbouring Continents and Oceans

By Cenomanian times, southern Africa was bordered along all its present day shorelines by oceanic areas. The South Atlantic to the south-west of Cape Town was 1 600 km wide, and sediments along the south-east and east coasts indicate open oceanic conditions (Dingle *et al.* 1983; Reyment and Dingle, 1987). By this time, Madagascar had reached its present day position (Reyment and Dingle, 1987). On the west coast the South Atlantic formed a narrow trough. To the south it was bound partially by the Falkland islands and Aghulas plateaus, and in the north it may have been in periodic contact with the North Atlantic via a shallow seaway between Africa and South America in the region of the Niger Delta (Reyment and Dingle, 1987). This seaway was established in the Early Albian (Reyment and Dingle, 1987) and, according to Owen (1983), the South and North Atlantic shared a common mid-Ocean ridge by the Turonian. However, Rand and Mabesoone (1982) cited palaeontological evidence that a land bridge may have existed periodically between South America and Africa in the region of the Niger Delta until the Maastrichtian.

During most of the Cretaceous the South Atlantic was split transversely into two basins by the Walvis Ridge and the Rio Grande Rise (Reyment and Dingle, 1987). In Cenomanian times the southern basin had well oxygenated benthic conditions due to a deep water connection with the Antarctic Ocean between the Falkland and Aghulas plateaus. The northern basin had anoxic benthic conditions until Santonian times (Dingle et al. 1983). An island chain along the Walvis Ridge and Rio Grande Rise may have provided a route for the dispersal of plants and animals until it broke up 50-60ma (Rand and Mabesoone, 1982).

In Late Cenomanian-Early Turonian times the south and east coasts were characterised by a general regression in sea level, the ocean along the west coast was transgessive (Dingle et al. 1983, Reyment and Dingle, 1987). In North Africa an epicontinental sea connected the Tethys Sea and the South Atlantic (Reyments and Dingle, 1987).

9.1.6 Palaeotopography

According to Dobbs (1978), between 50 and 100m (*See footnote on the following page) have been stripped from above the present ground surface at Orapa. This suggests that at the time of the emplacement of the Orapa kimberlite the general altitude of the landsurface was between 50 and 100m higher than it is today. However, subsequent to the emplacement of the kimberlite, the southern African subregion has been subject to periods of uplift, especially during the Miocene and the Pliocene (Partridge and Maud, 1987). According to Partridge and Maud this uplift in the southern Kalahari would have totalled some 225m. Assuming that the amount of uplift in the Central Kalahari was roughly the same, if this figure is subtracted from the above estimate of altitude for Orapa in the Cretaceous, a figure of between 125 and 175m lower than its present elevation (960m) is arrived at for Orapa at the time of emplacement.

---

[*] The relatively small amount of erosion that has taken place at Orapa suggests that the time between the eruption of the Orapa kimberlite and the formation of the Kalahari Basin (when erosion was replaced by deposition) was relatively short. This indicates that the sediments of the lower Kalahari Formation are probably of Upper Cretaceous age, which supports the estimate of Partridge and Maud's (1987) for the age of these sediments which was based on the age of diatremes emplaced in the southern Kalahari.

Using the estimates of Hawthorne (1975) for the amount of erosion undergone by kimberlites since their emplacement near Kimberley (a town in the west- central part of the southern African subcontinent), and in the Lesotho Highlands near the eastern escarpment (these kimberlites erupted at approximately the same time as the Orapa kimberlite), Partridge and Maud concluded that in the early Upper Cretaceous the elevations in the subcontinent would have varied between 2 350m near the eastern escarpment to 1 800m at Kimberly.

Highlying areas at the time, away from the eastern escarpment, would have included the Cape Fold Mountains, the Soutpansberg and Waterberg in the Transvaal, the Langeberg and Kuruman mountains in the Northern Cape, and a few remnants on the coastal hinterland which were left behind by the retreat of the escarpment (Partridge and Maud, 1987).

An overall picture of the southern African subregion in the mid-Cretaceous, therefore, includes a decline in elevation from some 2 500m at the south-east and eastern escarpment through 1 800m in the central region of the country to around 700m in the vicinity of Orapa with isolated highlands to the south and in the interior of the subcontinent.

The area in the vicinity of Orapa is likely to have been of moderate relief. Orapa was well away from the escarpment and there is no evidence for nearby highlands. The distribution of diamonds derived from the palaeovolcanic cone at Orapa suggests that the local drainage pattern was to the west (Rayner, personal communication). However, regional drainage was probably to the south. Analysis of clasts in alluvial gravels on the Orange river some 30km down stream of its confluence with the Vaal River suggests the former existence of a river which flowed into the Orange from the north (McCarthy, 1983). McCarthy suggested that this river may have contained up to four times the volume of water of the present day Orange and that it may have drained much of south-central Africa.

9.1.7 Sediments

Southern African Cretaceous sediments have been reviewed by Dingle et al. (1983). They are rare, and mainly of a marine origin. A summary of Cenomanian and Turonian sediments, and their palaeoenvironmental significance is given in Appendix 4.

According to Dingle et al. the high clay content of the Boane Formation and the sediments in the Orange Basin suggest that they were derived from a deeply weathered, well watered source. The coarseness of the fluviatile sediments in the Boane Formation, together with the high rates of deposition in the Orange Basin and Tugela Cone suggest high runoff rates from the interior and consequently humid conditions. The presence of large sedimentary slumps in the Orange Basin support the hypothesis of a high sedimentary input. Also, the deeply weathered, kaolinized nature of the Africa surface which was formed by erosion from the early Cretaceous to the Miocene (Partridge and Maud, 1987) suggests humid conditions (Partridge personal communication). In addition the, lowermost beds of the Kalahari Basin may be of a fluviatile origin (Dutoit, 1954; Truswell, 1977).

What do the sediments at Orapa indicate? Dobbs (1978) suggested that the predominance of mass flow mechanisms of deposition in the Orapa crater indicate an arid environment with occasional torrential rainstorms. This was presumably, because this type of sedimentation is usually found in arid environments today (Bull, 1977). However, Bull cited numerous instances of alluvial fans in humid regions. Vessel and Davies (1981) reported that debris flows form on the outside of the cone of the volcano Feugo in Guatamala. Here, debris flows are triggered by the saturation of loose, easily erodable volcanic ejecta by intense seasonal tropical rains. Therefore, mass flow mechanisms of deposition do not necessarily indicate arid regions.

The evaporite layers in the lacustrine sediments may indicate periods of drought, and the possibly varved nature of some of the lacustrine sediments suggest a seasonal climate. Seasonality may have been expressed as either seasonal fluctuations in temperature or seasonal fluctuations in rainfall, or both.

9.1.8 Distribution of Corals

As stated above, corals indicate water temperatures of greater than 21°C and tropical or subtropical conditions (Frakes, 1979). In southern Africa corals of Albian and Cenomanian age have been reported from the Mzinene Formation, on the Natal north coast (at approximately 30°S) (Dingle _et_ _al_., 1983) and the Igodo Formation, which is of Campanian to Maastrichtian age and is located at approximately 33° S near East London. During the Cretaceous these localities would have been located 14° to the south of their present day positions. Today, coral reefs, because of the influence of the Aghulas current which carries warm waters from the equator southwards, are only found as far South as 28° S on the east coast (Crossland, 1948; Williams, 1989). However, although there is some sedimentary evidence for periodic current action off the east coast in the Cretaceous (Dingle _et_ _al_., 1983), clear evidence for a Agulhas or proto-Agulhas current only dates from the Oligocene (Martin, 1981). Therefore, the distribution of corals off the southern African coast during the Cretaceous may be taken as an indication of general warmer conditions over the whole subregion than today.

9.1.9 Mid-Cretaceous Vegetation Studies in Southern Africa

The abundance of plant material in the Upper Sundays River Formation, Mzinene Formation, and Maputo Formation, suggest a well vegetated interior on the south and east southern

African coasts during the Cenomanian and Turonian (Appendix 4, Dingle _et al._ 1983). On the interior of the west coast the plant fragments and thin lignites from the Kangnas dinosaur site suggests abundant vegetation, however, the dating of this site is no more specific than Upper Cretaceous (Haughton, 1915; Dingle _et al._ 1983).

Axelrod and Raven (1978) inferred the character of the vegetation cover in Africa through the Upper Cretaceous and Palaeocene (75-55mya) from the distribution of modern plant taxa on the continent, from what little fossil evidence there is for this period, and from studies of fossil micro- and macro-floras on continents that were close by during that time (e.g. India and Australia). If vegetation zonation in the mid-Cretaceous was similar to that of today, then Orapa would have been situated in a region of subtropical evergreen forest perhaps fairly close to their subtropical woodland scrub zone. Vegetation of this type today is found in the wetter eastern regions of southern Africa (Axelrod and Raven, 1978). Axelrod and Raven's map suggests that a moist to dry subtropical climate (depending on the proximity to their drier woodland-scrub zone) existed at Orapa in the Upper Cretaceous.

Mid-Cretaceous pollen and spores from DSDP (Deep Sea Drilling Project) site 361, situated some 280 km west-southwest of Cape Town are diverse and indicate a favourable (warm and wet?) climate (McLachlan and Pieterse, 1978). The vegetation from this site apparently has affinities with temperate southern Gondwanaland (Australia, South America, and Antarctica) (Morgan, 1978). Pollen and spores, of mid-Cretaceous age, from DSDP site 364, situated far to the north of site 361 in the Angola basin are from a more restricted flora and suggest harsher possibly semi-arid conditions (Morgan, 1978). This flora has definite tropical affinities (Morgan, 1978). Coetzee et al. (1983) cited unpublished work on the palynology of Upper Cretaceous kimberlitic sediments (other than Orapa) from Botswana; these deposits are dominated by Ephredripites pollen which suggests a relatively dry climate. Ephredripites has also been reported from Orapa (Scholtz personal communication), but, because of the low diversity of palynomorphs from this site, this occurrence cannot be said to be significant. Therefore, palynological studies of mid-Cretaceous sediments in southern Africa indicate a climatic gradient, from moist at the southern tip to dry or even semi-arid on the west coast adjacent to the Angola Basin. Orapa would, presumably, have lain somewhere in the middle of this gradient. This gradient correlates roughly with the vegetation zonation of Axelrod and Raven (1978), which was constructed independently of the palynological knowledge cited above. However, it differs in that, unlike their pattern of zonation, no Notofagus pollen has been recovered from DSDP 361. This suggests that Notofagus never occurred at the southernmost tip of the subcontinent during the Cretaceous.

Coetzee et al. (1983) also inferred, from differences in the abundance of types of palynomorphs among the various sites mentioned above, that a climatic gradient and zonation of vegetation of some sort existed in southern Africa during that time period.

What little floral evidence there is for the palaeoclimate and palaeoenvironment at Orapa, is contradictory. Evidence that the climate was relatively moist is as follows.

i) The presence of abundant fern fragments.

ii) The presence of layers of lacustrine sediments rich in plant fragments, which suggest a well vegetated area in the vicinity of the lake.

Evidence that the climate was relatively dry is now given.

i) The presence of deciduous plants, with characteristic serrated leaves among the macroflora; this suggests seasonality (Bamford, personal communication).

ii) The small size of many of the leaves, suggesting a cold and/or dry climate (Bamford, personal communication).

iii) There is no evidence for thick layers of leaf litter, or for logs which would indicate forests (Bamford, personal communication) within the walls of the crater. However, factors other than climate could explain the lack of logs. Perhaps angiosperms of suitable size had not evolved yet, or conditions in the crater were so unstable as to preclude the growth of large trees.

iv) As stated above, the presence of pollen of the Ephredripites (Scholtz, personal communication) type suggests a relatively dry climate (Coetzee et al., 1983).

However there are also factors which confuse the issue.

i) The presence of compound and lobed leaves which suggest that much of the vegetation was of a successional nature (Bamford, personal communication), and is therefore probably not representative of the vegetation surrounding the crater. Such successional vegetation could have colonised portions of the crater laid bare by mudflows. The portion of the crater covered by successional vegetation would be dependent on the frequency and extent of the mudflows.

ii) The kimberlitic crater with a lake could have represented a unique microclimate, either because the crater with its lake provided a moist environment in an otherwise dry area (Dobbs, 1978), or because the silica-poor sediments derived from kimberlite could only support rather specialised vegetation. The latter seems unlikely because today grasses and trees from the surrounding area seem to colonise the Orapa pit easily.

How can this contradictory and confusing evidence be reconciled? Firstly, however the evidence is reconciled, the macrofossils all suggest a moister environment than that which exists at Orapa today. Even moist microenvironments (pans and river banks) in present day Botswana, perhaps with the exception of the Okavango delta, are not characterised by ferns and abundant vegetation. The ferns are good indicators of a moist environment, even if only in the interior of the crater. Therefore, the other plant macrofossils (unless they were somehow blown into the crater), whether they represent successional vegetation or not, must have also grown in moist conditions. The small leaves, and the <u>Ephredripites</u> pollen indicate relatively dry conditions, but presumably relative only to wet temperate climates or tropical rainforests. The lack of leaf litter contradicts the evidence provided by many of the insects (see below). The vegetation may, therefore, be taken to indicate a seasonal climate which is moister than that which occurs in most of Botswana today. It is possible though that conditions in the crater were moister than in the surrounding countryside.

9.1.10 The Orapa Insect Fauna

Caution must be exercised when using insects as indicators of palaeoenvironment. Firstly, insects are often highly mobile, and are sometimes found far away from their usual environment. For example, Nepidae (Insecta: Hemiptera) have been reported from the swimming pool at Gobabeb, which is situated in the Namib desert many kilometers away from the nearest permanent water source (Kleinjan, personal communication). Secondly, as taxa of progressively higher level than species are included, so they become less useful as palaeoenvironmental indicators. This is because members of larger taxa tend to be found in a greater variety of environments. The main reason why Quaternary beetles are such useful palaeoenvironmental indicators, is because it has been possible to identify them to the level of species (Coope, 1978). The best way of overcoming these problems is to consider entire insect faunas rather than individual specimens or taxa, as each specimen or taxon may then be used to test the environmental hypothesis suggested by the rest of the fauna.

The insect taxa described from Orapa, and the environments in which they are found are summarised in Appendix 5. Unfortunately, most of the insects belong to large diverse groups which do not make good palaeoenvironmental indicators. However, the presence of numerous phytophagous, scavenging, parasitic and predacious groups signifies a large, diverse insect fauna.

McKay and Rayner (1986) suggested, further, that the presence of numerous phytophagous groups, together with those that require decaying organic matter at some stage in their lifecycle, indicates continuous vegetation cover in the crater. This is now confirmed by the presence of Bibionidae, Tipulidae, Empididae, Hybotidae and the Promecognathinae, all of which indicate forest or thick bush. The first three taxa mentioned also indicate fairly high humidity and proximity to water.

9.1.11 The Nature of the Surrounding Countryside

Can the vegetation and microclimate in the Orapa crater be extrapolated to the surrounding countryside? As discussed above the Orapa Crater may have been a damp mini-environment in a more arid region. However, as mentioned previously, the topmost sediments surrounding the Orapa pipe are Kalahari Sands, of which the lowest layers may be Cretaceous in age. These lowest layers are possibly of a fluvial origin (Dutoit, 1954; Truswell, 1977) and probably do not, therefore, indicate an arid climate. Also Palaeoaxinidium orapensis was probably a forest species. This is indicated from the environments in which its extant relatives are found, and from the associated insect fauna. It is also probable that it was flightless, because its elytra were fused. It would, therefore, have been unlikely to disperse over extensive arid areas, and the most likely explanation for its presence at the pipe involves dispersal from surrounding forested or bushy areas (this could have included the entire area or just sections along the water courses). It is interesting to note, in this regard, that the extant genera of southern African promecognathines all occur in isolated patches of forest which are, in some cases, separated by semi-arid areas. Presumably, at some time in the past, the various patches of forest were joined and speciation occurred via isolation of small populations through the disintegration of this forested area. It is possible that such short term fluctuations in climate occurred in the Cretaceous. But it is doubtful, given the incompleteness of the sedimentary record in southern Africa for this time period and the inaccuracy of the dating methods, whether such short term fluctuations would be detected.

9.1.12 Conclusions

Studies and modelling exercises of the global climate in the Mid-Cretaceous suggest that southern Africa, despite its position 14° to the south of its present day position, was warmer than today. Modelling of mid-Cretaceous global climates also suggests that the climate in the interior of the sub-continent would have been wetter and more intensly seasonal than today. Greater warmth during the mid-Cretaceous is supported by the distribution of corals on the east coast of southern Africa during the Cretaceous at latitudes 14° further south than today. A wetter climate is supported by the theoretical consequences of warmer oceans on either side of the sub-continent. What little data are available from Cretaceous sediments also support a warmer more humid climate on the interior of southern Africa.

Vegetation studies suggest that a climatic gradient existed in southern Africa from wetter in the south and east to drier in the northwesterly parts of the subcontinent.

Orapa itself lay at a slightly lower elevation than its present day altitude, in a region of moderate relief. Local drainage was to the west, and the Orapa area had not yet been incorporated in the Kalahari Basin. Some of the vegetation in the crater was deciduous this, together with evaporites and varve-like layers in the sediments, suggests that the climate was seasonal. The presence of thick bush and ferns in the crater suggests, that the climate was much wetter than it is today, though evidence from both plants (small leaves and Ephredripites pollen) and sediments (evaporites and lack of fluvial sediments) suggests that it was on the dryish side. The presence of a flightless carabid Palaeoaxinidium indicates that the area surrounding the crater may have been similar to that in the crater though probably drier and not as intensly vegetated.

9.2 Concluding Remarks on the Carabid Fauna

Any conclusions drawn from the fossil carabid fauna must be tempered with the knowledge that many of the identifications are tentative. Also, where conclusions are drawn from the absence of taxa, it is possible that the taxa in question may have existed in the Orapa crater but have not been found, either through chance or through some peculiarity of the habit of its members.

Although compression and impression fossils have provided valuable information concerning the origins and relationships of the various adephagan taxa, they cannot ever provide similar information (unless the taxon concerned has a very characteristic shape such as the Promecognathinae) about the origins and relationships of the various taxa within the Carabidae. This is because the characters used to separate the various taxa (postion of setae, genitalia, sclerites, mouthparts etc.) are seldom preserved on compressions and impresssions. It is possible, however, that amber fossils may be useful in this regard.

One of the surprising aspects of the carabid fauna described, if only the fossil record is considered, is that all the carabids are at least superficially modern in form, and may be placed in more derived taxa (Haraplinae, Anchoneminae etc.). In contrast, the carabids described by Ponomarenko (1977, 1980, 1986) belong, either to the archaic Protorabinae or Conjunctini or the primitive Carabites; although a trace of the more derived taxa is preserved in the form a protibia of the harpaline type (sensu Crowson, 1955). This demonstrates how misleading the fossil record can be with regard to providing information about the origin of taxa.

A more precise prediction of the carabids present in the mid-Cretaceous has been made, independently of the fossil record, from the study of the distribution of modern taxa. Continental drift theory predicts that many of the continents that are today separate were fused in the past. Reconstructions of continental movements through time, using ocean floor spreading data and best fit of continental margins, have been made. Therefore, if a monophyletic taxon is present on two widely separated continents, which were once fused (assuming that dispersal between the continents did not occur) an idea of the minimum age of the taxon can be estimated.

Erwin (1979, 1985) and Noonan (1979, 1985) (also see references cited by these authors) identified a large number of taxa which had their distributions split by either the separation of Laurasia and Gondwanaland (an event which probably occurred in the Jurassic), or the separation of South America and Africa (a Cretaceous event). Erwin (1985) termed these taxa ancient, old or middle aged; he also confirmed that older "biogeographically speaking" taxa are also more pleisiotypic with respect to morphology. Many of these taxa could have potentially occurred at Orapa during the Cretaceous. In fact, all the fossils described here belong to these older groups, and, therefore, verify the biogeographic hypotheses.

The similarity of the carabids to modern forms indicates that they have been remarkably conservative in their evolution since the Cretaceous. In addition, if the Promecognathinae, Scaritinae and the Harpalinae had their origins in the Jurassic, they have been conservative for even longer. During the same period, the dinosaurs became extinct, and the mammals and birds underwent their major period of diversification.

The carabid fauna must have lived in and possibly around the outside of the crater. It was diverse, with the 14 specimens described here representing at least six different subfamilies, which included burrowing and non burrowing forms, and phytophagous and carnivorous forms. The carabids were dwellers in the thick bush or forest of the surrounding countryside. Some may have dwelt on the shoreline of the crater-lake, subsisting on insects that were washed up by wave action.

Dr. P. Basilewsky has examined an initial report on the various fossils. He suggested that the lack of Brachininae from the deposits supported the hypothesis that the water of the lake at Orapa was poisoned in some way as many of these carabids feed on the larvae of aquatic insects. According to Erwin (1985), the brachinines are a relatively old group, so it is probable that they had evolved by the mid-Cretacous. Dr. Basilewsky also suggested that the lack of arboreal carabids from the Orapa fauna is significant. Their absence is further evidence for lack of large trees in the vicinity. It is also possible that arboreal carabids had not yet evolved. Indeed Erwin (1985) suggested that arboreal carabids were only a later innovation. However, a rather earlier date of origin of the arboreal habit is suggested by the Ctenostomatinae which are, according to Erwin (1979), strictly arboreal. They are found on

Madagascar and in South America (Erwin, 1979) which suggests at least a Cretaceous age for this group.

The carabid fauna comprises both predominantly tropical [Siagoninae, Anchoneminae, Erwin (1985)] and temperate [Promecognathinae, Pterostichinae, Erwin (1985)] forms. This combination of taxa could be found in the forests of southern Africa today.

Eldredge and Gould (1972) identified two patterns of evolutionary change: gradual evolutionary change, the more traditional view, in which organisms are seen as changing slowly through time; and punctuated change, where organisms change rapidly over relatively short periods of time, which are interspersed by long periods of stasis. They regarded the latter pattern of change to have dominated throughout evolutionary history. The similarity of the fossil promecognathines to extant forms is, in my opinion, more supportive of the punctuated model of change than of the gradual model, as the promecognathines have apparently undergone very little morphological change in the past 90 million years. Not only does this conservatism apply to morphology, but also to preferred environment. It seems that fossil promecognathines occupied a forested environment, as do extant promecognathines. Such a relationship between morphology and environment would be predicted if there is a close relationship between the unique morphology of the promecognathines, and their habitat and lifestyle.

9.3 The Fossil Insect Fauna and the Age of the Orapa Sediments.

The fossil insect fauna can be used to provide an age for the Orapa sediments which is independent of that provided by the fossil plants or the radiometric dating methods. Unfortunately, using the insect fauna for dating purposes suffers from the disadvantage that, almost all other fossil insect sites are in the Northern Hemisphere. Therefore, any faunal differences (or similarities) observed between Orapa and Northern Hemisphere sites could be due to the position of the site, rather than just age. However, Jell and Duncan (1986) noted that the Lower Cretaceous insect fauna from the Australian Koonwarra fossil beds could all be placed in modern families and may even belong to extant genera. The modern aspect of many of the insects from Orapa, some may even belong to modern genera (see section which reviews the Orapa insect fauna), therefore, suggests a Cretaceous to recent age.

A more recent age is also suggested by the absence of Archostemata from the Orapa deposits. According to Ponomarenko (1977), archostematans are common in Asian and European Mesozoic sites but become rare in the Late Cretaceous. However, no Archostemata have been described from the Koonwarra site, though this is possibly because of the largely aquatic nature of this fauna.

A Mesozoic age is indicated by the presence of the archaic forms described in Chapter Four and the aquatic beetle of the family Coptoclavidae.

An older age is also suggested by the absence or rarity of Isoptera, Lepidoptera, Apoidea and Formicidae, which are all prominent constituents in African insect faunas today and presumably became more common from the Tertiary onwards.

An idea of the age of the sediments may also be obtained from the carabid fauna. As discussed in the previous chapter, biogeographic evidence suggests that all of the taxa of carabids discovered in the Orapa deposits originated in the Cretaceous or even earlier. Their presence, therefore, suggests a Cretaceous to recent age. However, the presence of a new genus Palaeoaxinidium indicates a pre-Eocene age, as most Carabids from the Eocene-Oligocene ambers of the Northern Hemisphere have been placed in modern genera (Spahr 1981a; 1981b). This may, however, only be taken as an indication of greater age, as generic designations are usually subjective.

Therefore, the insect fauna adds support to the radiometric and palynological dates of Upper Cretaceous, for the deposition of the epiclastic sediments.

9.4 Palaeoenvironmental Model

I suggest, following the palaeoenvironmental model of Dobbs (1978), that the following sequence of events lead to the formation of the fossiliferous sediments in the Orapa crater:

1) The Orapa kimberlite erupted through the sedimentary sequence and basalts of the Karoo series. At the time of the eruption the topography of the surrounding area was one of medium relief with a westward drainage pattern.

2) The eruption occurred at about 90 million years ago in the Upper Cretaceous (early Turonian).

3) The emplacement of the kimberlite resulted in a volcanic crater, 140m deep, surrounded by a volcanic cone approximately 114m high (Dobbs, 1978).

4) At some time after the kimberlite had cooled a crater lake formed. It probably had a deep centre with shallow mudflats round the perimeter. Occasionally the lake may have dried completely.

5) The cone collapsed into the crater and formed the poorly sorted massive boulder beds.

6) Avalanching from the walls of the crater resulted in the formation of talus slopes, preserved as the segregated clast beds.

7) Rainstorms, or seismic events triggered debris flows from the walls of the cone. These would have been large fan shaped structures which carried coarse material towards the centre of the crater.

8) Caving from the sides of the debris flows, distal thinning of the debris flows, or perhaps muddy slurry flows succeeding and preceding the debris flows during their formation are all explanations for the formation of the finer grained granular mass flows.

9) Settling of turbidity currents formed by mudflows passing through the lake, mud charged streams flowing into a thermally stratified lake, and distal thinning of mud flows are possible causes of the unlaminated mudstones and fine sandstones.

10) Fluvial deposits were deposited by streams tansporting material down the crater walls.

11) Settling of organic material in undisturbed deep-water lacustrine conditions resulted in the formation of dark organic rich layers. In places these are separated by thin lighter layers forming paired laminations reminiscent of seasonally formed varves.

12) The inside of the crater and possibly the surrounding area was heavily forested or covered by thick bush, which

included primitive angiosperms and ferns. Vegetation on fresh debris flows would have been of a successional nature. The angiosperms included herbs, shrubs and small trees but there were probably few or no large trees (Bamford, personal communication).

13) In addition to the plants, the crater supported a diverse, thriving population of insects. Many of them fed on the plants, pollinated them, took shelter in the plants, or were scavengers, predators or parasites. Indeed, the insect population, like any analogous modern population of insects, appears to have been represented by all the links in the ecological web and all the normal plant/insect interactions probably occurred. However, aquatic insects (except those that flew into the lake) were absent. In fact, all forms of aquatic life were absent which suggests that the lake waters were probably poisonous to animal life.

14) The insect fauna consisted of both archaic and modern forms, sometimes even modern genera. Also, the composition of the insect fauna differed from an extant African fauna in that the Isoptera, Lepidoptera, Apoidea, and Formicidae were absent or rare.

15) There were apparently few or no vertebrates in the area, or else, vertebrates were simply not preserved.

16) The climate of the area was seasonal, and both warmer and wetter than the climate in the same area today. It was intermediate between temperate and tropical and perhaps resembled that of the higher rainfall areas in the eastern part of the subcontinent today.

17) The plants and Insects became trapped in the fine grained sediments within the lake and buried. As the sedimentary sequence accumulated they were exposed to increasing pressure and thus eventually fossilised. Post-deformational alteration of some of the sediments occurred, perhaps through the oxidising action of ground waters.

18) Gradually the crater filled with sediments. After this between 50 and 100m from the top of crater were eroded away. Eventually the area became incorporated in the Kalahari basin, erosion stopped and the Kalahari sediments were deposited. The result of this sequence of events was the sedimentary sequence that remained before mining operations commenced.

REFERENCES

ADAMSON, R. S. 1931. Notes on some petrified wood from Banke, Namaqualand. Transactions of the Royal Society of South Africa 19:255-258.

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

ALLEN, P. A. and COLLINSON, J. D. 1986. Lakes. In Sedimentary Environment and facies. -2nd edition, (Reading, H. G., ed.) 63-94. London: Blackwell Scientific Publications.

ALEXANDER, C. H., and BYERS, G. W. 1981. Family Tipulidae. In: Manual of Nearctic Diptera (Mc Alpine, J.F., ed.) 153-190. Hull: Canadian Government Publishing Center.

ANDERSON, J. M., and ANDERSON, H. M. 1983. Palaeoflora of Southern Africa: Molteno Formation (Triassic) Volume 1. Rotterdam: Balkema.

ASHWORTH, A. C. 1979. Quaternary Coleoptera studies in North America: Past and Present. In: Carabid Beetles: Their Evolution, Natural History, and Classification

(Erwin T. L., Ball, G. E., and Whitehead, D. R., eds) 395-407. The Hague: Junk.

AXELROD, D. I., and RAVEN, P. H. 1978. Late Cretaceous and Tertiary vegetation history of Africa. In: *Biogeography and Ecology of Southern Africa* (Werger, M. J. A., ed.) 77-130. The Hague: Junk.

BAGNOLD, R. M. 1956. The flow of cohesionless grains in fluids. *Philosophical Transactions of the Royal Society of London. Series A* 249:235-297.

BALL, G. E. 1979. Conspectus of carabid classification: history, holomorphology, and higher taxa. In: *Carabid Beetles: Their Evolution, Natural History, and Classification*. (Erwin, T. L., G. E. Ball, and Whitehead D. R., eds) 63-111. The Hague: Junk.

BARNARD, P. W. D. 1973. Mesozoic floras. In: *Organisms and Continents Through Time.* (N. F. Hughes ed.) 175-187. *Special Papers in Paleontology of the Palaeontological Association (London)* 12.

BARRACLOUGH, D. A., and LONDT, J. G. 1985. Diptera. In: *Insects of Southern Africa*. (Scholtz, C. H., and Holm, E., eds) 283-321. Durban: Butterworths.

BARRON, E. J. 1983. A warm, equable Cretaceous: the nature of the problem. *Earth-Science Reviews* 19: 305-338.

BARRON, E. J. and WASHINGTON, W. M. 1982. Cretaceous climate: a comparison of atmospheric simulations with the geologic record. *Palaeogeography, Palaeoclimatology, Palaeoecology* 40:103-133.

BASILEWSKY, P. 1950, Révision generale des Harpalinae d'Afrique et de Madagascar. Part 1. *Annales du Musee du Congo Belge*, 8°, *Zool*. 6:1-238.

BASILEWSKY, P. 1951, Révision generale des Harpalinae d'Afrique et de Madagascar. Part 2. *Annales du Musee du Congo Belge*, 8°, *Zool*. 9:239-571.

BASILEWSKY, P. 1958. Coleoptera: Carabidae. In: *South African Animal Life: results of the Lund University expedition in 1950-1951*. (Hanström, B., Brinck, P., and Rudebeck, G., eds) Volume 5:212-317. Stockholm: Almqvist Wiksell.

BASILEWSKY, P. 1963. Révision des Promecognathinae d'Afrique (Coleoptera, Carabidae). *Annals of the Transvaal Museum* 24:305-319.

BATTEN, R. L. and SCHWEICKERT R. A. 1981. Discussion concerning the paper of Nur, A. and Ben-Avraham, Z.: Lost Pacifica continent: a mobilistic speculation. In: *Vicariance Biogeography: a Critique* (G. Nelson and D.E. Rosen eds) 359-366. New York: Columbia University Press.

BEATY, C. B. 1970. Age and estimated rate of accumulation of an alluvial fan, White Mountains, California, U.S.A. *American Journal of Science* 268:50-77.

BELL, R. T. 1967. Coxal cavities and the classification of the Adephaga (Coleoptera). *Annals of the Entomological Society of America* 60:101-107.

BELL, R. T., and BELL, J. R. 1962. The taxonomic position of the Rhysodidae (Coleoptera). *The Coleopterists' Bulletin* 16:99-106.

BLATT, H., MIDDLETON, G., and MURRAY, R. 1980. *Origin of Sedimentary Rocks*. New Jersey: Prentice-Hall.

BOOMKER, J. 1985. Elateroidea. In: *Insects of Southern Africa*. (Scholtz, C. H., and Holm, E., eds) 228-232. Durban: Butterworths.

BOUSQUET, Y, and SMETANA, A. 1986. A description of the first instar larva of *Promecognathus* Chaudoir (Coleoptera: Carabidae). *Systematic Entomology* 11:25-31.

BULL, W. B. 1977. The alluvial-fan environment. Progress in Physical Geography 1:220-270.

CHEN, S., and CHUAN-CHIEN, T. 1973. A new family of Coleoptera from the Lower Cretaceous of Kansu. Acta Entomologica Sinica 11:169-178.

COETZEE, J. A., SCHOLTZ, A., and DEACON, H. J. 1983. Palynological Studies and vegetation history of the fynbos. In: Fynbos Palaeoecology: a Preliminary Synthesis. South African National Scientific Programmes Report 75:156-173.

COOPE, G. R. 1978. Late Cenozoic fossil Coleoptera: evolution, biogeography and ecology. Annual Review of Ecology and Systematics 10:247-267.

COOPE, G. R. 1979. The Carabidae of the glacial refuge in the British isles and their contribution to the post glacial colonization of Scandinavia and the North Atlantic Islands. In: Carabid Beetles: Their Evolution, Natural History, and Classification. (Erwin, T. L., G. E. Ball, and Whitehead D. R., eds) 407-424. The Hague: Junk.

CROSSLAND, C. 1948. Reef corals of the South African coast. Annals of the Natal Museum 11:169-207.

CROWSON, R. A. 1955. The Natural Classification of the Families of the Coleoptera. London: Nathaniel Lloyd.

CROWSON, R. A. 1960. The phylogeny of the Coleoptera. Annual Review of Entomology 5:111-134.

CROWSON, R. A. 1981. The Biology of the Coleoptera. London: Academic Press.

CURRY, R. R. 1966. Observation of alpine mudflows in the Tenmile Range, central Colorado. Bulletin of the Geological Society of America 77:771-766.

DARLINGTON, P. J. 1967. A fossil carabid beetle from the Miocene of Montana. Contributions from the Museum of Palaeontology, University of Michegan 22:193-197.

DAVIS, D. L. 1977. The ages and Uranium contents from Kimberlites and associated rocks. Extended abstracts of the second International Kimberlite Conference, Santa Fe.

DAWSON, J. B. 1980. Kimberlites and their Xenoliths. Berlin: Springer-Verlag.

DE VILLIERS, W. M. 1985. Orthoptera. In: Insects of Southern Africa. (Scholtz, C. H., and Holm, E., eds) 78-95. Durban: Butterworths.

DINGLE, R. V., SIESSER, W. G. and NEWTON, A. R. 1983. Mesozoic and Tertiary Geology of Southern Africa. Rotterdam: A.A. Balkema.

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).

DONN, W. L. 1982. The enigma of high-latitude paleoclimate. Palaeogeography, Palaeoclimatology, and Palaeoecology 40:199-212.

DOUGLAS J. G. and WILLIAMS G. E. 1982. Southern polar forests: the early Cretaceous floras of Victoria and their palaeoclimatic significance. Palaeogeography, Palaeoclimatology, and Palaeoecology 39: 171-185.

DU TOIT, A. L. 1954. The Geology of South Africa. 3rd ed. Edinburgh: Oliver and Boyd.

EDWARDS, C. B., and HOWKINS, J. B. 1966. Kimberlites in Tanganyika, with special reference to the Mwadui occurrence. Economic Geology 61:537-554.

ELDREDGE, N., and GOULD, S. J. 1972. Punctuated equilibria: an alternative to phyletic gradualism. In: Models in Paleobiology (Schopf, T. J., ed.) 82-115. San Francisco: Freeman Cooper.

ENOS, P. 1977. Flow regimes in debris flow. Sedimentology 24:133-142.

ERWIN, T. L. 1978. The larva of neotropical *Enceladus gigas* Bonelli (Coleoptera: Carabidae: Siagoninae: Enceladini) with notes on the phylogeny and classification of some of the more primitive tribes of ground beetles. The Coleopterists Bulletin 32:99-106.

ERWIN, T. L. 1979. Thoughts on the evolutionary history of ground beetles: hypotheses generated from comparative faunal analyses of lowland forest sites in temperate and tropical regions. In: Carabid Beetles: Their Evolution, Natural History, and Classification. (Erwin, T. L., Ball G. E. and Whitehead D. R., eds) 539-592. The Hague: Junk.

ERWIN, T. L. 1981. Taxon pulses, vicariance, and dispersal: an evolutionary synthesis illustrated by carabid beetles. In: Vicariance Biogeography: A Critique. (Nelson G. and Rosen D. E., eds) 159-183. Columbia University Press: New York.

ERWIN, T. L. 1985. The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles. In: Taxonomy, Phylogeny and Zoogeography of Beetles and Ants. (Ball, G. E., ed.) 437-472. Dordrecht: Junk.

ESTES, R. 1977. Relationship of the South African fossil frog *Eoxenopoides reuningi* (Anura, Pipidae). *Annals of the South African Museum* 73:49-80.

EVANS, G. E. 1977. Locomotion in the Coleoptera Adephaga, especially Carabidae. *Journal of Zoology* 181:189-226.

EVANS, G. E. 1980. The phylogenetic evidence of functional characters in ground beetles (Coleoptera: Caraboidea). *Entomologia Generalis* 6:303-310.

EVANS, G. E. 1982. Early evolution of the Adephaga - some locomotor speculations. *The Coleopterists' Bulletin* 36:597-607.

EVANS, G. E. 1985. Hydradephagan comparative morphology and evolution: some locomotor features and their possible phylogenetic implications. *Proceedings of the Academy of Natural Sciences of Philadelphia* 137:172-181.

EVANS, M. G. and FORSYTHE T. G. 1985. Feeding mechanisms, and their variation in form, of some adult ground-beetles (Coleoptera: Caraboidea). *Journal of the Zoological Society of London (A)* 206: 113-143.

FRAKES, L. A. 1979. *Climates Throughout Time.* Amsterdam: Elsevier.

FRIIS, E. M. and CREPET, W. L. 1987. Time of appearance of floral features. In The origins of angiosperms and their biological consequences. (Friis, E. M. ed.) 145-179. Cambridge: Cambridge University Press.

FUJUYAMA, I. 1978. Some fossil insects from the Tedori Group (Upper Jurassic-Lower Cretceous), Japan. Bulletin of the National Science Museum, Ser. C (Geol) 4:181-194.

GALTON, P. M. 1977. The ornithopod dinosaur Dryosaurus and a Laurasia-Gondwanaland connection in the Upper Jurassic. Nature 268:220-232.

GALTON, P. M. 1981. A juvenile stegosaurian dinosaur, Astrodon pusillus from the Upper Jurassic of Portugal, with comments on Upper Jurassic and Lower Cretaceous Biogeography. Journal of Vertebrate Palaeontology. 1:245-256.

GILES, E. T. 1970. In: Insects of Australia. (MacKerras I.M., ed.) CSIRO, 303-313. Melbourne: Melbourne University Press.

HAGGERTY, S. E., RABER, E., and NAESER, C. W. 1983. Fission track dating of kimberlitic zircons. Earth and Planetary Science Letters 63:41-50.

HALLAM, A. 1981. Relative importance of plate movements, eustasy, and climate in controlling major biogeographical changes since the early Mesozoic. In. Vicariance Biogeography: a Critique (G. Nelson and D. E. Rosen eds). New York: Columbia University Press.

HALLAM, A. 1984. Continental humid and arid zones during the Jurassic and Cretaceous. Palaeogeography, Palaeoclimatology, Palaeoecology, 47: 195-223.

HALLAM, A. 1985. A review of Mesozoic Climates. Journal of the Geological Society of London 142:433-445

HAMPTON, M. A. 1972. The role of subaqueous debris flow in generating turbidity currents. Journal of Sedimentary Petrology 42:775-793.

HARDY, D. E. 1981. Family Bibionidae. In: Manual of Nearctic Diptera (McAlpine, J.F., ed.) 212-222. Hull: Canadian Government Publishing Centre.

HARMS, J. C., SOUTHARD, J., SPEARING, D. R. and WALKER, R. G. 1975. Depositional environments as interpreted from primary sedimentary strutures and stratification sequences. Lecture notes Soc. econ. Paleont. Miner., Short Course 2. Dallas, Texas, 161pp.

HATCH, M. H. 1953. The beetles of the Pacific Northwest, Part 1: introduction and Adephaga. University of Washington Publications in Biology 16:1-340.

HAUGHTON, S. H. 1915. On some dinosaur remains from Bushmanland. Transactions of the Royal Society of Southern Africa. 15:259-264.

HAUGHTON, S. H. 1924. The fauna and stratigraphy of the Stormberg series in South and Central Africa. Annals of the South African Museum 12:323-497.

HAUGHTON, S. H. 1931. On a collection of fossil frogs from the clays at Banke. Transactions of the Royal Society of Southern Africa 19:233-249.

HAWTHORNE, J. B. 1975. Model of a kimberlite pipe. Physics and Chemistry of the Earth 9:1-15.

HLAVAC, T. F. 1975. The prothorax of the Coleoptera (except Bostrichiformia-Cucujiformia). Bulletin of the Museum of Comparative Zoology at Harvard College 147:137-183.

HONG, Y. -C. 1982. Mesozoic Fossil Insects of Juiguan Basin in Gansu Province. Peking: Geological Publishing House.

HONG, Y. -C. 1983. Middle Jurassic Fossil Insects in North China. Peking: Geologial Publishing House.

HOOKE, R. LeB. 1967. Processes on arid-region alluvial fans. Journal of Geology 75:438-435.

HOOKE, R. LeB. 1968. Steady state relationships on arid region alluvial fans in closed basins. American Journal of Science 266:609-629.

HUMPHRIES, C. J. and PARENTI, L. R. 1986. Cladistic Biogeography. Oxford Monographs on Biogeography no. 2. Oxford: Clarendon Press.

JACKSON, S. P, and TYSON, P. D. 1971. Aspects of weather and climate over Southern Africa. Environmental Studies Occasional Paper 6:13pp Department of Geography and Environmental Studies, University of the Witwatersrand, Johannesburg.

JACOBS, D. H. 1985. Hemiptera. In: Insects of Southern Africa. (Scholtz, C. H., and Holm, E., eds) 111-175. Durban: Butterworths.

JARZEMBOWSKI, I. A. 1981. An Early Cretaceous termite from Southern England. Modern Geology 9:71-93.

JEANNEL, R. 1941. Coleopteres Carabiques. Part 1. Fauna de France 39:1-571.

JEANNEL, R. 1942. Coleopteres Carabiques. Part 2. Fauna de France 40:573-1173.

JELL, P. A. and DUNCAN, P. M. 1986. Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra fossil bed (Korumburra Group), Victoria. In Plants and invertebrates from the Lower Cretaceous Koonwarra fossil bed, South Gippsland, Victoria. (Jell, P.A. and Roberts, J. eds) Memoir 3 of the Association of Australasian Palaeontologists. 111-205.

JOHNSON, A. M. 1970. Physical Processes in Geology. San Francisco: Freeman Cooper.

KAVANAUGH, D. H. 1979. Investigations on present climatic refugia in North America through studies on the distributions of carabid beetles: concepts, methodology and prospectus. In: Carabid Beetles: Their Evolution, Natural History, and Classification. (Erwin, T. L., Ball, G. E. and Whitehead D. R., eds) 63-111. The Hague: Junk.

KAVANAUGH, D. H. 1985. On wing atrophy in carabid beetles (Coleoptera: Carbidae), with special reference to Nearctic Nebria. In Taxonomy, Phylogeny and Zoogeography of Beetles and Ants. (Ball G. E., ed.) 408-429. Dordrecht: Junk.

KAVANAUGH, D. H. 1986. A systematic review of amphizoid beetles (Amphizoidae: Coleopetera) and their phylogenetic relationships to other Adephaga. _Proceedings of the California Academy of Sciences_ 44:67-109.

KEIGWIN L. D. 1980 Palaeoceanographic change in the Pacific at the Eocene-Oligocene boundary. _Nature_ 287: 319-355.

KENT, L. E. 1980. Malvernia Formation. In: South African Committee for Stratigraphy (SACS), Part 1 (Comp. L.E. Kent). Lithostratigraphy of the Republic of South Africa, South West Africa/Namibia, and the Republics of Bophutatswana, Transkei and Venda. _Handbook of the Geological Survey of Southern Africa_ 8: 595-598.

KEY, K. H. 1970. Orthoptera. In: _Insects of Australia_. (Mackerras, I.M., ed.) 323-347. Melbourne: Melbourne University Press.

KIRCHHEIMER, F. 1934. On pollen from the Upper Cretaceous dyosil of Banke, Namaqualand (South Africa). _Transactions of the Royal Society of Southern Africa_ 21:41-45.

KRYZHANOVISKIY, O. L. 1976. An attempt at a revised classification of the Family Carabidae (Coleoptera). _Entomological Review_ 1:56-64.

KUSCHEL, G. 1959. Un Curculionido del Cretaceo superior primer insect fosil de Chile. Investigaciones Zoologicas Chilenas 5:49-54.

LAWRENCE, J. F., and NEWTON, A. F., 1982. Evolution and classificaion of beetles. Annual Review of Ecology and Systematics 13:261-290.

LECLERQUE S. 1960. Refundage d'une roche fossilifère et dégagement de ses lemeiles. Senckenberheana Lethaea 41:483-487.

LINDROTH, C. H. 1957. The faunal connections between Europe and North America. New York: Almquist and Wiksell/Wiley and Sons.

LINDROTH, C. H. 1961. The ground beetles (Carabidae excl. Cicindelidae) of Canada and North America. Part 2. Opuscula Entomologica Suppl. 20: 1-200.

LINDSAY, J. F. 1968. The development of clast fabric in mudflows. Journal of Sedimentary Petrology 38: 1242-1253.

LIN, Q. -B., 1983. Some insect fossils from the east of Heilongjiang province. In: Fossils from the Middle-Upper Jurassic and Lower Cretaceous in Eastern Heilongjiang Province China. Part 1. 113-118. Heilongjiang: Heilongjiang Publishing House.

LIN, Q. -B, 1986. Early Mesozoic fossil insects from South China. Palaeontologica Sinica 21: 1-112.

LLOYD, C. R. 1982. The mid-Cretaceous earth: paleogeography; ocean circulation and temperature, atmospheric circulation. Journal of Geology 90:393-413.

MACKERRAS, J. M. 1970. Blattodea. In: Insects of Australia. (MacKerras, I. M. ed.) 262-275. Melbourne: Melbourne University Press.

MACSWAIN, J. W., and GARNER, W. V. 1956. Notes on two millipede-feeding carabids. The Pan-Pacific Entomologist 32:54.

MARSHALL, J. 1985. Blattodea. In: Insects of Southern Africa. (Scholtz, C. H., and Holm, E., eds) 49-52. Durban: Butterworths.

MARTIN, A. K. 1981. Evolution of the Agulhas Current and its palaeo-ecological implications. South African Journal of Science 77:547-554.

MATTHEWS, J. V. 1979. Late Tertiary Carabid Fossils from Alaska and the Canadian Archipelago. In: Carabid Beetles: Their Evolution, Natural History, and Classification. (Erwin, T. L., Ball, G. E., and Whitehead D. R., eds) 425-445. The Hague: Junk.

MCCARTHY, T. S. 1983. Evidence for the existence if a major, southerly flowing river in Griqualand West. Transactions of the Geological Society of Southern Africa 86:37-49.

MCKAY, I. J., and RAYNER, R. J. 1986. Cretaceous fossil insects from Orapa, Botswana. Journal of the Entomological Society of Southern Africa 49:7-17.

MCLACHLAN, I. R. and PIETERSE, E. 1978. Preliminary palynological results: Site 361, leg 40. Deep Sea Drilling Project. Initial reports of the Deep Sea Drilling Project 4:857-881.

MOORE, B. P. 1965. Studies on Australian Carabidae (Coleoptera). 4- The Pterostichinae. Transactions of the Royal Entomological Society of London. 17: 1-32.

MORGAN, R. 1978. Albian to Senonian palynology of Site 364, Angola Basin. Initial Reports of the Deep Sea Drilling Project 4:915-951.

NAYLOR, M. A., 1980. The origin of inverse grading in muddy derbris flow deposits- a review. Journal of Sedimentary Petrology. 50: 1111-1116.

NICHOLS, S. W. 1985. Omophron and the origin of Hydradephaga (Insecta: Coleoptera: Adephaga).

Proceedings of the Academy of Natural Sciences of Philidelphia 137:182-201.

NICHOLSON S. E. and FLOHN H. 1980. African environmental and climatic changes and the general atmospheric circulation in the Late Pleistocene and Holocene. Climatic Change 2:313-348.

NOONAN, G. R. 1979. The science of biogeography with relation to carabids. In: Carabid Beetles: Their Evolution, Natural History, and Classification. (Erwin, T. L., Ball, G. E., and Whitehead D. R., eds) 295-317. The Hague: Junk.

NOONAN, G. R. 1985. The influences of dispersal, vicariance and refugia on patterns of biogeographical distribution of the beetle family Carabidae. In: Taxonomy, Phylogeny and Zoogeography of Beetles and Ants (Ball, G. E., ed.) 322-349. Dordrecht: Junk.

NUR, A. and BEN-AVRAHAM, Z. 1981. Lost Pacifica continent: a mobilistic speculation. In: Vicariance Biogeography: a Critique (G. Nelson and D.E. Rosen eds) 341-358. New York: Columbia University Press.

OBERPRIELER, R. G., and LOUW, S. 1985. Curculionoidea. In: Insects of Southern Africa. (Scholtz, C. H., and Holm, E., eds) 270-280. Durban: Butterworths.

O'FARRELL, A. F. 1970. Odonata. In: Insects of Australia. (MacKerras, I. M. ed.) 241-261. Melbourne: Melbourne University Press.

O'SULLIVAN, P. E., 1983. Annually-laminated lake sediments and the study of Quaternary envirnonmental changes-a Review. Quaternary Science Reviews 1: 245-313.

OWEN, H. G. 1983. Atlas of continental displacement, 200 million years to the present. Cambridge: Cambridge University Press.

PARRISH, J. T., ZEIGLER, A. M., and SCOTESE, C. R. 1982. Rainfall patterns and the distribution of coals and evaporites in the Mesozoic and Cenozoic. Palaeogeography, Palaeoclimatology, and Palaeoecology 40:67-101.

PARTRIDGE, T. C. and MAUD, R. R. 1987. Geomorphic evolution of southern Africa since the Mesozoic. South African Journal of Geology 90:179-208

PONOMARENKO, A. G. 1977. Suborder Adephaga. In Mesozoic Coleoptera (in Russian). (Arnoldy, L. V., Nikritin, V. V., and Ponomarenko, A. G., eds). Trudy Palaeontological Institute Akadamie Nauk USSR 161:1-204.

PONOMARENKO, A. G. 1980. The new Coleoptera species from the Manlay locality. Trudy Sovm. sov. -mongol. palaeont. eksped. 130: 52-56.

PONOMARENKO, A. G. 1985. Beetles from the Jura of Siberia and Western Mongolia. In: Jurassic Insects of Siberia and Mongolia. (Rasnitsyn, A. P., ed.) Trudy Palaeontological Institute Akadamie Nauk USSR 211:47-88.

PONOMARENKO, A. G. 1986. Insects in the Early Cretaceous ecosystems of W. Mongolia. Descriptions of fossil Coleoptera. Trudy Sovm. sov. -mongol. palaeont. eksped. 28:84-108.

PONOMARENKO, A. G. 1987. New Mesozoic water beetles (Insecta, Coleoptera) from Asia. Palaeontological Journal 21:79-92.

PRINSLOO, G. L. 1985. Hymenoptera, section Parasitica. In: Insects of Southern Africa. (Scholtz, C. H., and Holm, E., eds.) 402-422. Durban: Butterworths.

PRUVOST, P. 1934. Description d'un insecte fossile des couches de la Lukuga (Kivu). Memoirs of the Institute of Geology. University of Lovaine 9:1-8.

RAND, H. M. and MABESOONE, J. M. 1982. Northeastern Brazil and the final separation of South America and

Africa. Palaeogeography, Palaeoclimatology, Palaeoecology. 38:163-183.

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

RAYNER, R. J., and COVENTRY, M. K., 1985. A Glossopteris flora from the Permian of South Africa. South African Journal of Science 81:21-32.

RAYNER, R. J., and MCKAY, I. J. 1987. The treasure chest at Orapa diamond mine. Botswana Notes and Records 18:55-61.

RAYNER, R. J., and WATERS, S. 1989a. A new aphid (Homoptera: Aphididae) from the Cretaceous of Botswana. Palaeontology 32: still to be published

RAYNER, R. J., and WATERS, S. 1989b. A Cretaceous crane-fly (Diptera, Tipulidae): 93 million years of stasis. Unpublished manuscript.

RENNIE, J. V. 1931. Note on fossil leaves from the Banke clays. Transactions of the Royal Society of South Africa 21:33-39.

REUNING, E. 1931. A contribution to the geology and palaeontology of the western edge of the

Bushmanland plateau. Transactions of the Royal Society of South Africa 19:215-232.

REUNING, E. 1934. The composition of the deeper sediments to the pipe at Banke, Namaqualand, and their relation to kimberlite. Transactions of the Royal Society of South Africa 21:33-39.

REYMENT, R. A. and DINGLE, R. V. 1987. Palaeogeography of Africa during the Cretaceous period. Palaeogeography, Palaeoclimatology, Palaeoecology 59:93-116.

RIEK, E. F. 1970. Fossil history, 168-186. In: Insects of Australia (Mackerras I. M., ed.). Melbourne: Melbourne University Press.

RIEK, E. F. 1970. Hymenoptera, 867-959. In: Insects of Australia (Mackerras, I.M., ed.). Melbourne: Melbourne University Press.

RIEK, E. F. 1973. Fossil insects from the Upper Permian of Natal, South Africa. Annals of the Natal Museum 21:513-532.

RIEK, E. F. 1974a. A fossil insect from the Dwyka series of Rhodesia. Palaeontologia Africana 17:15-17.

RIEK, E. F. 1974b. Upper Triassic insects from the Molteno "Formation", South Africa. Palaeontologia Africana 17:19-31.

RIEK, E. F. 1976a. An entomobryid collembolan (Hexapoda: Collembola) from the Lower Permian of South Africa. Palaeontologia Africana 19:141-143.

RIEK, E. F. 1976b. Fossil insects from the Middle Ecca (Lower Permian) of southern Africa. Palaeontologia Africana 19:145-148.

RIEK, E. F. 1976c. An unusual mayfly from the Triassic of South Africa. Palaeontologia Africana 19:149-151.

RIEK, E. F. 1976d. A new collection of insects from the Upper Triassic of South Africa. Annals of the Natal Museum 22:791-820.

RIEK, E. F. 1976e. New Upper Permian insects from South Africa. Annals of the Natal Museum 22:755-789.

RODINE, J. D., and JOHNSON, A. M. 1976. The ability of debris, heavily freighted with coarse clastic material, to flow on gentle slopes. Sedimentology 23:213-234.

ROGERS, A. W. 1915. The occurrence of dinosaurs in bushmanland. Royal Society of South Africa. 15:265-268.

ROUGHLEY, R. E. 1981. Trachypachidae and Hydradephaga (Coleoptera): a monophyletic unit? Pan-Pacific Entomologist 57:273-285.

RUIZ, L. A. and DELCLÒS, X. M. 1986. Nuevo género fósil de insecto Isóptero (Hodotermitidae) de las calizas neocomienses del Montsec. Lleida: Institut D'estudis Ilerdencs Diputacion Provincial de Lleida.

SAVIN S. M. 1977. The history of the earth's surface temperature during the past 100 million years. Annual Revue of Earth Planet Science 5:319-355.

SCHILDKNECHT, H. 1970. The defensive chemistry of land and water beetles. Angewandte Chemie (international edition) 9:1-9.

SCHOLTZ, A. 1985. The palynology of the upper lacustrine sediments of the Arnot pipe, Banke, Namaqualand. Annals of the South African Museum 95:1-109.

SCHOLTZ, C. H., and HOLM, E. 1985. Scarabaeoidea. In: Insects of Southern Africa. (Scholtz, C. H., and Holm, E., eds) 214-223. Durban: Butterworths.

SCHOPF, J.M. 1975. Modes of fossil preservation. Review of Palaeobotany and Palynology 20:27-53.

SCHWEICKERT, R. A. 1981. Discussion concerning A. Hallams paper: Relative importance of plate movements, eustasy, and climate in controlling major biogeographical changes since the early Mesozoic. In: Vicariance Biogeography: a Critique (G. Nelson and D. E. Rosen eds) 331-334. New York: Columbia University Press.

SHARP, R. P., and NOBLES, L. H. 1963. Mudflow of 1941 at Wrightood, Southern California. Bulletin of the Geological Society of America 64:547-560.

SIESSER W. G. 1980. Late Miocene origin of the Benguela upwelling system of northern Namibia. Science 208:283-285.

SLOAN, T.G. 1923. The classification of the family Carabidae. Transactions of the Royal Entomological Society of London 1923:234-250.

SMETANA, A. 1985. Staphylinoidea. In: Insects of Southern Africa. (Scholtz, C. H., and Holm, E., eds) 209-213. Durban: Butterworths.

SMITH, K. G. V. 1969. The Empididae of Southern Africa. Annals of the Natal Museum 22:275-288.

SMITH, R. M. 1986. Sedimentation and palaeoenvironments of crater-lake deposits in Bushmanland, South Africa. Sedimentology 33:369-386.

SPAHR, V. U. 1981. Bibliography der bernstein- und kopalkafer (Coleoptera). Stuttgarter Beitrage zur Naturkunde Serie B (Geologie und Palaontology) 72:1-21.

SPAHR, V. U. 1981. Systematischer katalog der Bernstein- und Kopal-Kafer (Coleoptera). Stuttgarter Beitrage zur Naturkunde Serie B (Geologie und Palaeontology) 80:1-107.

STEINMANN, H. 1985. Dermaptera. In: Insects of Southern Africa. (Scholtz, C. H., and Holm, E., eds) 66-69. Durban: Butterworths.

STRANEO, S. L. 1958. Coleoptera: Carabidae: Pterostichinae: a revision of the South African Pterostichinae. In: South African Animal Life (Hanstrom, B., Brinck, P., and Rudebeck, G., eds). 5:318-455. Stockholm: Almqvist Wiksell.

TAYLOR, T. N. 1981. Palaeobotany, an Introduction to Fossil Plant Biology. New York: McGraw-Hill Book Company.

TEDFORD, R. H. 1981. Discussion concerning the paper of

Nur, A. and Ben-Avraham, Z.: Lost Pacifica continent: a mobilistic speculation. In: Vicariance Biogeography: a Critique (G. Nelson and D.E. Rosen eds) 367-370. New York: Columbia University Press.

THIELE, H. U. 1977. Carabid Beetles in their Environments. A Study on Habitat Selection by Adaptations in Physiology and Behaviour. New York: Springer-Verlag.

TINDALE, N. B. 1980. Origin of the Lepidoptera with a description of a new Triassic species and notes on the origin of the butterfly stem. Journal of the Lepidopterists' Society 34:263-285.

TRUSWELL, J. F. 1977. The Geological Evolution of South Africa. London: Purnell.

VAN DIJK, D. E. 1985. An addition to the fossil Anura of Southern Africa. South African Journal of Science 81:207-208.

VESSEL R. K., and DAVIES, D. K. 1981. Nonmarine sedimentation in an active fore arc basin. Special Publications of the Society of Economic Palaeontologists and Mineralogists 31:31-45.

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. 1989a. A Cretaceous dance fly (Diptera: Empididae) from Botswana. Systematic Entomology 14:133-241.

WATERS, S. 1989b. A new hybotine dipteran from the Cretaceous of Botswana. Palaeontology 32: still to be published.

WIGHTON, D. C. 1987. Gomphaeschna obliqua spec. nov. a new species of Gomphaeschinae from the lower Cretaceous of N. E. Brazil (Anisoptera: Aeshnidae). Odonatalogica 16:311-314.

WILLIAMS, G. C. 1989. A review of recent research on the sublittoral coral reefs of Northern Natal with a provisional assessment of findings regarding the distribution of octocorals on Two-Mile Reef, Sodwana Bay. South African Journal of Science 85:140-141.

WILSON, E. O. 1987. The earliest known ants: an analysis of the Cretaceous species and an inference concerning their social organisation. Palaeobiology 13:44-53.

WILSON, E. O. 1987. The earliest known ants: an analysis of the Cretaceous species and an inference concerning their social organisation. Palaeobiology 13:44-53.

WHITE, M. E. 1986. The Greening of Gondwana. Australia: Reed Books.

ZEUNER, F. E. 1939. Fossil Orthoptera, Ensifera. London: British Museum of Natural History.

ZEUNER, F. E. 1955. A fossil blattoid from the Permian of Rhodesia. Annals and Magazine of Natural History 8:685-688.

ZEUNER, F. E. 1961. A Triassic insect flora from the Molteno beds of South Africa. Proceedings of the 11th International Congress of Entomology. 1:304-306.

APPENDIX 1. List of species of Carabidae examined

Most species examined are from the National Insect Collection, Pretoria. A * indicates a specimen from the Transvaal Museum, ** indicates the South African Museum Cape Town and *** indicates the California Academy of Science.

FAMILY CARABIDAE

SUBFAMILY CARABINAE

Calosoma frigidum Kirby
C. schayeri Erichson
Caminara chorostictum (Dejean)
Ctenoste planicolle (Chaudoir)
C. senegalense (Dejean)

SUBFAMILY CAMARAGNATHINAE

Camaragnathus oxygonus Chaudoir

SUBFAMILY OMOPHRONINAE

Omophron americanus Dejean
O. capicola Chaudoir
O. picturatus Boheman
O. suturalis Guérin
Phrator depressus (Klug)

SUBFAMILY PROMECOGNATHINAE

Promecognathus sp.
Axinidium angulatum Basilewsky
**A. africanum Sturm
*Paraxinidium andreaei Basilewsky
*Metaxinidium leleupi Basilewsky
*M. namum Basilewsky
*Holaxinidium fitsomonsi Basilewsky

SUBFAMILY SIAGONINAE

Siagona australis Péringuey

SUBFAMILY SCARITINAE

Acanthoscelis ruficornis (Fabricius)
Antireichia promontorii (Péringuey)
Bohemania minor Péringuey
Clivina americana Dejean
C. caffra Putzeys
C. cognata Péringuey
C. natalensis Putzeys
C. rugiceps Klug
Distichus picicornis (Dejean)
Dyshyrius capensis Péringuey

Dyschyrius ornatus Péringuey
Haplotrachelus atropis Bates
H. capicola Dejean
H. ignobilis Chaudoir
H. latesulcatus Bates
H. oviventris Chaudoir
H. pasimachoides Chaudoir
H. politus Wiedemann
H. polypleuris Bates
H. punctuliger Bates
H. subcrenatus Chaudoir
H. transvaalensis Chaudoir
Passalidius fortipes (Boheman)
Pseudoclivinia grandis (Dejean).
Scallophorites doquereaui (Gory)
S. exaratus (Dejean)
S. molassus (Klug)
S. natalensis (Boheman)
S. nigrita (Boheman)
S. rugiceps (Wiedemann)
S. rugosus (Wiedemann)
Scarites aestuans (Klug)
S. herbsti Dejean
S. polites Boheman
S. perplexus Dejean
S. praevius Peringuey
S. senegalensis Dejean
S. simogonus Chaudoir

SUBFAMILY APOTOMINAE

Apotomus annulaticornis Péringuey

SUBFAMILY BEMBIDIINAE

Bembidium sp.
Elaphropus aethiopicus (Chaudoir)
Eotachys caffer (Péringuey)
E. leptocerus (Chaudoir)
Notaphocampa foveolatum (Dejean)
Omatophus mixtum (Schaum)
Polyderis brevicornis (Chaudoir)
Sphaerotachys haemorrhoidalis (Dejean)
Tachys coruscus Léconte
T.crassescens Péringuey
T. flavicauda Say
T. similis Blackburn
Tachylopha optimus (Péringuey)
Tachyphanes bisignatus (Boheman)
Tachyura capicola (Péringuey)
T.faustus (Péringuey)
T. spurius (Péringuey)

SUBFAMILY POGONINAE

Pogonus lamprus Wiedemann

SUBFAMILY MELAENINI

Melaenus elegans Dejean

SUBFAMILY TRECHINAE

Perileptus sp.
Plocamotrechus bohemani Jeannel
P. tabulae (Péringuey)
P. rufipes (Boheman)
P. vivax (Péringuey)
Trechus ambiguus Péringuey
T. ovipennis Motschulsky

SUBFAMILY PANAGAEINAE

Craspedophorus bonvouloiri Chaudour
C. impictus Boheman
Epigraphus amplicollis Schaum
Euschizomerus elongatus Chaudoir
E. junodi Péringuey
Microcosmus laetiusculus (Chaudoir)
M. natalensis (Péringuey)
M. tenuipunctatus (Laferté)
Tefflus delugorguei Guérin

SUBFAMILY ANTHIINAE

Anthia sp.
Atractanotus mulsanti Perroud
Baeoglossa melanaria (Boheman)
Cycloloba alveolata (De Breme)
C. aenigma (Dohrni)
C. amatonga Péringuey
C. boucardi Chaudoir
C. consobrina Péringuey
C. divisa Boheman
C. fritschi Péringuey
C. septemguttata (Fabricius)
Eccoptoptera cupricollis Chaudoir
E. mutilloides (Bertoloni)
Thermophilum andersoni Chaudoir
T. biguttata Boheman

SUBFAMILY GRAPHITERINAE

Graphoterus albolinealus (Wallengren)
G. amabilis Boheman
G. amicus Péringuey
G. ancora Dejean
G. atremidius Chaudoir
G. bilineatus Chaudoir

G. bivittus Chaudoir
G. bonvouloiri Chaudoir
G. cicindeloides Swederus
G. cinctus Chaudoir
G. curcumcinctus Boheman
G. lateralis Boheman
G. limbatus Castelnau
G. lineelus Péringuey
G. lugens Chaudoir
G. macrocephalus Boheman
G. mashunas Pêringuey
G. mouffleti Chaudoir
G. obliteratus Boheman
G. plagiatus Boheman
Piezia algoensis Péringuey
P. *selousi* Péringuey
P. *spinolae* (Bertoleni)

SUBFAMILY PELECIINAE

Dyschiridium chleninus Chaudoir

SUBFAMILY PTEROSTICHINAE

Abacetus agilis Péringuey
A. congruens Péringuey
A. confinis Péringuey
A. conformis Péringuey
A. crenulatis Dejean
A. delagoensis Péringuey
A. dilucidus Péringuey
A. lucidulus Boheman
A. majorinus Péringuey
A. minutus (Dejean)
A. nanus Chaudoir
A. natalensis Chaudoir
A. obtuses Bóheman
A. olivaceus Tschitscherine
A. optimus Péringuey
A. pavoninus Péringuey
A. percoides Fairmaire
A. pertubator Péringuey
A. perplexus Péringuey
A. pilosellus Péringuey
A. propinquus Péringuey
A. pygmaeus Boheman
A. setulosus Chaudoir
A. trechoides Péringuey
A. vertagus Péringuey
Capabatus raffrayi Péringuey
Camptoscelus hottentota (Olivier)
Cophsomorpha arnoldi Straneo
C. caffra (Dejean)
C. similis Straneo
C. soror Tschitscherine
Melanchiton rectangulum Chaudoir

Morion guineensis Imhoff
Ogmophora peringueyi Tschitscherine
Stereostoma corpulentum Chaudoir
Stigomerus ferrugineus (Péringuey)
Rhathymus melanaria Klug
Wahlbergia undulatorugosa Tschitscherine

SUBFAMILY ANCHOMENINAE

Agonum alacre Boheman
A. natalense Boheman
A. rufipes Dejean
Agonidium fallaciosum (Péringuey)
A. striatitarse (Péringuey)
Enoicus fallax Péringuey
Euleptus albicornis Kolbe
E. caffer Boheman
E. gracilis Péringuey
Geobaenus ingenuus Péringuey
G. lateralis Dejean
Laemosthenes complanatus Dejean
Lasiocera tessellata Klug
Metagonum capicola (Péringuey)
M. crenatostriatus (Peringuey)
M. gilvipes (Boheman)
M. insolitus (Peringuey)
M. lattipennis (Boheman)
M. latuisculum (Péringuey)
M. umtalianus (Péringuey)
Selina westermanni Motschulsky

SUBFAMILY LICININAE

Rembus capensis Péringuey

SUBFAMILY CHLAENIINAE

Baldochlaenius cham (Chaudoir)
B. clarsoni (Barker)
B. piceus (Chaudoir)
B. natalensis (Chaudoir)
B. trapezicollis (Chaudoir)
Callistoides fulvicollis (Chaudoir)
C. pulchellus (Boheman)
C. kirki (Chaudoir)
C. viticollis (Boheman)
Chlaenionus dohrni (Bertolini)
Chlaeniostenodes coeruleipennis (Boheman)
Chlaeniostenus angustatus (Dejean)
C. cylindricollis (Dejean)
C. leucoristus (Chaudoir)
C. sulcipennis (Boheman)
C. tenuicollis (Fabricius)
C. validicornis (Boheman)
Chlaenites comes (Péringuey)
C. cyanipennis (Boheman)

Chleanius communimacula Chaudoir
C. coscinoderus Chaudoir
C. dichrous Wiedemann
C. nitidiceps Dejean
C. notabilis Laferte
C. senagalensis Dejean
C. signatus Boheman
C. quadrisignatus Boheman
Epomis circumscriptus (Duftschmidt)
Leptorembus verecundis (Péringuey)
Ocybatus reichei (Laferté)
Pachydinodes bipustulatus (Boheman)
P. simplex (Wiedemann)
Prochlaeniellus limbatus (Wiedemann)
P. limbipennis (Boheman)
Pseudochlaeniellus cribricollis (Péringey)
P. paenulatus (Ericson)
Rhopalomelus angusticollis Boheman
Spilochlaeniellus discrepans (Dejean)
S. cruciatus (Dejean)
S. discrepans Basilewsky
S. dusaulti Basilewsky
Stenodinodes asseila (Laferté)
S. cribellatus (Chaudoir)
S. fasciger (Chaudoir)
S. fenestratus (Chaudoir)
S. goryi (Gray)
S. perspicillaris (Erichson)
Wilmerstenus capicola (Chaudoir)
W. laetus (Fabricius)
W. latipennis (Sternberg)

SUBFAMILY OODINAE

Oodes fluvialus Leconte
O. natalensis Chaudoir
O. senegalensis Dejean
O. similatus Boheman
Systolocranius ampliolatus Péringuey
S. validus Klug

SUBFAMILY HARPALINAE

Acupalpus egenus Péringuey
A. elegantulus Péringuey
A. simplex Péringuey
A. umpbripennis Péringuey
A. vittiger Klug
Africobatus harpaloides (Guèrin)
Amblystomus amabilis (Boheman)
A. blandus Péringuey
A. ornatipennis (Boheman)
A. promontorii Péringuey
A. natalicus Péringuey
A. plagifer (Klug)
A. quadrisignatus (Boheman)

Anoplogenius agilis (Péringuey)
A. angustatus Chaudoir
A. gratus (Péringuey)
Aulacoryssus aciculatus (Dejean)
A. natalicus (Péringuey)
A. venustulus (Boheman)
Batoscelis promintorii Péringuey
Boeomimetes ephippium (Boheman)
Bradybaenus opulentis Boheman
Cratognathus capensis (Castelnau)
C. mandibularis Dejean
Dichaetochylis caffer (Boheman)
D. incrassatus (Boheman)
D. moestus (Chaudoir)
Diatypus picinus (Chaudoir)
Egadroma capensis Péringuey
E. nitidulus (Chaudoir)
E. terminalis (Péringuey)
E. tesselatum (Péringuey)
E. scapulare (Dejean)
Harpalus agilis Péringuey
H. capicola Dejean
H. cursorius Péringuey
H. defector Péringuey
H. dubius Boheman
H. exiguus Boheman
H. fimetarius Dejean
H. fulvicornis Thunberg
H. fuscipennis Wiedemann
H. fuscoaenus Dejean
H. hybridus Boheman
H. lugubrus Boheman
H. miles Péringuey
H. nanniscus Péringuey
H. natalensis Boheman
H. parvulus Dejean
H. rufocinctus Chaudoir
H. spurius Péringuey
H. venator (Boheman)
Harpalodes xanthoraphus (Wiedemann)
Harpalomorphus aeneipennis Péringuey
Heterohyparpalus caffer (Boheman)
H. tomentosus (Dejean)
Neosiopelus interstitialus (Boheman)
N. melancholicus (Boheman)
N. punctatellus (Reiche)
Oidius dorsiger (Klug)
Omostropus palangoides (Reiche)
O. tersulus Péringuey
O. vicarius Péringuey
Platymetopus seriatis (Chaudoir)
P. tesselatus Dejean
Pseudohyparpalus audens (Péringuey)
P. puncticollis (Boheman)
Pseudoselenophorus imitator (Péringuey)
Selenophorus rufomarginatus (Boheman)

SUBFAMILY MASOREINAE

Aephnidius madagascariensis Chaudoir
Microus mocquerysi Chaudoir
Somoplatus substriatus Dejean

SUBFAMILY TETRAGONODERINAE

Cyclosomus buqueti Dejean
Cyclicus insignicollis (Chaudoir)
Tetragonoderus dispar Péringuey
T. sericatus Dejean
Tilius subsericeus Dejean

SUBFAMILY LEBIINAE

Apristus latipennis Chaudoir
Arsinoe caffra Péringuey
A. fraterna Péringuey
A. grandis Péringuey
A. notabilis Péringuey
A. plausabilis Peringuey
A. quadriguttata Castelnau
Catascopus rufofemoratus Chaudoir
Coptodera fasciata Boheman
Cylindrocranius errans Péringuey
C. ruficollis Péringuey
Haplopeza violacea Boheman
Hystrichopus agilis Péringuey
H. atratus Chaudoir
H. altecostatus Péringuey
H. angusiticollis Boheman
H. dorsalis (Thunbergen)
H. gracilis Péringuey
H. praedator Péringuey
H. rufipes Dejean
H. sulcatus Dejean
H. vigilans (Sturm)
Klepteromimus ornatus Péringuey
Lebia adamtina Péringuey
L. cognata (Péringuey)
L. congruens Péringuey
L. crucifera Boheman
L. dubia Péringuey
L. durbanensis Barker
L. eximia Péringuey
L. fortuita Péringuey
L. fraterna Péringuey
L. immaculata Boheman
L. insidiosa Péringuey
L. lytata Motschulsky
L. modesta Boheman
L. natalensis Chaudoir
L. natalis Péringuey
L. peregrinator Péringuey
L. plagiata Boheman

L. sebakuana Boheman
L. simulatoria Péringuey
L. speciosa Péringuey
L. tetragramma (Chaudoir)
L. vaciva Péringuey
L. vagans Péringuey
L. verisimilis Barker
Lebiomorpha sanguinea (Boheman)
Leptosarcus porrectus (Péringuey)
Libistina peringueyi Liebke
L. subcruciata Fairmaire
Lionychus cinctus Chaudoir
Lipostratia elongata Boheman
Mesolestes affinis (Péringuey)
Mesolestinus flavosignatus (Boheman)
M. fusculus (Péringuey)
Metaxymorphys affinis Peringuey
M. agilis Péringuey
M. cycloderus Chaudoir
M. decepter Péringuey
M. goryi Chaudoir
M. inconspicuus Péringuey
M. namaquensis Péringuey
M. stigmatellus Péringuey
M. vicinus Peringuey
Microlestes capensis Motsch~~o~~ulsky
M. tibialis Péringuey
Paralebia vicaria Péringuey
Parena africana Allard
Plagiopyga cymindiodes Péringuey
*_Periphobus confusus_ Basilewsky
P. nigra Péringuey
Stenocallida affinis (Chaudoir)
S. angusticollis (Boheman)
S. fervida (Péringuey)
Thyreopterus flavosignatus Dejean

SUBFAMILY PENTAGONICINAE

Pentagonica gracilis Peringuey
P. O'neili Barker

SUBFAMILY HEXAGONIINAE

Hexagonia immaculata Chaudoir
H. natalensis Chaudoir
H. praeusta Chaudoir
H. terminalis Gemminger and Harold
H. umtalina Péringuey
H. venusta Péringuey

SUBFAMILY ODACANTHINAE

Archicolliuris rufopicea (Chaudoir)
Erectocolluris Fairmairei (Gestro)
Eucolliuris amoenula (Péringuey)

E. dorsalis (Péringuey)
E. natalensis (Chaudoir)
E. Olivieri (Buquet)
Smeringocera mashuna (Péringuey)
Stenidia abdominalis Chaudoir
S. angusta Péringuey
S. elegantula Péringuey
S. fraterna Péringuey
S. jucunda Péringuey

SUBFAMILY DRYPTINAE

Desera australis Péringuey
Deserida distincta (Rossi)
Drypta brevis Péringuey
D. dentata (Rossi)
D. mashona Péringuey
D. melanarthra Chaudoir
D. ruficollis Dejean
D. thoracica Boheman
Galerita janus Fabricius
Galeritiola angustipennis (Gerstaecker)

SUBFAMILY ZUPHIINEA

Parazuphium debile (Péringuey)
Planetes quadricollis Chaudoir
Zuphium bohemani Chaudoir
Z. caffrum Boheman

SUBFAMILY HELLUONINAE

Macrochilus dorsalis Klug
M. viduatus Péringuey
Triaenogenius corpulentus Chaudoir
T. vicinus Péringuey

SUBFAMILY ORTHOGONIINAE

Neoglyptus brevicornis (Péringuey)
Orthogonius aemulus Péringuey
O. caffer Boheman
O. capucinus Boheman
O. impuctipennis Quedenfeldt

SUBFAMILY BRACHYNIINAE

Aploa nobilis (Dejean)
Brachinus algoensis Péringuey
B. armiger Dejean
B. axillaris Chaudoir
B. caffer Boheman
B. diffusus Chaudoir
B. fuscipennis Dejean
B. leprieuri Gory
B. longulus Chaudoir

B. mactus Péringuey
B. natalicus Péringuey
B. promontorii Péringuey
B. subcostatus Dejean
B. vitaticollis Péringuey
Crepidogaster bimaculata Boheman
C. caffra Peringuey
C. consobrina Péringuey
C. costata (Dejean)
C. infuscata (Dejean)
C. insignis Péringuey
C. neglecta Basilewsky
C. nonstriata Chaudoir
C. rufescens (Motsch~~o~~ulsky)
Mastax albonotata Péringuey
M. extrema Péringuey
M. ornatella Boheman
Pherosophus angolensis Erickson
P. Bohemani Chaudoir
P. capensis Chaudoir
P. Dregei Chaudoir
P. fastigiatus Linnaeus
P. Planti Chaudoir
P. mashunus Péringuey
Styphlomeris equestris Dejean
S. montana (Péringuey)

APPENDIX 2. Summary of dimensions of specimens. LB = length of body, LE = length of elytra, LMF = length of the metathoracic femora, LMT = length of the metathoracic trochanters, LP = length of prothorax, MWE = maximum width of the elytra, MWP = maximum width of the prothorax, WA = width of the head between the antennae, WEHA = width of elytra at the humeral angles, WN = width of the head at the neck, WPAA = width of the prothorax between the anterior angles, WPPA = width of the prothorax between the posterior angles.

Dimensions	Specimen Number BP/2/...												
Measurements (mm)	18302	26253a	26253b	18669a	18669b	26255	26260	24006	26256a	26256b	27356	24004a	24004b
LB	8.56	14.67	14.50	9.98	6.16	7.70	7.04	4.84	7.40	6.88	8.45	7.70	7.86
LP	1.56			2.40		1.78	1.76	1.18	1.72	1.60	1.97	1.90	1.94
WPAA	1.72	3.80	3.80	2.50		1.76	1.80	1.36	1.64	1.60	2.16		2.16
WPPA	1.12	3.80	3.80	3.32		2.00	1.76	1.28	1.60	1.52			
MWP	1.72	3.80	3.80	3.49		2.64	2.40	1.60	2.20	2.08	2.50	2.40	2.51
LE	4.32	7.58	7.75	5.80		4.52	4.08	2.86	4.28	4.20	4.56	4.44	4.48
WEHA	1.84					2.72		1.60	2.20	2.08			
MWE	2.24	3.80	3.80	4,84		2.88		1.88	2.48	2.40	2.57	2.76	2.81
Ratios													
WA/WN	0.53			0.67		0.72	0.72	0.51	0.72	0.67	0.56	0.79	0.73
MWP/LP	1.10	1.00	1.00	1.45		1.48	1.32	1.36	1.28	1.30	1.27	1.20	1.29
WPAA/WPPA	1.54			0.72		0.88	1.02	1.06	1.05	1.05			
LP/LE	0.36			0.41		0.39	0.43	0.41	0.40	0.38	0.43	0.43	0.43
MWP/MWE	0.77	1.00	1.00	0.60		0.92		0.85	1.00	1.00	0.86	0.87	0.89
WPPA/WEHA	0.61							0.80	0.73	0.73			
LMT/LMF	0.31	0.407		0.54	0.57	0.48		0.53	0.43		0.49	0.49	0.48

APPENDIX 2 (continued). LB = length of body, LE = length of elytra, LMF = length of the metathoracic femora, LMT = length of the metathoracic trochanters, LP = length of prothorax, MWE = maximum width of the elytra, MWP = maximum width of the prothorax, WA = width of the head between the antennae, WEHA = width of elytra at the humeral angles, WN = width of the head at the neck, WPAA = width of the prothorax between the anterior angles, WPPA = width of the prothorax between the posterior angles.

Dimensions	Specimen Number BP/2/...							
Measurements (mm)	27583a	27583b	27584	27586a	27586b	27585a	27585b	27587
LB	6.47	6.57	7.43	8.32	7.78	8.74	8.61	6.23
LP	1.66	1.77	2.07			2.08	2.16	1.55
WPAA	1.54	1.63	1.95			2.21	2.18	1.65
WPPA	1.32	1.32	1.18				1.48	
MWP	1.89	1.86	2.23		2.14	2.50	2.55	
LE	3.52		3.89	4.43	4.22	4.87	4.77	3.38
WEHA	1.81	1.91	2.05	2.41	2.18	2.45	2.50	
MWE	1.89	1.86	2.27	2.91	2.64	3.02	3.05	2.51
Ratios								
WA/WN	0.66							0.57
MWP/LP	1.14	1.05	0.43			1.20	1.17	
WPAA/WPPA	1.17	1.24	1.65			1.39	1.48	
LP/LE	0.47		0.53			0.43	0.45	0.46
MWP/MWE	0.85	0.84	0.98		0.81	0.83	0.84	
WPPA/WEHA	0.72	0.69	0.58			0.65	0.59	
LMT/LMF			0.41	0.51	0.54	0.57		0.55

APPENDIX 3. List of Carabid specimens recovered from Orapa but not described in this thesis.

BP/2/22218
BP/2/24001
BP/2/24003 a&b
BP/2/24005
BP/2/25893
BP/2/25906
BP/2/25929
BP/2/26247
BP/2/26248 a&b
BP/2/26249
BP/2/26250
BP/2/26254
BP/2/26256
BP/2/26257
BP/2/26267
BP/2/26637
BP/2/26639
BP/2/26658
BP/2/26950
BP/2/27037
BP/2/27247
BP/2/27256
BP/2/26257
BP/2/26261
BP/2/26710
BP/2/26797
BP/2/27118
BP/2/27494 a&b
BP/2/27495 & BP/2/27496 (part and counterpart)
BP/2/27497
BP/2/27498
BP/2/27499
BP/2/27588
BP/2/27589 a&b
BP/2/27590
BP/2/27591
BP/2/27592

APPENDIX 4. Summary of Cenomanian and Turonian sediments in Southern Africa and the palaeoclimate and palaeoenvironment which they indicate. Unless otherwise indicated the information is taken from Dingle et al. (1983).

Position of Sediments.	Sedimentary Formation, System, etc.	Age	Nature of sediments	Palaeoclimate or environment which they indicate.
Outeniqua Basin (SE Coast)	Upper Sundays River Formation	Barremian to Cenomanian	Deltaic deposition in elongate sedimentary basins.	Abundant lignite and plant material indicating well vegetated coastal river catchment areas
	Alphard Formation	Cenomanian to Maastrichtian	Shallow water environment with open ocean influences	
Natal, Zululand and Mozambique (E Coast)	Tugela Cone	Cenomanian to Maastrichtian (but continues down into the lower Cretaceous and up into the Palaeocene and beyond)	Mildly anoxic shallow marine conditions with a large supply of fresh water and sediments from the Tugela river.	
	Mzinene Formation	Albian to Cenomanian	Shallow water marine environment with a diverse fauna and abundant plant remains.	Corals and carbonates indicate warm water conditions. Plant remains indicate well vegetated interior.
	Boane Formation	Cenomanian to Coniacian	Fluviatile sands and conglomerates.	Coarseness of the fluviatile sediments indicates a high runoff rate of coastal rivers. Abundance of clay indicates deep weathering in the river catchment areas.
	Sena Formation	Upper Jurassic to ?Santonian.	Conglomeratic sandstones interbedded with larvas. Represent fluviatile continental infill of fault basin.	
	Maputo Formation	Aptian to Cenomanian	Shallow water marine environment with rich fauna.	Carbonates indicate warm water conditions.
	Domo Formation	Albian to Turonian	Distal marine sediments deposited in anoxic conditions.	
	Grudja Formation	Coniacian to Palaeocene	Shallow marine sediments with a dwarf fauna and deep water sediments deposited in oxygenated conditions.	

APPENDIX 4 (continued).

Position of Sediments.	Sedimentary Formation, System, etc.	Age	Nature of sediments	Palaeoclimate or environment which they indicate.
West Coast	Orange River basin	Albian to Maastrichtian (continues down into lower Cretaceous and up into Palaeocene and beyond.)	A large lense of sedi-deposited in marine conditions mainly by the Orange river.	High clay content, rapid rates of deposition and large sedimentary slumps indicate high sediment input by Orange river and therefore a well watered, warm catchment area. Diverse pollen content indicates well vegetated coastline.
	Wanderfeld 1V beds	Cenomanian	Shallow marine conditions.	
Continental Interior	Kagnas sediments	Upper Cretaceous	terrestrial, with dinosaur remains, silicified wood and lignite.	Silicified wood and lignite suggests well vegetated interior.
	Malvernia formation	Upper Cretaceous (Kent, 1980)	Continental alluvial fan and valley fill sediments.	Indicate existance of the limpopo river in the Cretaceous. (Partridge and Maud, 1987).
	Lowermost Kalahari System	Upper Cretaceous	Conglomerates, calcareous grits and sandstones, marls. Fluviatile origin? Du Toit (1954).	

APPENDIX 5. Summary of insect taxa found at Orapa and their use as environmental indicators.

Taxon	Biology
Zygoptera	A cosmopolitan group which occur in most environments. The nymphs are aquatic and, although they are generally found in fresh water, may be found in brack waters and ephemeral habitats such as rain pools (O'Farrell, 1970)
Blattodea	A large group with 4 000 species world-wide. Most are nocturnal and found near the ground, under rocks, bark or logs. They occur in a wide variety of environments, ranging from caves, and arid regions through to tropical forests (Mackerras, 1970; Marshall, 1985).
Dermaptera	Nearly 1 200 species are known. This is a cosmopolitan group. Adults are nocturnal, and spend their days under rocks, bark, logs, etc. They are omnivorous, feeding on a wide variety of plant and animal matter (Giles, 1970; Steinmann, 1985)
Orthoptera	A large cosmopolitan order with over 20000 described species. They are found in almost every conceivable environment, ranging from caves and forest, through to arid regions. They may be phytogphagous or omnivorous, although a few are carnivorous (Key, 1970; De Villiers, 1985).
Hemiptera	Over 60 000 species from a wide variety of environments, including aquatic ones, have been described. Many are phytophagous, and some are carnivorous (Jacobs, 1985).
Coleoptera:	
Coptoclavidae	Adults were aquatic predators living at the waters surface. Larvae were nectonic actively swimming forms. Known from the Jurassic and Cretaceous of Southern Europe, Asia and North Africa (Ponomarenko, 1977).

APPENDIX 5 (continued).

Taxon	Biology
Carabidae:	
Promecognathinae	Eight species distributed in the southern part of South Africa, and the west coast of north-west North America (Basilewsky, 1963). They are found in temperate and riverine forest, (Basilewsky, 1963; Kavanaugh, personal communication), and possibly in thick bush with abundant leaf litter. In southern Africa they occur in regions which receive rainfall ranging from less than 500mm to over 1000mm per year. The American species *P. laevissimus* has been observed eating millipedes and tipulid larvae (Macswain and Garner, 1956).
Scaritinae	A cosmopolitan group, with approximately 1 500 species, found in almost every conceivable environment (Erwin, 1979).
Siagoninae	With two genera; *Siagona* and *Luperca* (Erwin, 1985). *Siagona* is found on the ground in damp areas with decaying vegetation or under bark, while *Luperca* have been found associated with termitaria (Erwin, 1979).
Harpalinae	A cosmopolitan group, with approximately 2000 species (Kryzhanovskiy, 1976). They are found in most climates (Erwin, 1979). Many are phytophagous and, in particular, granivorous (Basilewsky, 1950; 1951).
Pterostichinae	A cosmopolitan group found in a wide variety of environments (Erwin, 1979).
Anchomeninae	A cosmopolitan group found in a wide variety of environments (Erwin, 1979).
Staphylinidae	A large family with 30 000 species and a cosmopolitan distribution. They occupy almost all terrestrial habitats and may be semi-aquatic. Most are predators and live in ground litter (Smetana, 1985).

APPENDIX 5 (continued).

Taxon	Biology
Scarabaeidae	A large family with a world wide distribution. Adults and larvae may be phytophagous, carrion feeders, or feed on dung (Scholtz and Holm, 1985).
Elateroidea	This superfamily has a world-wide distribution. Adults are found in foliage, on flowers or under bark. The adults and larvae may be phytophagous or carnivorous (Boomker, 1985).
Curculionoidea	A very large cosmopolitan superfamily. Most are phytophagous, though a few may be parasitic or predacious (Oberprieler and Louw, 1985).
Diptera:	
Tipulidae	The Tipulidae is a cosmopolitan group. Members may be found in a wide variety of environments, although most occur in moist temperate environments alongside streams or lakes. Some tipulid larvae are aquatic (Alexander and Byers, 1981; Barraclough and Londt, 1985; Rayner and Waters, 1989b).
Bibionidae	Little is known of the Afrotropical species. In other regions they are found in wooded or forested areas, and larvae may be phytophagous or scavengers (Hardy, 1981; Barraclough and Londt, 1981; Rayner, 1987).
Empididae	This family is cosmopolitan. Adults are usually found among undergowth in shady woods, bush, grassland and moist vegetation near water. Larvae live in soil, leaf-litter, rotting wood or dung, some are semi-aquatic and a few are aquatic. They are rare in dry open regions. Empids are predators (Smith, 1969; Waters, 1989a)).
Hybotidae	Adults and larvae are in found in similar situations to the Empididae (Waters, 1989b).

APPENDIX 5 (continued).

Taxon	Biology
Hymenoptera:	
Ichneumonidae	A diverse family which is found in environments of relatively high humidity (Riek, 1970). They are parasitic, and their hosts include Lepidoptera, Coleoptera, Hymenoptera and Neuroptera (Prinsloo, 1985).
Braconidae	Parasitic wasps whose hosts include, Lepidoptera, Hemiptera, Coleoptera, Diptera and Aphids (Prinsloo, 1985).
Proctotrupoidea	Wasps which parasitise the immature stages of insects, and in a few cases, spiders (Prinsloo, 1985).

CRETACEOUS CARABIDAE (COLEOPTERA) FROM ORAPA, BOTSWANA

VOLUME TWO- FIGURES

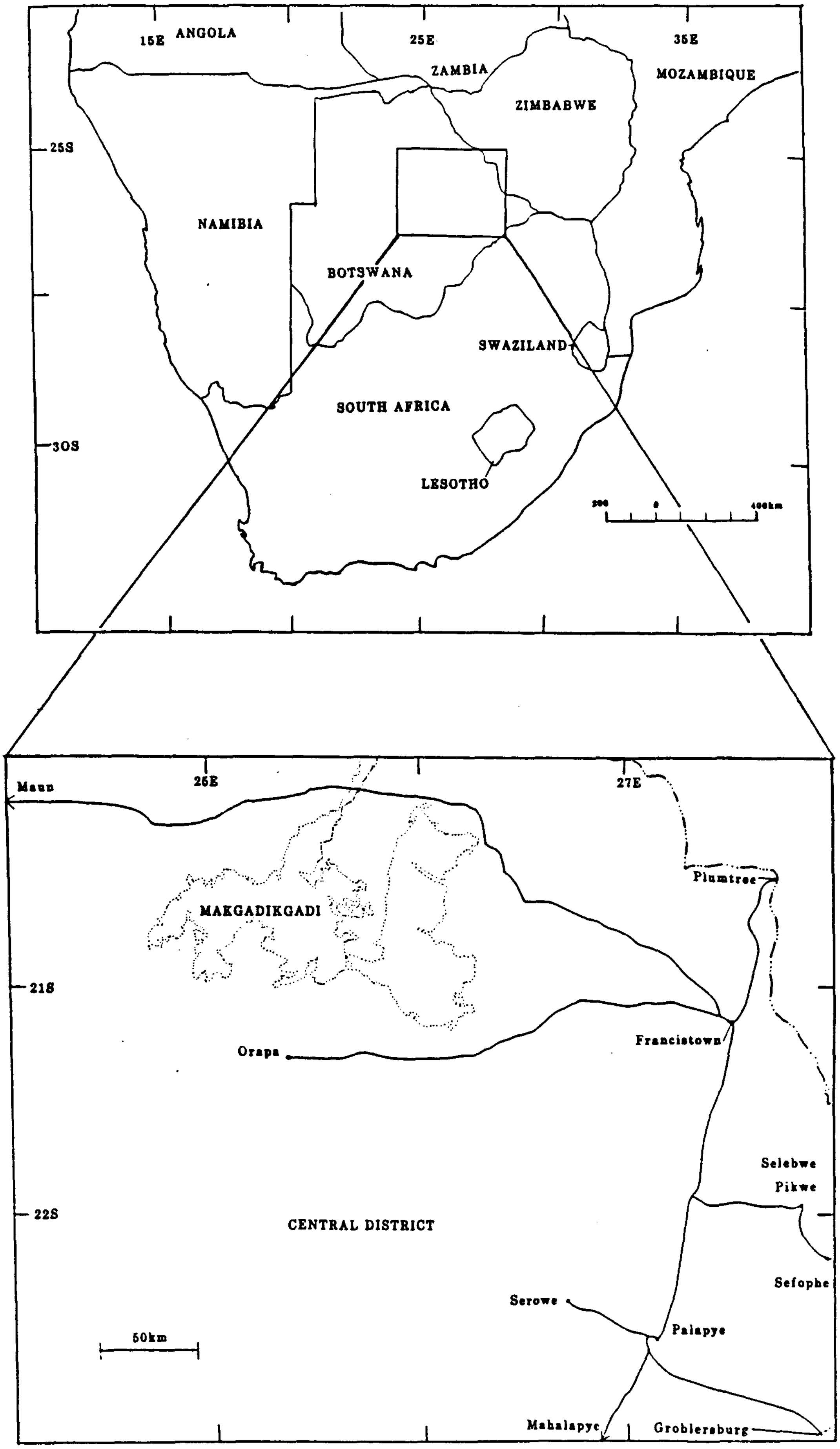
(Volume one- text)

Ian James McKay

Thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, for the degree of Doctor of Philosophy.

Johannesburg, January 1990.

Fig. 1. Locality map of Orapa.



15E
ANGOLA
25E
35E
ZAMBIA
MOZAMBIQUE
ZIMBABWE
25S
NAMIBIA
BOTSWANA
SWAZILAND
SOUTH AFRICA
30S
LESOTHO
200
0
400km
Maun
26E
27E
Plumtree
MAKGADIKGADI
21S
Francistown
Orapa
Selebwe
Pikwe
22S
CENTRAL DISTRICT
Sefophe
Serowe
Palapye
50km
Mahalapye
Groblersburg

Fig. 2. Generalised model of a kimberlite pipe showing the relation of the kimberlite to the overlying sediments, and surrounding strata (after, Hawthorne 1975)

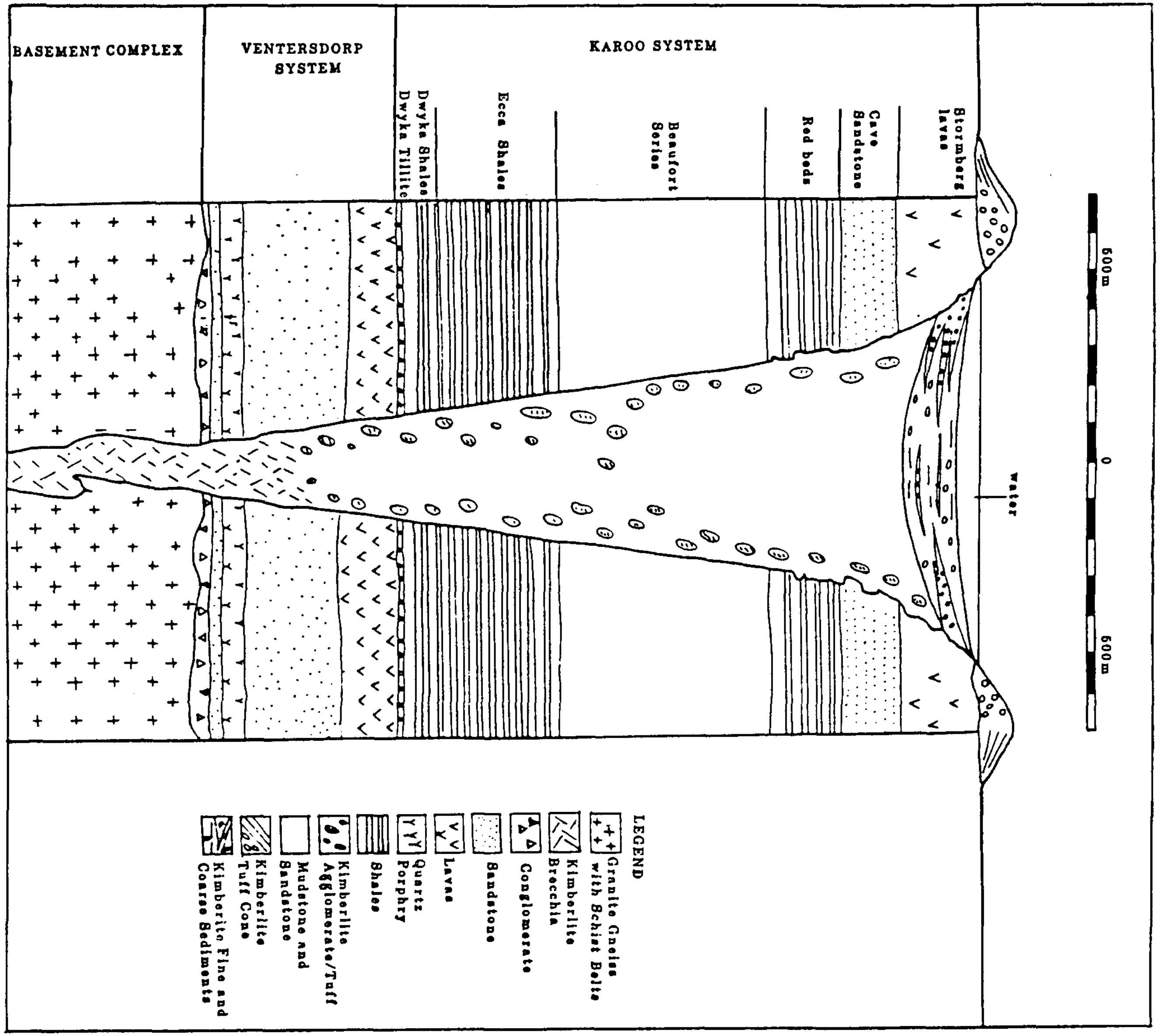

BASEMENT COMPLEX
VENTERSDORP SYSTEM
KAROO SYSTEM
Dwyka Tillite
Dwyka Shales
Ecca Shales
Beaufort Series
Red beds
Cave Sandstone
Stormberg lavas
water
600m
0
600m
LEGEND
Granite Gneiss with Schist Belts
Kimberlite Breccia
Conglomerate
Sandstone
Lavas
Quartz Porphry
Shales
Kimberlite Agglomerate/Tuff
Mudstone and Sandstone
Kimberlite Tuff Cone
Kimberlite Fine and Coarse Sediments

Fig. 3. View of the Orapa mine from the east.

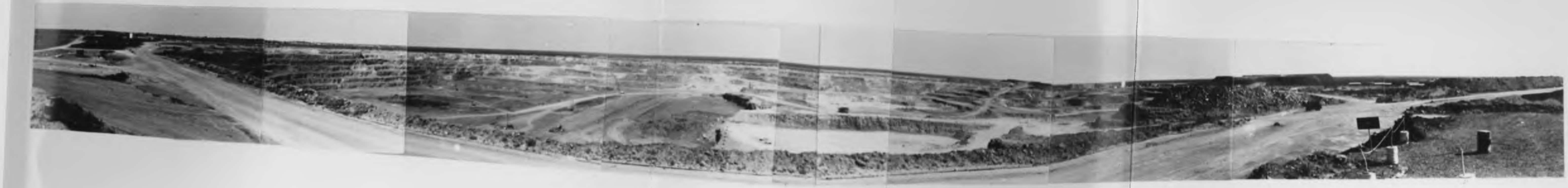
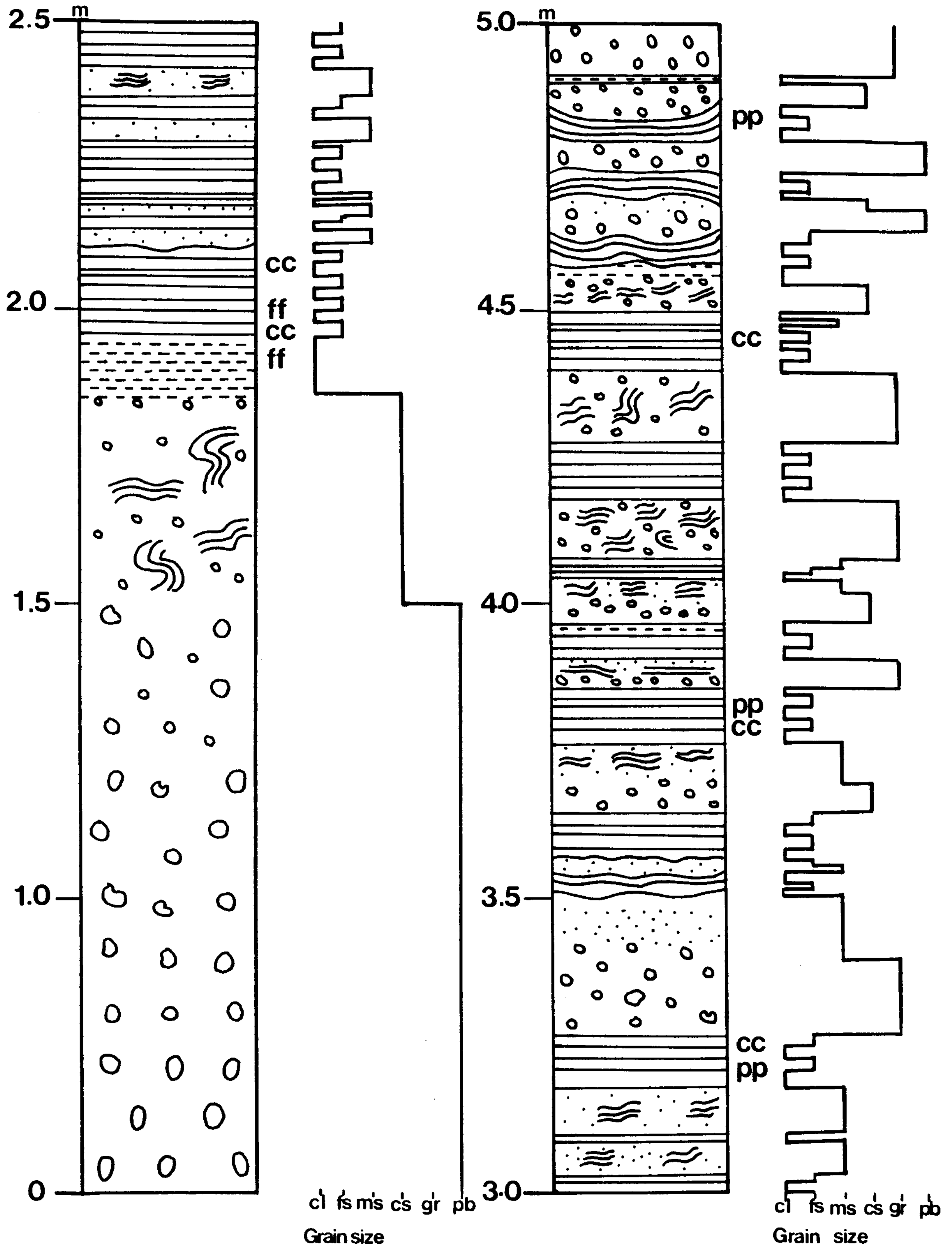


Fig. 4 Section through the fossiliferous, lacustrine sediments at locality 11.

Fig. 4 Section through the fossiliferous, lacustrine sediments at locality 11.



▨ Conglomerate with shale clasts, Facies 3

▨ Poorly sorted sandstone, Facies 3

☰ Interbedded thin layers of very fine sandstone, mudstone, and organic rich layers, Facies 3&4

▨ Non laminated mudstone, Facies 3.

PP= Plant material
CC= Calcite layers

Cl= Clay
FS= Fine Sandstone
MS= Medium Sandstone
CS= Coarse Sandstone
GR= Granules
PB= Pebbles

Fig. 5. Interbedded fine and coarse sediments at locality 11.

Fig. 6. Close up view of interbedded granular mass flows and fine grained sediments

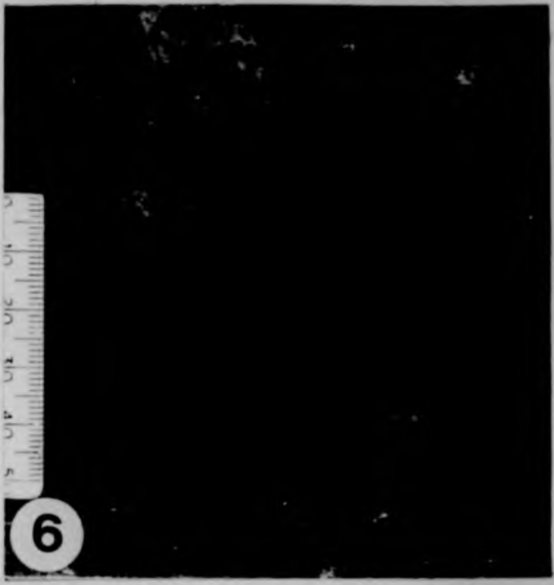
Fig. 7. Laminated fine grained sediments.

Fig. 8. Section showing apparent varved nature of some of the mudstones.

Fig. 9. Raindrop impressions?

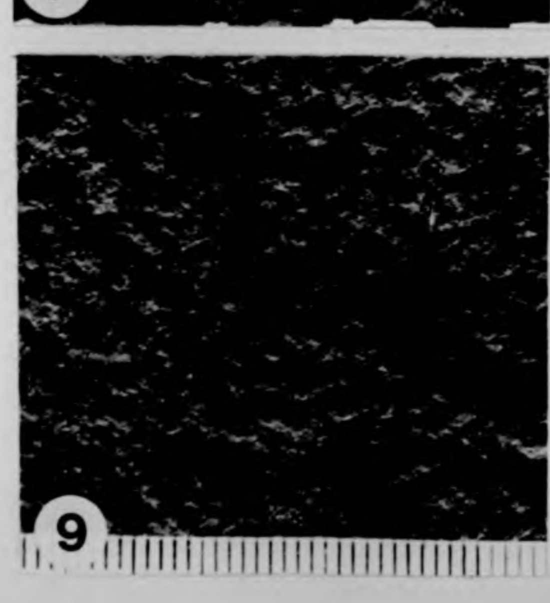
Fig. 10. Assemblage of almost complete plants together with numerous beetles.


5


6


7


8


9

10

Fig. 11. BP/2/27534. Coptoclavidae? Polarised light.

Fig. 12. BP/2/27534. Coptoclavidae? Non-polarised light.

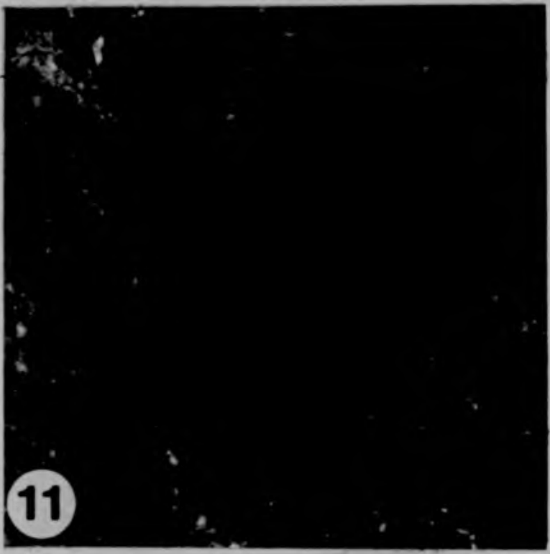
Fig. 13. BP/2/27593a. Zygoptera. Polarised light.

Fig. 14. BP/2/27593a. Unidentified insect, form 1, polarised light.

Fig. 15. BP/2/22153a. Unidentified insect, form 2, polarised light.

Fig. 16. BP/2/27302. Unidentified insect, form 3, polarised light.

Captions for figs 11-16: a= antenna, c= cerci, e= eye, el= elytron, l= leg, 0= ovipositor.



11

12

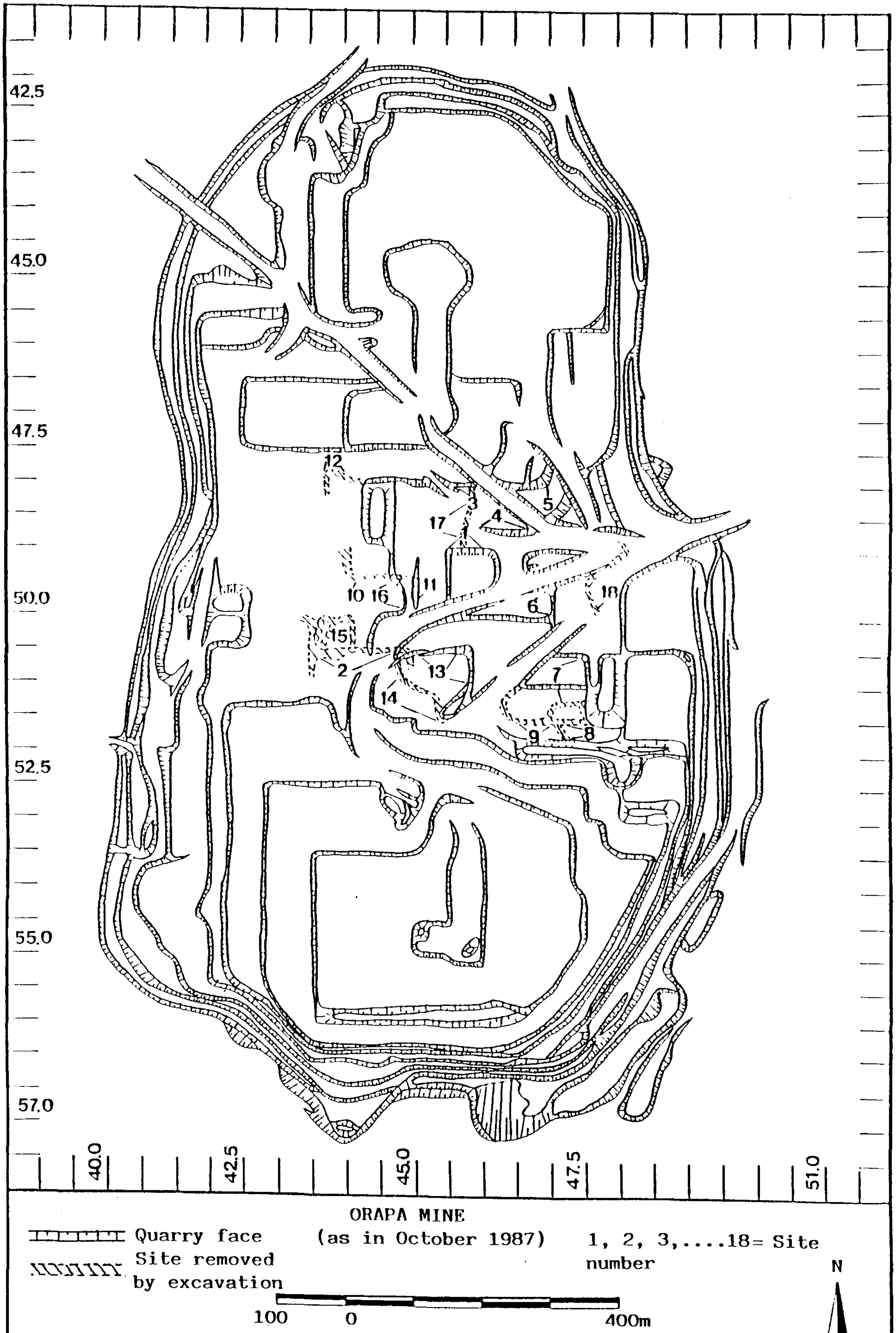
13

14

15

16

Fig. 17. Position of fossil sites in the Orapa mine.



ORAPA MINE
(as in October 1987)

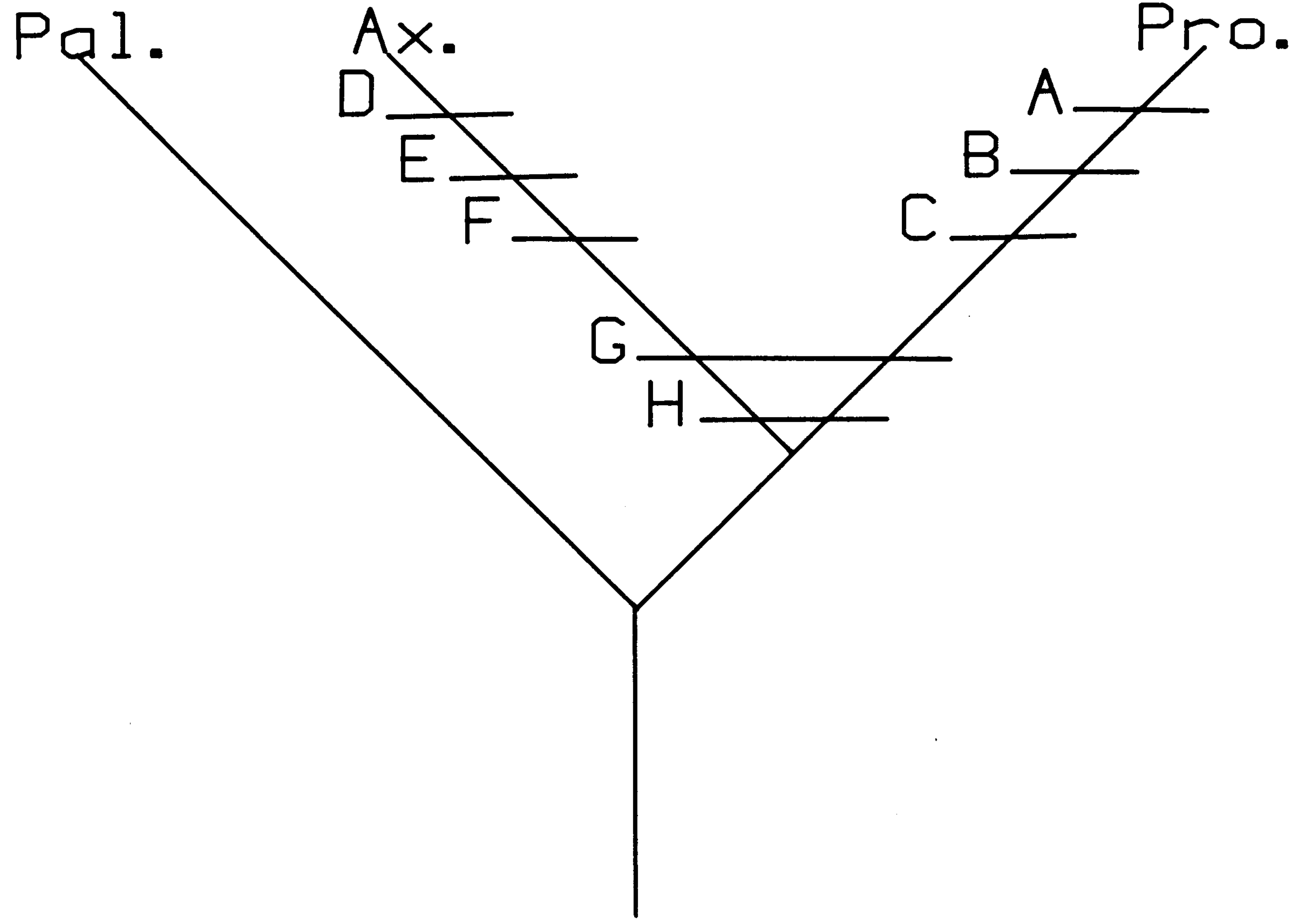
Figs 18-20. *Palaeoaxinidium orapensis* gen. nov. sp. nov. holotype, BP/2/18302: 18, polarised light; 19, line diagram; 20, non-polarised light.

18

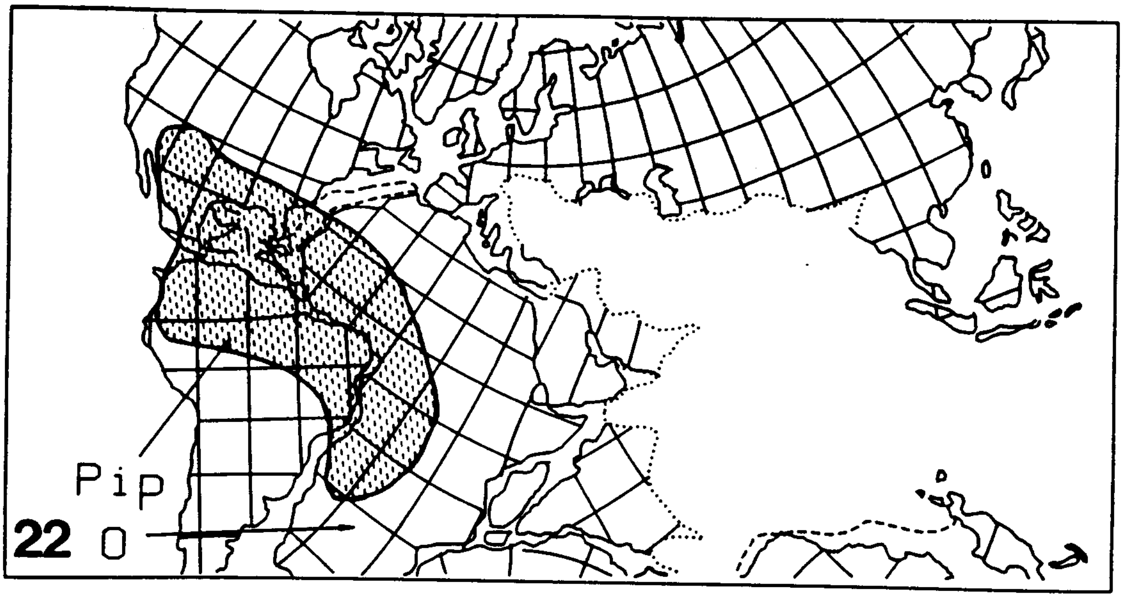
19

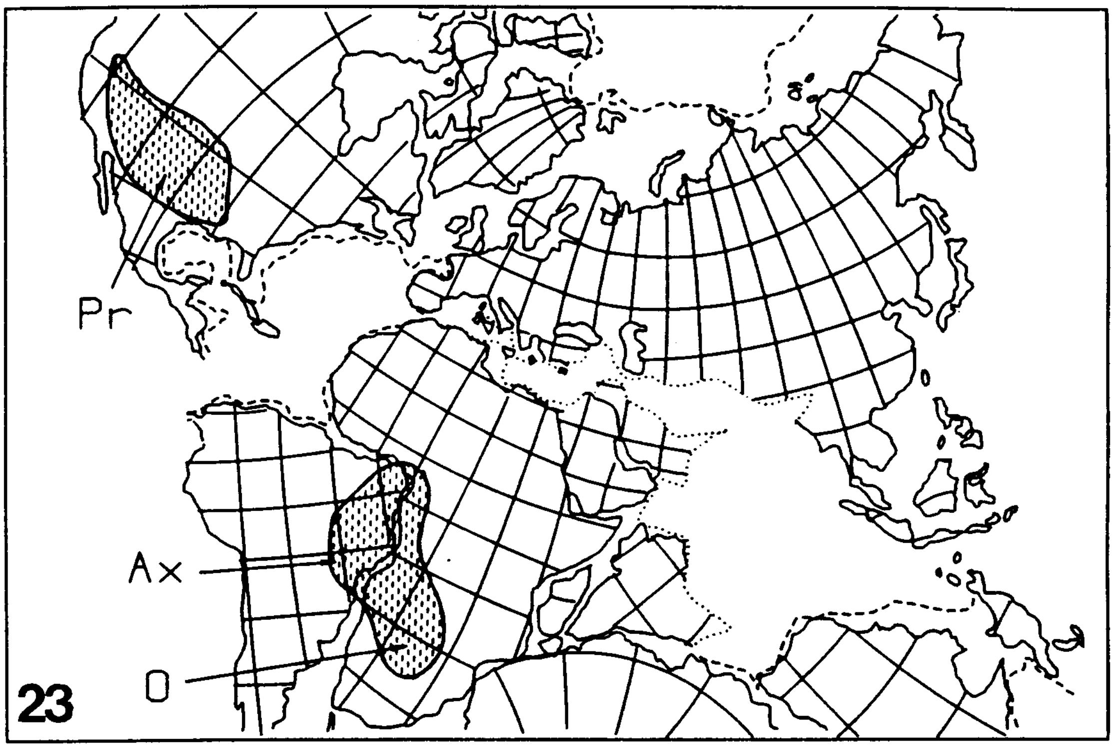
20

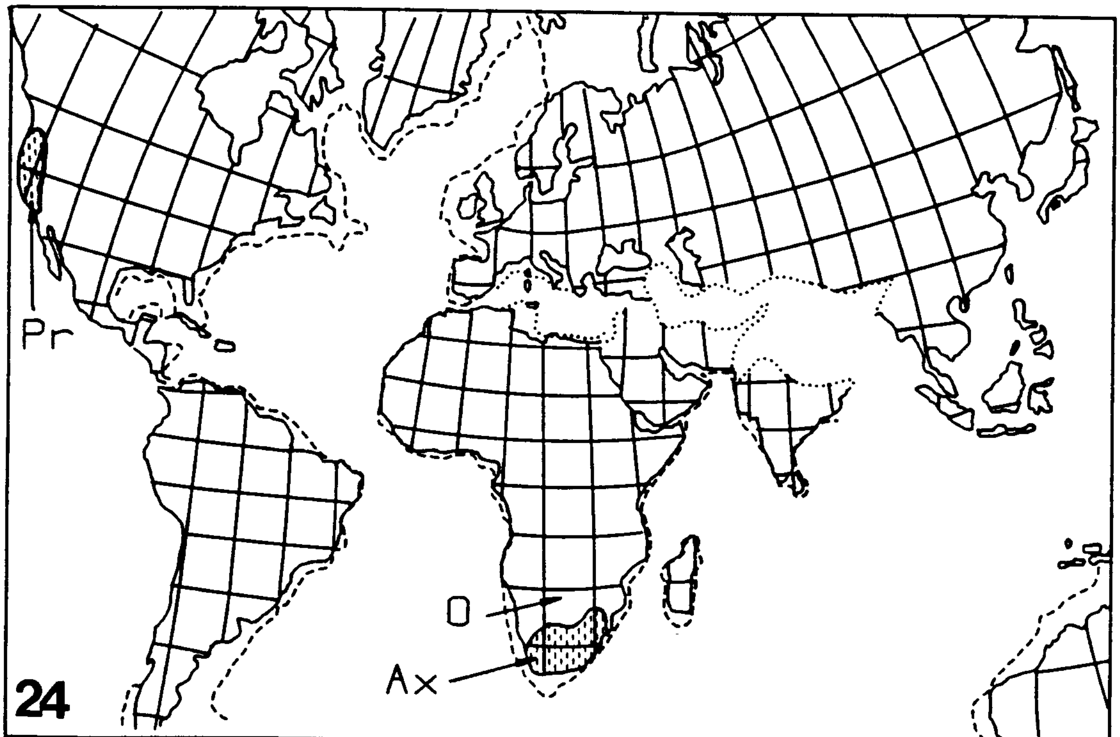
Fig. 21. Cladogram showing the relationships between extant and fossil promecognathines. Ax.=Axinidiini, Pal=*Palaxinidium*, Pro.=Promecognathini.


Pal.
Ax.
Pro.
D
E
F
G
H
A
B
C

Figs 22-24. Maps illustrating Erwin's (1979, 1981) hypothesis for the changing distribution of the Promecognathinae through time: 22, Distribution of the initial promecognathine stock during the Jurassic (about 170mya); 23, Vicariance of Jurassic range and movement into temperate climates during the Cretaceous (about 100mya); 24, Distribution in the Eocene (about 50mya) after extinction in the tropics.


22


23


24

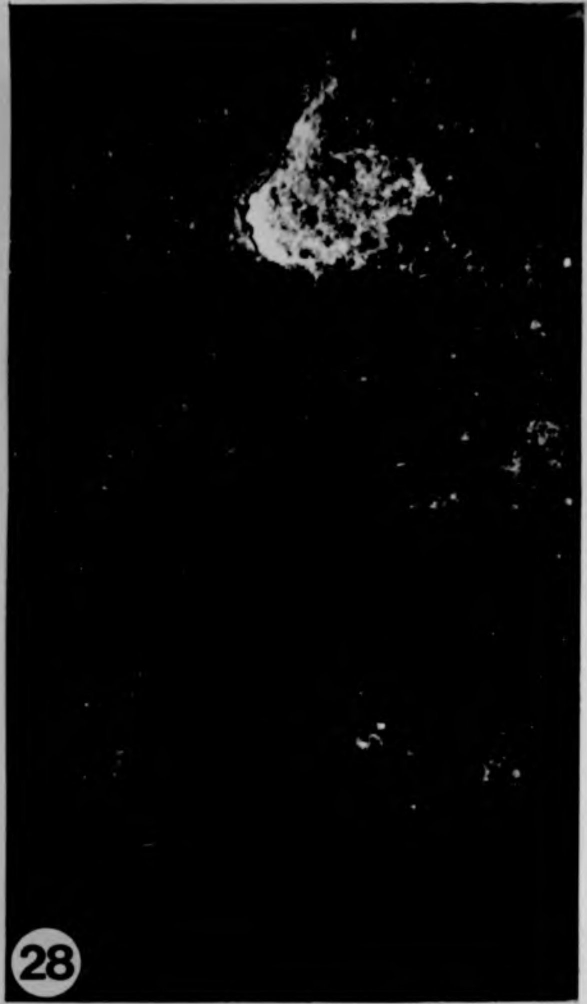
Figs 25-27. Scaritinae, part, BP/2/26253a: 25, polarised light; 26, line diagram; 27, non-polarised light.

25

26

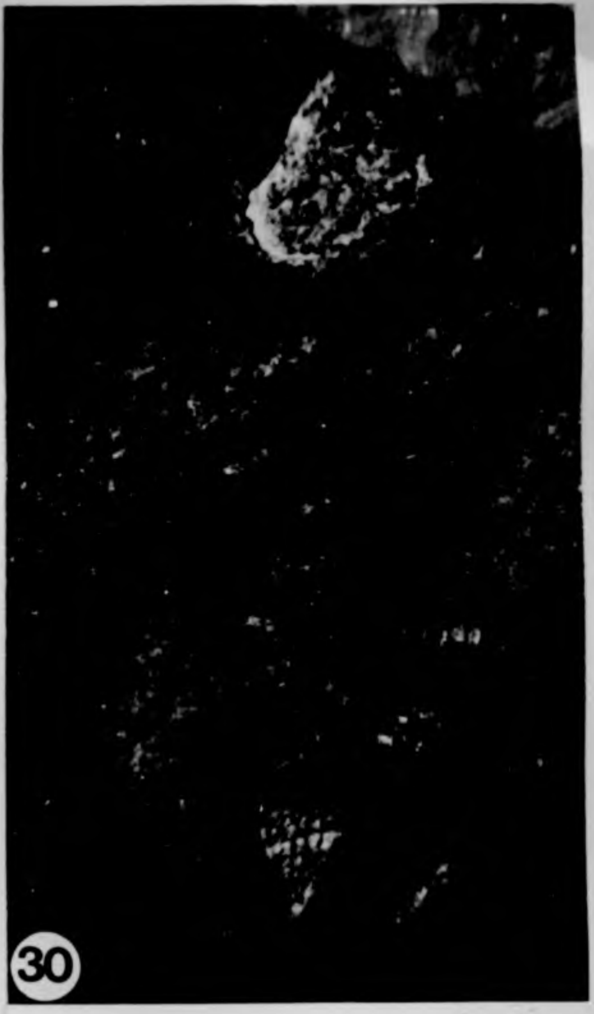
27

Figs 28-30. Scaritinae, counterpart, BP/2/26253b: 28, polarised light; 29, line diagram; 30, non-polarised light.



28

29

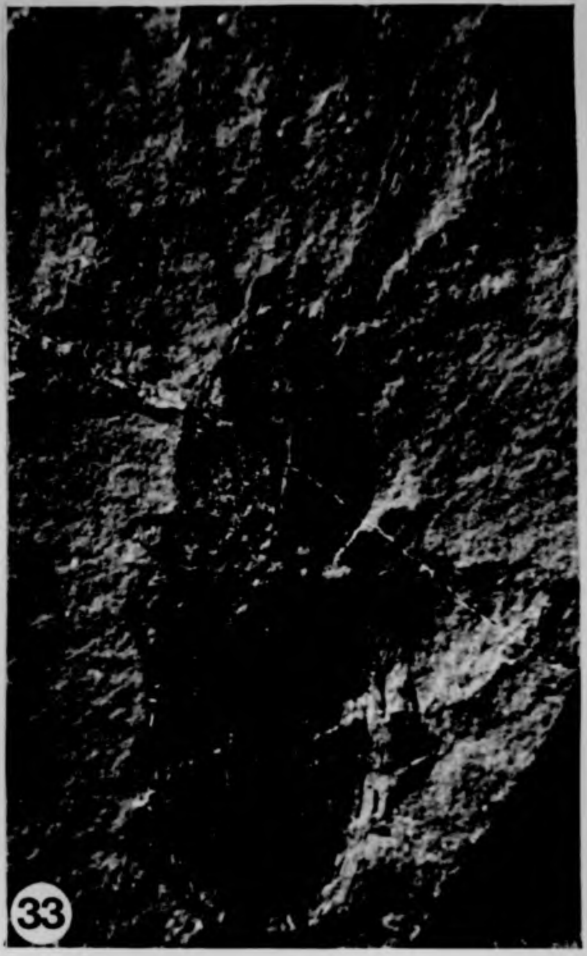


30

Figs 31-33. Siagoninae? BP/2/27536: 31, polarised light; 32, line diagram; 33, non-polarised light.


31

32


33

Figs 34-36. Siagoninae? Part, BP/2/24004a: 34, polarised light; 35, line diagram; 36, non-polarised light.


34

35


36

Figs 37-39. Siagoninae? Counterpart, BP/2/24004b: 37, polarised light; 38, line diagram; 39, non-polarised light.

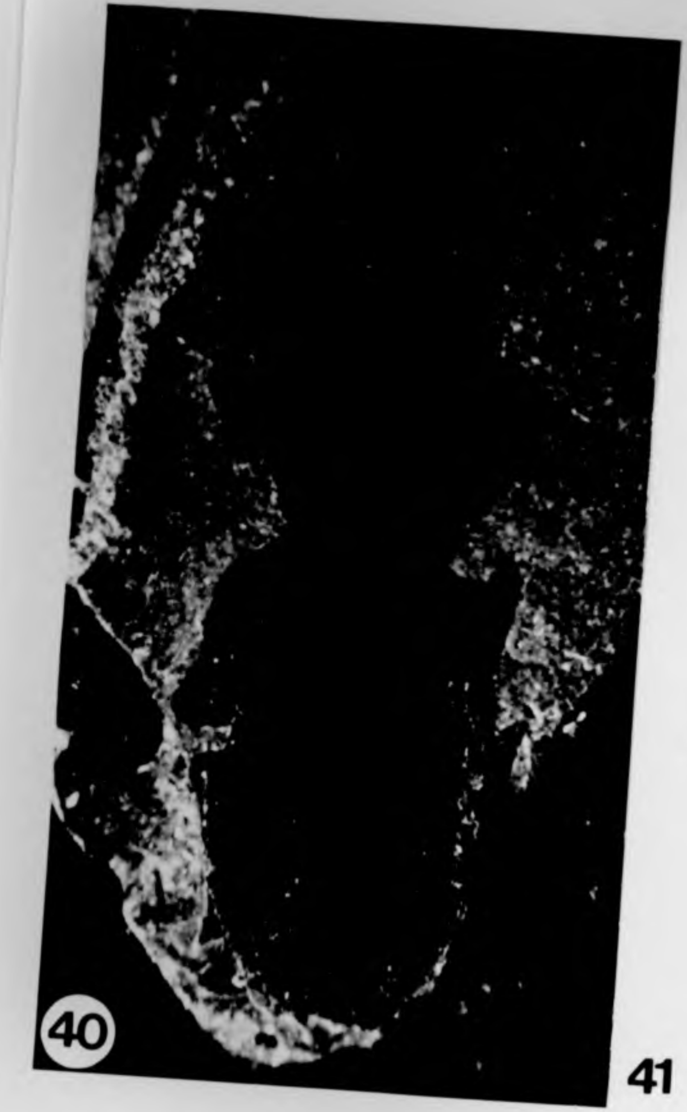

37


38


39

Figs 40-42. Pterostichinae? Part, BP/2/27583a: 40, polarised light; 41, line diagram; 42, non-polarised light.

40



41

42

Figs 43-45. Pterostichinae? Counterpart, BP/2/27583b: 43, polarised light; 44, line diagram; 45, non-polarised light.

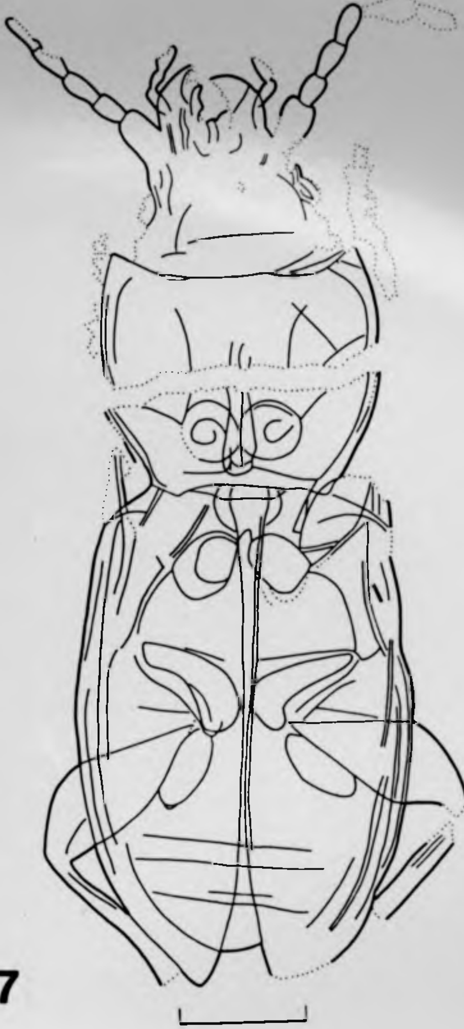
43

44

45

Figs 46-48. Pterostichinae? BP/2/27584: 46, polarised light; 47, line diagram; 48, non-polarised light.


46


47


48

Figs 49-51. Pterostichinae? Part, BP/2/27586a; 49, polarised light; 50, line diagram; 51, non-polarised light.

49

50

51

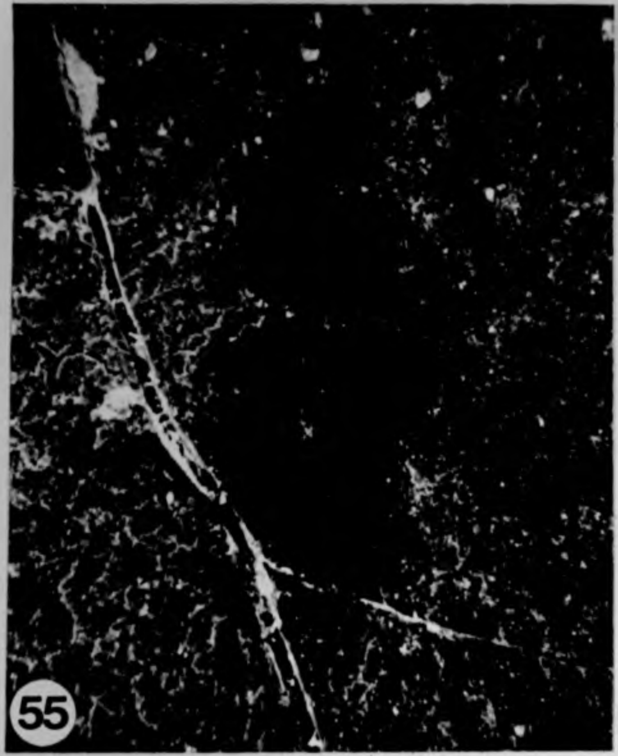
Figs 52-54. Pterostichinae? Counterpart, BP/2/27586b: 52, polarised light; 53, line diagram; 54, non-polarised light.

52

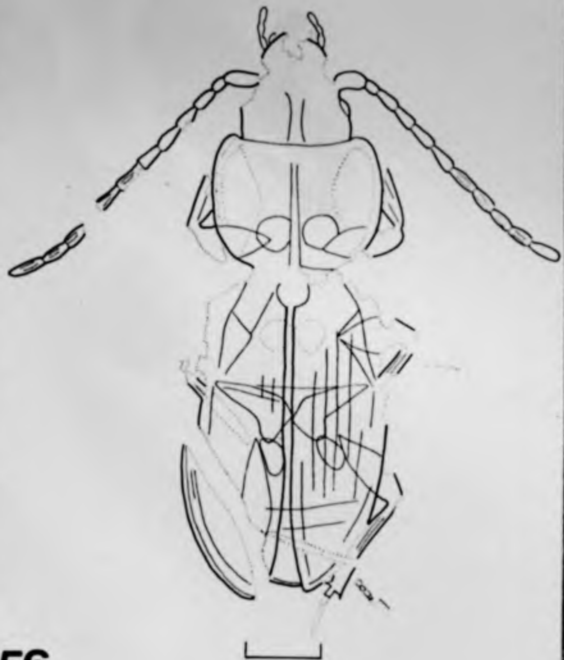
53

54

Figs 55-57. Anchomeninae? Part, BP/2/27256a: 55, polarised light; 56, line diagram; 57, non-polarised light.



55

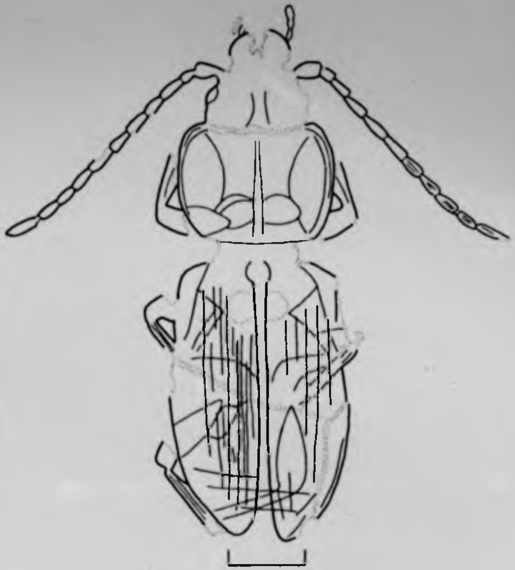


56

57

Figs 58-60. Anchomeninae? Counterpart, BP/2/27256b: 58, polarised light; 59, line diagram; 60, non-polarised light.

58



59

60

Figs 61-63. Harpalinae? Part, BP/2/18669a: 61, polarised light; 62, line diagram; 63, non-polarised light.

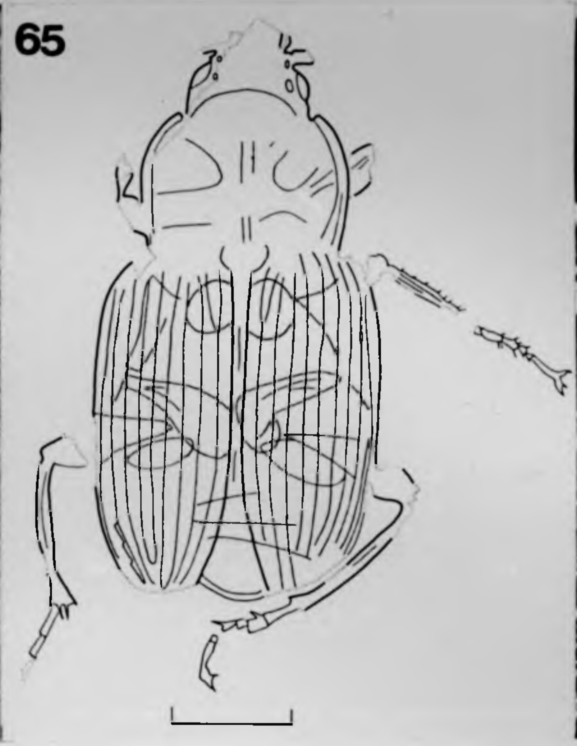

61


62


63

Figs 64-66. Harpalinae? Counterpart, BP/2/18669b: 64, polarised light; 65, line diagram; 66, non-polarised light.

64



65

66

Figs 67-69. Harpalinae? BP/2/26255: 67, polarised light; 68, line diagram; 69, non-polarised light.

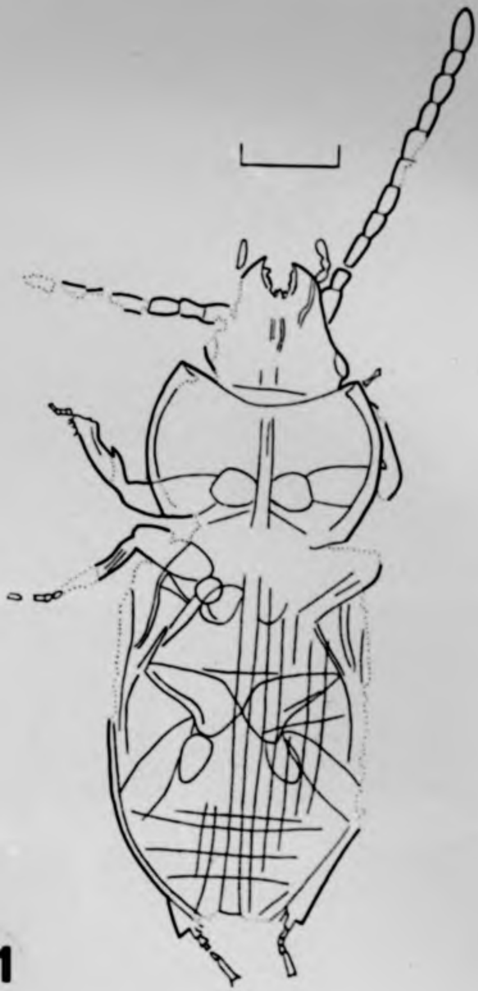

67


68


69

Figs 70-72. Harpalinae? BP/2/26260: 70, polarised light; 71, line diagram; 72, non-polarised light.

70



71

72

Figs 73-75. Harpalinae? BP/2/24006: 73, polarised light; 74, line diagram; 75, non-polarised light.

73

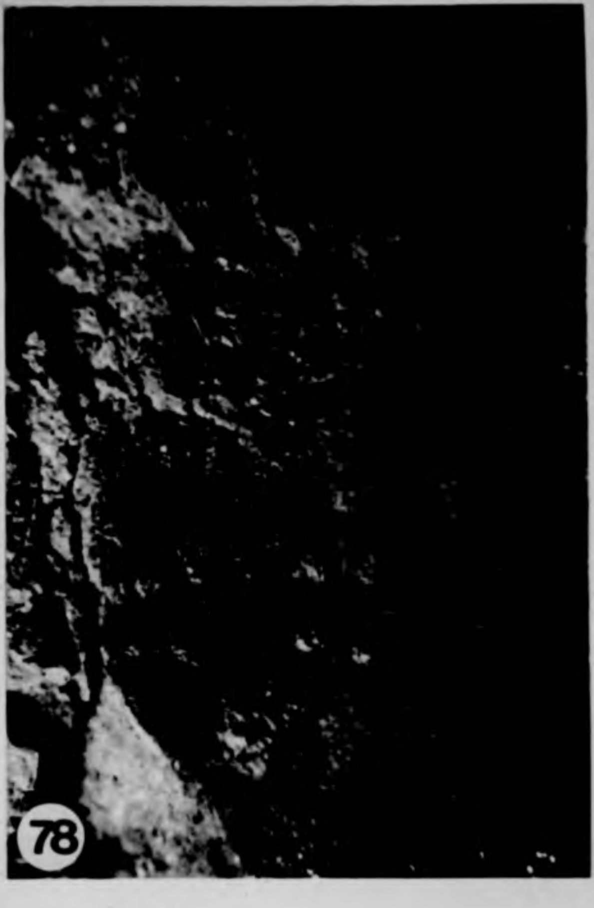
74

75

Figs 76-78. Carabidae, *incertae sedis*, part, BP/2/27585a: 76, polarised light; 77, line diagram; 78, non-polarised light.

76

77

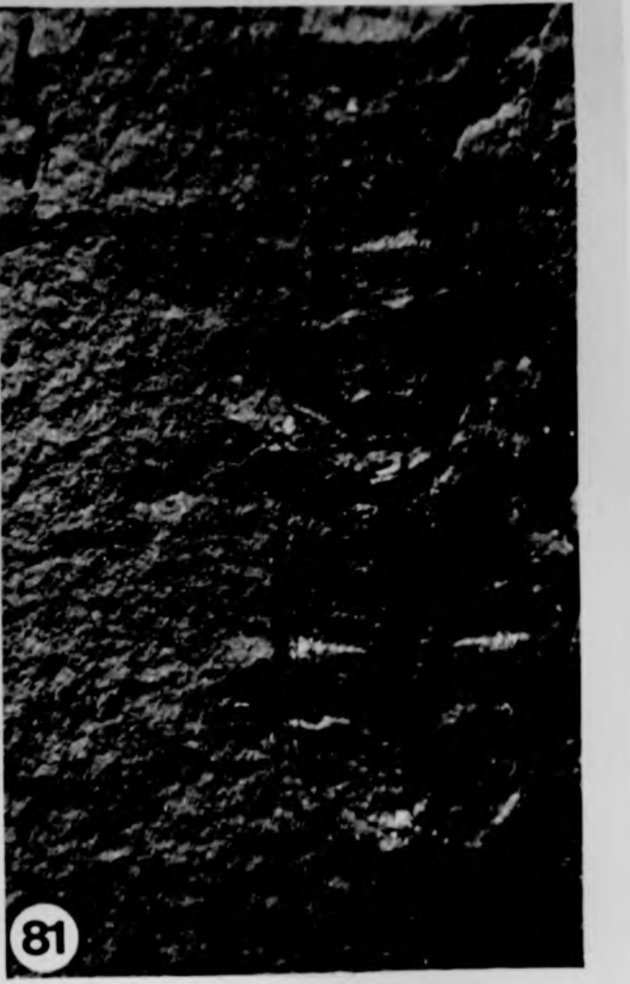


78

Figs 79-81. Carabidae, *incertae sedis*, counterpart, BP/2/27585b: 79, polarised light; 80, line diagram; 81, non-polarised light.

79

80



81

Figs 82-84. Carabidae, *incertae sedis*, BP/2/27587: 82, polarised light; 83, line diagram; 84, non-polarised light.


82

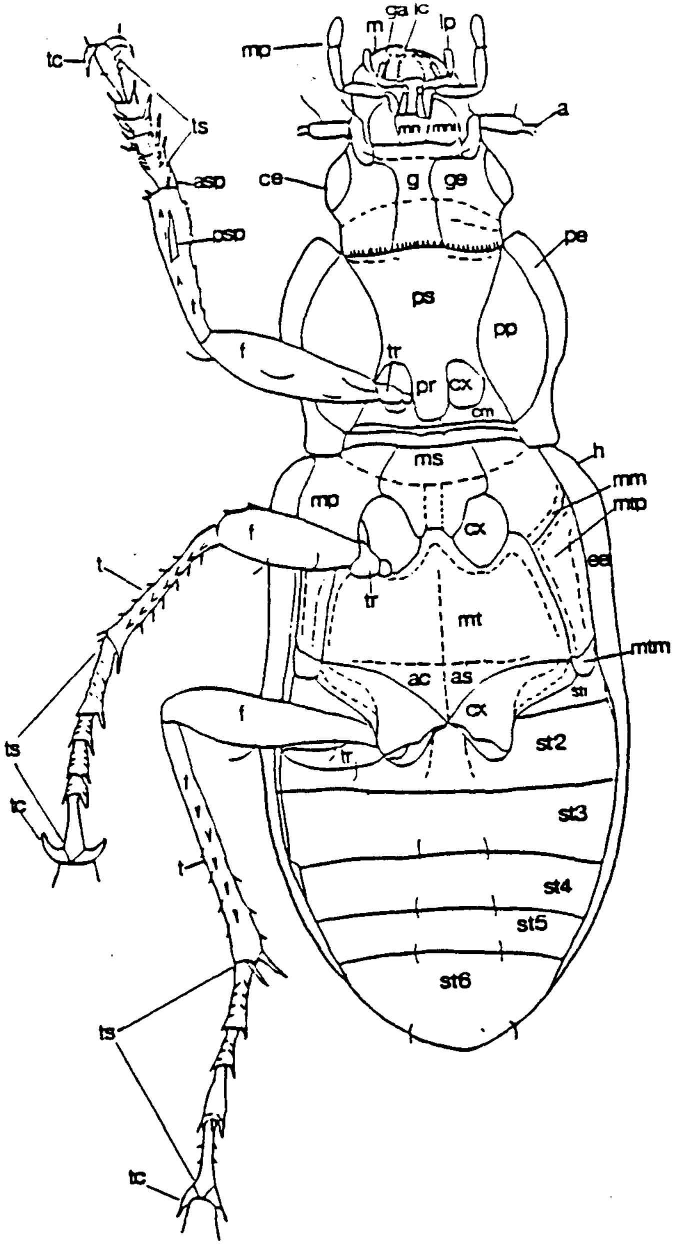
83


84

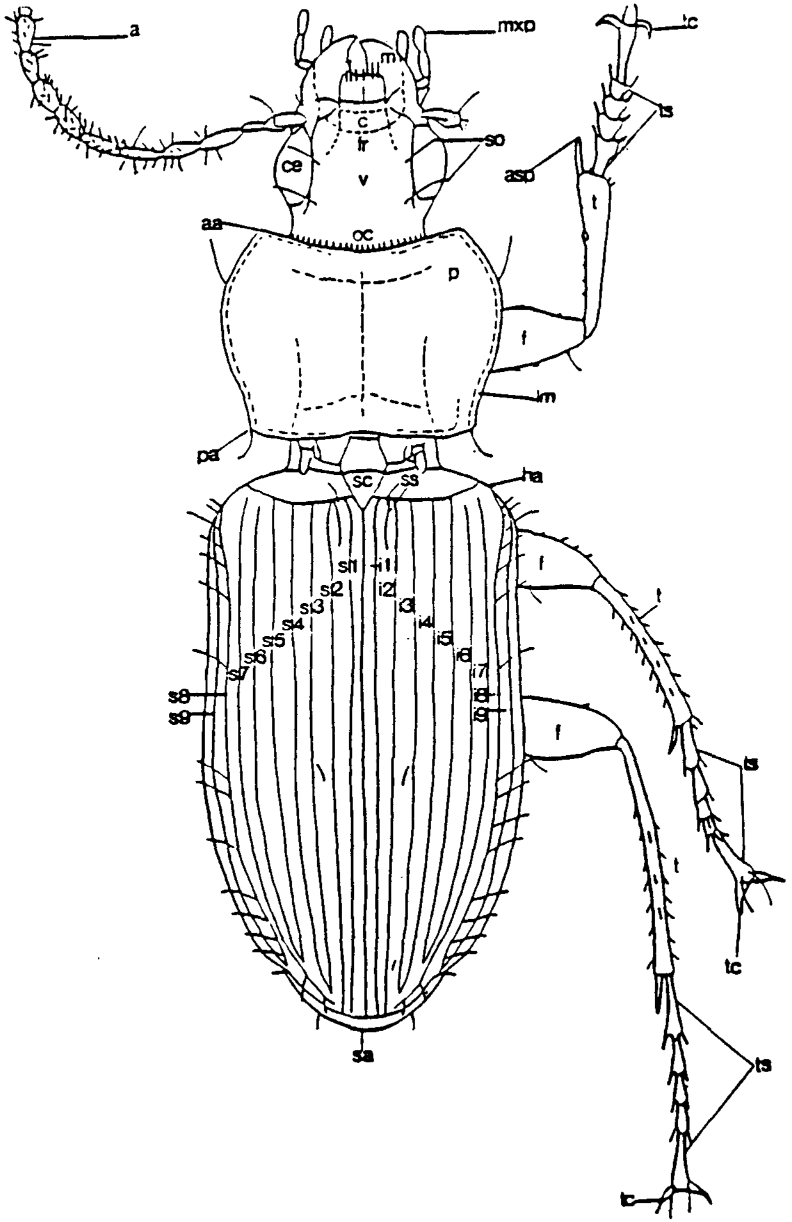
1. Ventral view. 2. Dorsal view.

List of Abbreviations

a, antenna
aa, anterior angle
ac, antecoxal piece
asp, anterior tibial spur
as, antecoxal suture
c, clypeus
ce, compound eye
cs, clypeal suture
cx, coxa
d, disc
ee, elytra epipleura
f, femur
fr, frons
fs, frontal suture
g, gula
ga, galea
g, gena
gs, gula suture
h, humeral angle
i1, first or sutural interval
i2-i8, second to eighth sutural interval
i9, ninth or marginal interval
l, labium
lc, lacinia
lp, labial palp
m, mandible
mm, mesepimeron
mn, mentum
mnl, lobe of mentum
mp, mesepisternum
ms, mesosternum
mt, metasternum
mtm, metepimeron
mtp, metepisternum
mxp, maxillary palp
oc, occiput
p, pronotum
pa, posterior angle
pe, epipleura of pronotum
pl, prosternal lobe
pm, proepimeron
pp, proepisternum
pr, prosternal process
ps, prosternum
s, scape
s1, first or sutural stria
s2-s7. second to seventh stria
s8, eighth or marginal stria
sa, sutural angle
sc, scutellum
so, supraorbital setae
ss, scutellar stria
st1-st6, sternites
su, sutural margin
t, tibia
tc, tarsal claws
tr, trochanters
ts, tarsal segments 1-5
v, vertex



tc
mp
m
ga
lc
lp
ts
a
asp
ce
g
ge
psp
pe
ps
pp
f
tr
pr
cx
cm
h
ms
mp
mm
mtp
f
cx
t
ee
tr
mt
mtm
ac
as
sn
f
cx
st2
ts
tr
tc
st3
t
st4
st5
st6
ts
tc

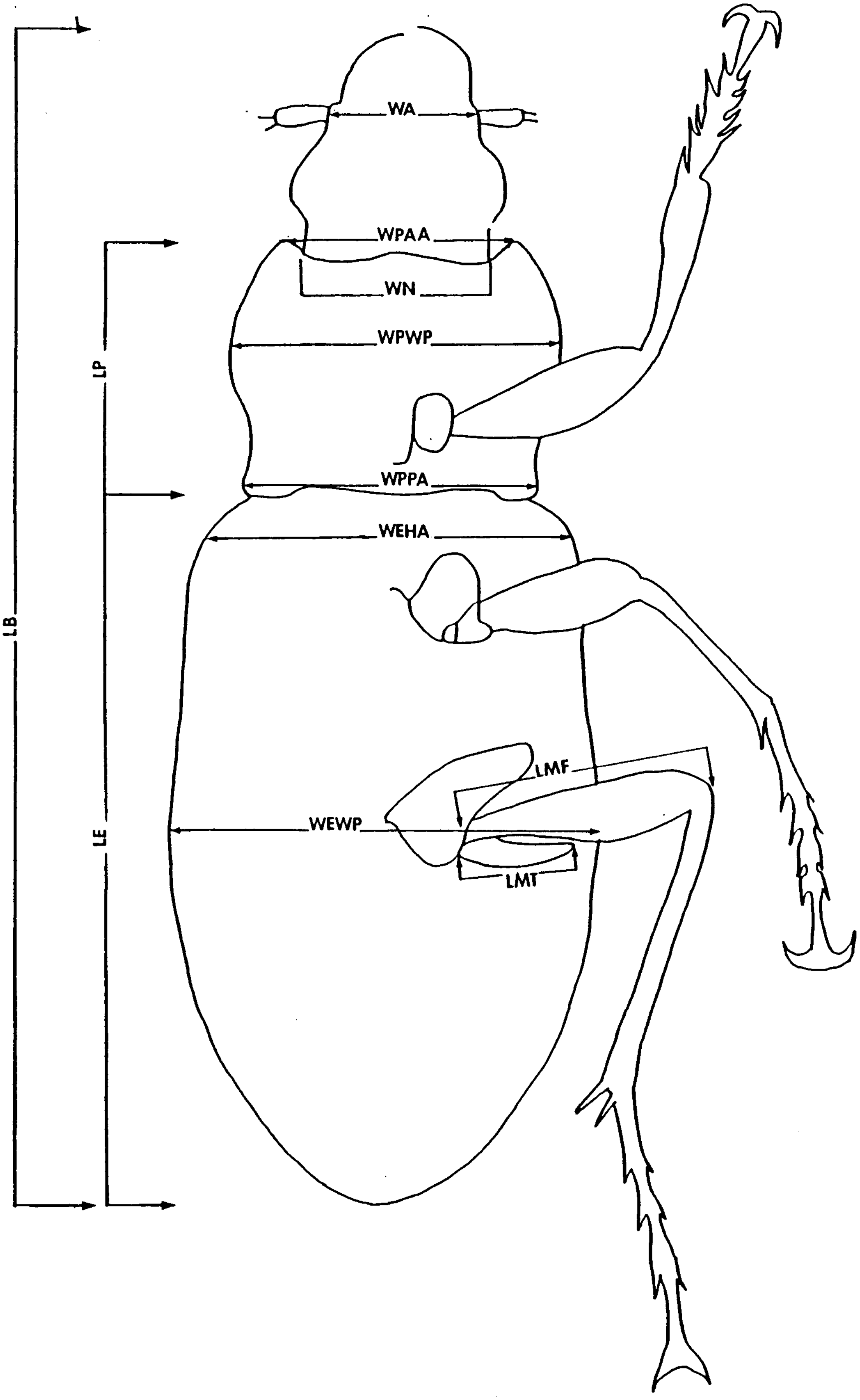


a
mxp
tc
m
c
ts
fr
so
ce
v
asp
t
aa
oc
p
f
lm
pa
sc
ss
ha
st1
i1
f
s2
i2
s3
i3
t
s4
i4
s5
i5
s6
i6
s7
i7
s8
i8
s9
i9
f
ts
t
tc
ts
sa
tc

Fig. 86. Parameters measured on the specimens.

Abbreviations

LB, length of body, from the anterior of the mandibles to the posterior of the elytra or abdomen (whichever is the longest.
LE, length of the elytra, from the attachment of the elytra to the prothorax to the tip of the elytra or abdomen (which ever is the longer).
LMF, length of the metathoracic femora.
LMT, length of the metathoracic trochanters.
LP, length of the prothorax.
WA, width of the head between the antennae.
WEHA, width of the elytra between between the humeral angles.
WEWP, maximum width of the elytra.
WN, width of the head at the occipital region.
WPAA, width of the prothorax at the anterior angles.
WPPA, width of the prothorax at the posterior angles.
WPWP, maximum width of the prothorax.


LB
WA
WPAA
WN
LP
WPWP
WPPA
WEHA
LMF
WEWP
LE
LMT