The geological history and development of the terrain at the Riversleigh World Heritage Area during the middle tertiary

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The geological history and development

of the terrain at

the Riversleigh World Heritage Area

during the middle Tertiary

Derrick A. Arena

CERTIFICATE OF ORIGINALITY

I hereby declare that this submission is my own work and to the best of my knowledge it contains no materials previously published or written by another person, nor material which to a substantial extent has been accepted for the award of any other degree or diploma at UNSW or any other educational institution, except where due acknowledgement is made in the thesis. Any contribution made to the research by others, with whom I have worked at UNSW or elsewhere, is explicitly acknowledged in the thesis.

I also declare that the intellectual content of this thesis is the product of my own work, except to the extent that assistance from others in the project's design and conception or in style, presentation and linguistic expression is acknowledged.

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Chapter 1

Introduction

More than 200 deposits containing Cainozoic fossil vertebrate faunas have been recognised at Riversleigh during the last 30 years. Prior knowledge of the Australian Tertiary vertebrate fossil record was based primarily on a limited number of faunas collected mainly from remote central Australian localities (Stirton *et al.* 1968, Archer *et al.* 1994).

Fossil vertebrate faunas from Riversleigh have played a significant role in developing an understanding of the evolutionary history of the Australian terrestrial vertebrate fauna during the middle Tertiary (Archer *et al.* 1999, see Appendix F). Because Riversleigh deposits are rich in well-preserved fossil material that spans the period from the Oligocene to the Pleistocene, Riversleigh faunas provide unique opportunities to understand individual taxa and groups in greater detail; study the evolutionary changes in taxa over time; study the palaeoecological implications of contemporaneous taxa and faunas and changes in these faunas over time; more clearly resolve temporal and taxonomic relationships of taxa that have biocorrelative significance; and consider the role of environmental change in the evolution and development of the Australian fauna during the last 25-30 Ma.

However, while the faunas from the Oligo-Miocene are so well known, interpretations of palaeoenvironmental conditions at Riversleigh during that period have been the subject of controversy because of the poor palaeobotanical record there, and because many aspects of the middle Tertiary geological history of Riversleigh have not been well understood. Interpretations of palaeoenvironmental conditions have been challenged by the lack of an adequately resolved depositional framework for the deposits containing fossil faunas.

During the last four decades, various authors have described and interpreted aspects of the middle Tertiary geology at Riversleigh (Tedford 1967, Williams 1978, Day *et al.* 1983, Megirian 1992, Archer *et al.* 1989, 1994, 1997, Creaser 1997, Arena 1995, 1997,

Arena and Black 1997, Price 2002, Morrell 2002). The cumulative result is a variety of interpretations and depositional models at the local and regional scale. However, the majority of these were based on limited geological data and/or lacked application of key concepts and processes occurring in karst systems, which are essential for the exploration of viable interpretations and models of events at Riversleigh during the middle Tertiary.

This is due in part to the combination of complex geology and the remoteness and inaccessibility of the terrain at Riversleigh that hinders collection, observation and assessment in the field. Significantly, until recently there has been a lack of information in the geological literature regarding karst processes. Without proper acknowledgement or application of these concepts, certain aspects of the geological history of Riversleigh cannot be properly addressed, restricting the applicability and parsimony of resulting depositional models.

This work explores new approaches to the interpretation of geology, palaeontology and modelling of depositional environments at Riversleigh during the middle Tertiary. New data and recent advances in the understanding of terrestrial carbonate systems allow the consideration of viable alternatives to some of the outcomes of previous work. The primary objective is to provide a well-founded and testable framework for the interpretation of faunas, palaeoenvironments and the study of individual fossil deposits at Riversleigh.

1.1 Aims and structure of this work

The middle Tertiary carbonate deposits at Riversleigh are here recognised as constituting a karst system. This work addresses and applies relevant karst concepts, proposes a scheme of standardised terminology, and offers interpretation of the geology based on recent advances in the understanding of depositional processes in karst. These outcomes are reconciled with the 'Systems' biocorrelative concept of Archer *et al.* 1989, 1994, 1997). Key aspects of karst systems including speleogenesis, hydrogeology and landform development are applied to depositional models and thus used to resolve a sequential pattern of geological development of the terrain at Riversleigh during the middle Tertiary.

The regional and geological context of Riversleigh is outlined in Chapter 2. A review of literature describes previous study of the geology of Riversleigh, provides estimated palaeolatitudes for Riversleigh during the middle Tertiary, and a new synthesis of Oligo-Miocene palaeoclimatic data.

Chapter 3 provides a review of concepts and processes occurring in karst. A scheme of standardised terminology, including new geological terms, is defined and proposed. Terrestrial carbonates and the key aspects of processes occurring in karst are discussed. These are speleogenesis, karst terrain development and the deposition of tufa. Syntheses of these key areas are thus provided, including processes occurring in caves, sequential patterns of karst terrain development, diagnosis of tufaceous lithologies and deposits, depositional models and facies types of tufaceous lithologies and the poor representation of tufaceous lithologies in the geological record. A classification scheme of tufaceous lithologies at Riversleigh is proposed, depositional rates of tufa formation over long periods are estimated and concepts of environmental variation in karst are explored.

The materials and methods used in research undertaken during this project are described briefly in Chapter 4.

Chapter 5 deals with the interpretation of the middle Tertiary carbonates at Riversleigh. Lithological, faunal and taphonomic criteria used to distinguish two broad categories of deposits at Riversleigh are recognised. These broad categories are cave deposits and primary heterogeneous carbonate host. Key lithotextures for use in petrographic analyses are described. Previous descriptions and interpretations of each major facies type are discussed in detail and each facies component is described and interpreted. Issues challenging previous interpretations are identified and alternative approaches to interpretation considered. Facies of the primary heterogeneous carbonate host are interpreted as forms of tufa and diagnostic criteria identified. Diagnosis of flowstone is included in interpretation of cave facies. New depositional models of primary host facies and cave facies are described. Representative deposits of each major facies type are described and discussed in more detail

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Chapter 6 combines karst concepts and processes, Riversleigh vertebrate biocorrelation and the interpretations of Riversleigh lithotypes to formulate a sequence of 4 depositional phases during the development of the terrain at Riversleigh during the middle Tertiary. Models of depositional processes and landscape evolution during these depositional phases are described. Aspects of the 4-phase model including palaeoclimatic implications and influences on palaeoenvironments and fossil faunal assemblages are discussed in Chapter 7. A revised interpretation of the Carl Creek Limestone based on this research is offered in Chapter 8. Problems with the interpretations and models in this work are discussed in Chapter 9.

Chapter 2

The regional and geological context of Riversleigh

2.1 Description of study area at Riversleigh

Riversleigh Station is in northwest Queensland, approximately 280km northwest of Mt Isa at 19°S 139°E, which is about 55km east of the Queensland border with the Northern Territory (see Figures 2.1, 2.2, 2.3, 2.4). To the north and east, the terrain is dominated by Proterozoic siliclastics, including conglomerate, sandstone and siltstone, of the McNamara and South Nicholson Groups. To the south and west is the karst terrain formed by the Cambrian Thorntonia Limestone, which is comprised of limestone and dolomite with bands of chert nodules and beds of chert. Carbonate facies dominate this unit to the east of the study area, and the sediments to the west of the study area are dominated by chert beds.

The major channels of Verdon Creek and the Gregory and O'Shanassy Rivers flow northeast from the karst terrain and converge north of Riversleigh Homestead. Carl Creek is a small distributary that runs between the Gregory and O'Shanassy Rivers south of the main confluence. Poorly consolidated alluvium and colluvium deposits in the Gregory River valley were mapped as ?Pliocene by Megirian (1992).

10 isolated outcrops of Tertiary carbonate overlying the Proterozoic basement have been recognised (referred to as mesas 1-10, Figures 2.2, 2.3, 2.4). A further three major outcrops are associated with the Cambrian terrain to the west. D Plateau lies at the junction of the Proterozoic and Cambrian terrains, overlying the former and lying upon and adjacent to carbonate-dominated deposits of the latter. Gag Plateau lies on and adjacent to Cambrian chert-dominated sediments to the north east and adjacent to chert-dominated deposits to the south and west. Southern Gag Plateau lies adjacent to, and probably upon Cambrian chert-dominated deposits. Because deposits in the area encompassing D Plateau, Gag Plateau and Southern Gag Plateau have been the main focus of palaeontological exploration and collection they are the main source of data for this project. Approximately 200 fossil localities have been mapped in that area so far (see Figures 2.5, 2.6).
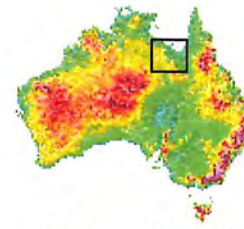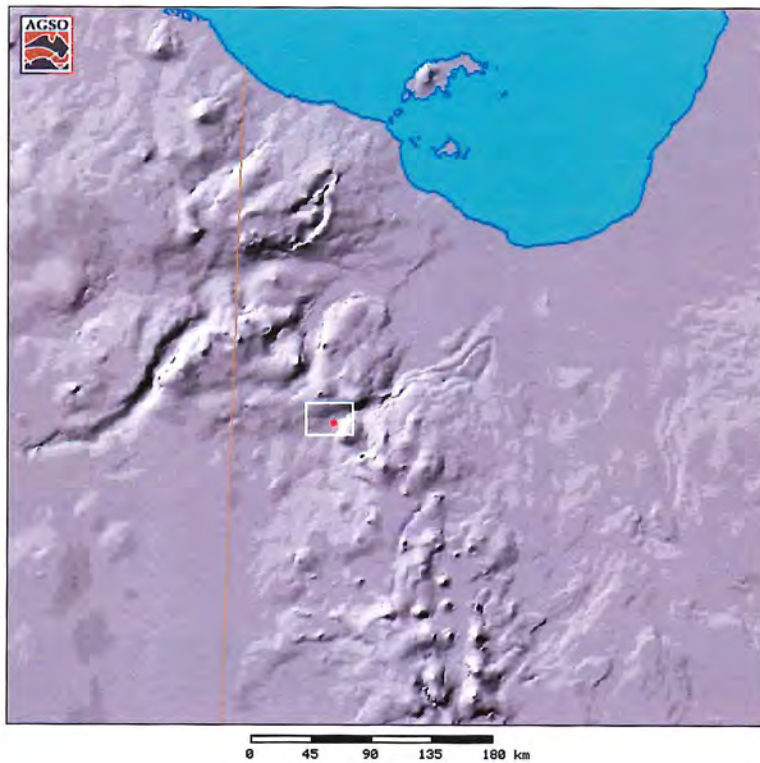
Figure 2.1: Location of the Riversleigh area on the Australian mainland and relationships with regional topography. The Riversleigh deposits occur in a wide valley forming part of the Gregory River drainage system. The white box indicates the position of area depicted in figures 2.2 and 2.3. Courtesy of AGSO Online Mapping www.agso.gov.au.

0   45   90   135   180 km

Legend

	?Pliocene alluvium and colluvium
	Tertiary carbonates
	Cambrian chert-dominated sediments
	Cambrian carbonate-dominated sediments
	Proterozoic sediments
∿	Drainage channel of Gregory River System

Figure 2.2: 3-dimensional terrain reconstruction of the Riversleigh area showing relationships between topography and major rock types and major drainage channels. The distinction between carbonate-dominated and chert-dominated Cambrian sediments is inferred from field observation and aerial photographs and is not a formal boundary. Note the Gregory River valley cuts through Proterozoic highs to the northeast. a) Looking north. b) Looking southeast. Model width approximately 23 km, vertical exaggeration x12. Geographic names are given in figure 2.4.

Figure 2.3: Geology of the Riversleigh area after Megirian (1992). The outcrops mapped as Riversleigh Tertiary carbonates are equivalent to Carl Creek Limestone. They show the known areal extent of the primary heterogeneous carbonate facies described in the text. The Proterozoic and Mesozoic sediments are shallow marine siliclastics, the Cambrian sediments are dominated by marine limestone, dolomites and chert. The ?Pliocene Armraynald Beds are discontinuous alluvium and colluvium deposits that post-date the Riversleigh Tertiary carbonates (corresponding regions are mapped as dominated by Cambrian or Proterozoic in the geological map in Figure 5.3 because outcrops of these older sediments occur in, and appear to underlie, the younger colluvium and alluvium deposits). The ?Freshwater carbonates/tufa of unknown age were mapped as part of the Carl Creek Limestone by Megirian (1992), however because these outcrops have not been sampled or dated using vertebrate biocorrelation, they are not included here with the Riversleigh Tertiary carbonates. It is possible that some of those outcrops could be more recent tufa deposits. Outline delineates area mapped in Figure 2.4 below.
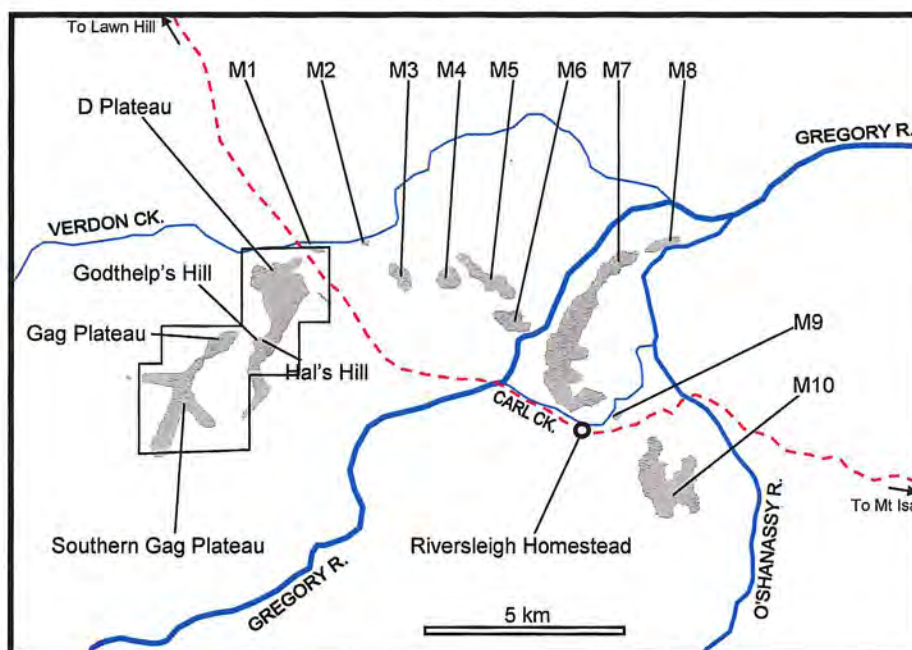
Figure 2.4: Geographic map of the Riversleigh area showing landmarks and informal placenames used in the text and earlier publications. 'M' denotes 'Mesa'. Shows approximate dimensions of maps and terrain models in Figures 2.5, 2.6 and 5.3. After Megirian (1992).

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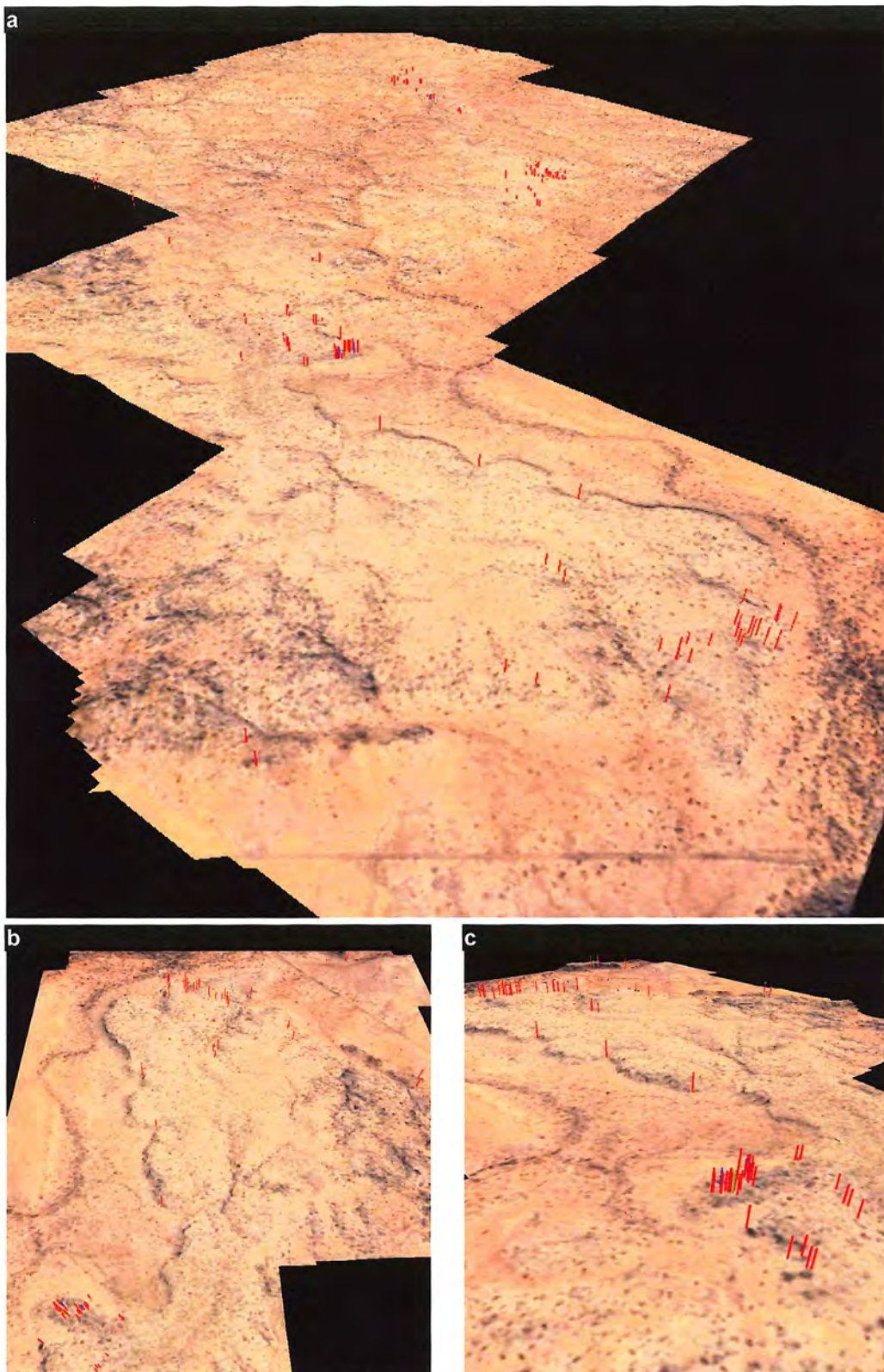
Figure 2.5: 3-dimensional reconstruction of key outcrops in the north of the main study area. a) General view looking southwest across D Plateau, Godthelp's and Hal's Hills in the background. In the distance are Gag and Southern Gag Plateaux. Positions of fossil localities are indicated with red markers. Tertiary deposits are greyish in colour compared to the orange/brown of Cambrian and surficial deposits. Note the low relief. b) Looking north down on D Plateau with Godthelp's and Hal's Hills at lower left. Note deep weathering structures on D Plateau. c) View northeast over Godthelp's Hill (with concentration of red markers) toward D Plateau. Total width of model is approximately 5750m.
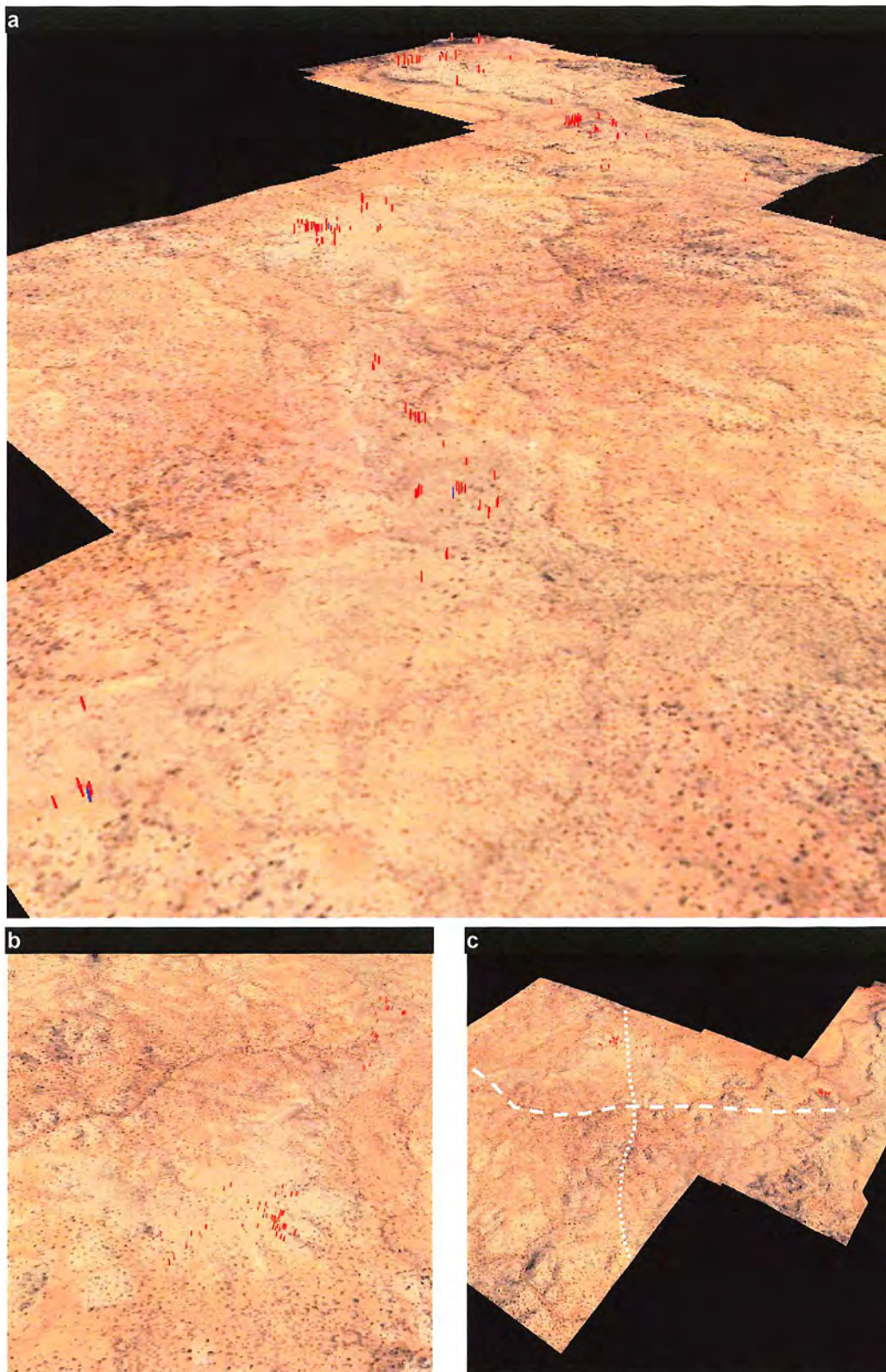
Figure 2.6: 3-dimensional reconstruction of key outcrops in the south of the main study area. a) General view looking northeast across Southern Gag Plateau, to Gag Plateau. Godthelp's and Hal's Hills and D Plateau are in the distance. b) Looking south over Gag Plateau and the northern end of Southern Gag Plateau. Middle Miocene faunas are found at the cluster of localities at lower centre right informally called Rays Amphitheatre and in other scattered localities across the western part of the plateau. c) Looking northwest at the SW/NE trending lineament south of Gag Plateau that could be interpreted as a fault, a NW/SE trending lineament mapped as a fault by Megirian (1992) is also marked. Total width of model is approximately 5750m.

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Tertiary outcrops at Riversleigh occur between 140 m and 200 m altitude. While elevation in the area spans 100m in the valley floor to 260m on Proterozoic highs, and the Cambrian karst of the Barkly Tableland further to the south and west reaches elevations of up to 300m, there is little difference in relief between outcrops of Cambrian sediments and Tertiary carbonates at Riversleigh.

2.1.1 Modern karst processes in the Tertiary carbonates at Riversleigh

The modern Tertiary karst terrain at Riversleigh can be considered to be at a mature stage of development. The pattern of landforms formed by outcrops of middle Tertiary carbonates (Figures 2.2, 2.3, 2.4, 2.7a) can be interpreted as karst residuals in a corroded landscape. Ongoing karst processes occurring in the middle Tertiary carbonates in the terrain at Riversleigh include:

1. Denudation producing typical karst weathering morphology on outcrops including various forms of rills, lapies and kamenitzas (Figure 2.7d, e). These solution features are indicative of ongoing denudation.

2. Epikarstic development, including formation of deep fissures and chimneys, pipes, grikes and cleftkarren occurs throughout the system (Figure 2.7b, c, f).

3. Epikarst in high points is often characterised by reduced soil and vegetation cover and exposed rock surfaces, providing potential access to subsurface cavities (Figure 2.7b, c).

4. Development of collapse dolines (Figure 2.7g).

5. Retraction of residual high-point landforms by erosion and corrosion (2.7a).

In the Riversleigh area, tufa formation occurs in fluvial barrage systems at Carl Creek, the Gregory River and at Louie Creek and Lawn Hill Creek north of Riversleigh (Drysdale 1995, Drysdale and Head 1994, Drysdale and Gale 1997, Drysdale and Gillieson 1997, Drysdale *et al.* 2002, Carthew *et al.* 2003).

2.2 Previous study of Riversleigh geology

The history of research of Riversleigh geology from the period prior to 1995 was summarised by Megirian (1992) and Arena (1995). Research to date is described briefly here.
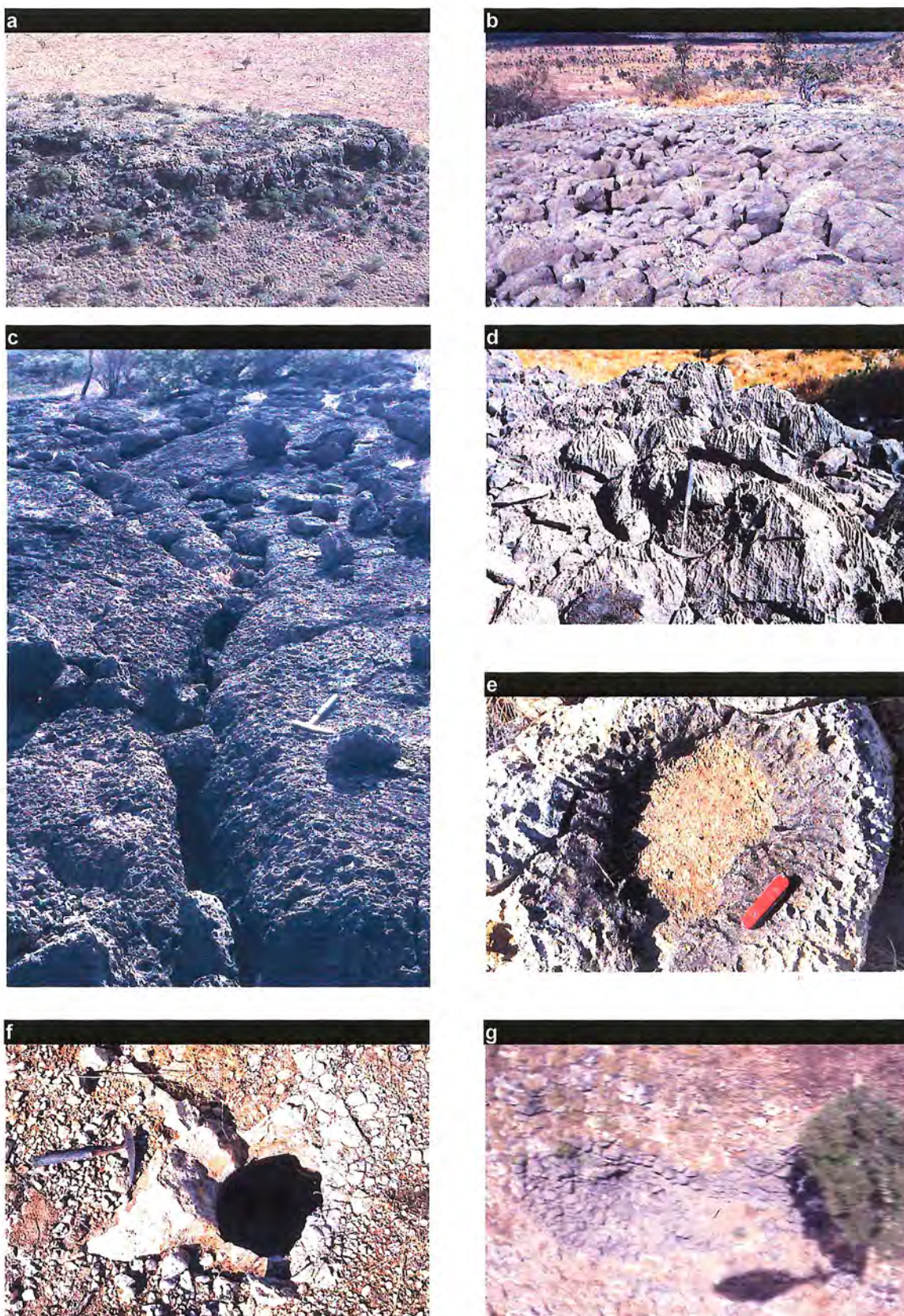
Figure 2.7: Modern karst processes in the Tertiary carbonates at Riversleigh. a) Mesa 3 as a representative high-point undergoing karst processes with an active solution fissure system can be considered analogous to inter-doline crest environments related to solution fissure systems in which vadose karst deposits formed during the Tertiary. The surface is characterised by exposed rock with vegetation and soil limited

to small patches or crevices. The surface is deeply corroded with many solution fissures of different depths and widths. Looking east. b) Deeply fissured surface of Mesa 3 pictured in a. This type of surface may resemble the surface beneath which the extensive vadose karst deposits of Godthelp Hill formed. c) Deep solution fissure, considered analogous to solution fissures that connected spelaean environments with the surface during the Tertiary. The fissure is many metres deep and appears to descend for some distance beyond that discerned visibly. d) Rillenkarren, south of Two Trees Site. This solution sculpture morphology is a very common feature of Tertiary outcrops at Riversleigh and indicates that denudation is an ongoing process. e) Kamenitza, another common form of solution sculpture at Riversleigh, Southern Gag Plateau. f) Vertical chimney descending more than two metres, 25m north of Encore Site. g) Collapse doline, indicating that vadose karst processes are actively corroding high points in the landscape that have greater soil and vegetation cover. Diameter is approximately 10-15 m, top of D Plateau looking south.

Previous investigation of the Riversleigh geology can be divided into two main areas:

1. Regional geology.

2. Local geology including recognition and interpretation of lithofacies, fossils and their modes of deposition.

2.2.1 Regional geology

Key aspects of the geological history of northern Australia, including tectonics and the cyclic phases of weathering and deposition were identified and discussed by Doutch (1976), Grimes (1979), Smart *et al.* (1980) and Day *et al.* (1983). The Tertiary geological development of northern Australia is characterised by three cycles of deposition and hiatus (Figure 2.8), recorded by sediments and exposure surfaces of the Karumba Basin, which encompasses the Gulf of Carpentaria, southern New Guinea, western Cape York, north western Queensland, north eastern Northern Territory and eastern Arnhem Land (Figure 2.9). The development of this regional setting was influenced by tectonic activity caused by the convergence of the northern margin of the Australian Plate as it drifted northward during the Cainozoic (Veevers 1984, 2000, Müller *et al.* 2000). The western parts of the Riversleigh region became enclosed within the southwestern margin of the Karumba Basin when the Barkly Tableland was uplifted during the Oligocene (Grimes 1979, Smart *et al.* 1980, Day *et al.* 1983). At this time the region was subject to the sedimentary hiatus of the late Bulimba Cycle. Events at Riversleigh were imprecisely related to this regional history (i.e. in Grimes 1979, Smart *et al.* 1980, Day *et al.* 1983), mainly because there was limited understanding of the age and depositional history of the Riversleigh Tertiary geology at the time. The relationships of some of these regional events to some aspects of the Riversleigh Tertiary geological development are clarified in this work.

2.2.2 Local geology

Tedford (1967) provided the first detailed description of Tertiary lithologies in outcrops at Riversleigh situated along the road to Lawn Hill, from which vertebrates of the Riversleigh Local Fauna were first collected. Based on the stage of evolution of certain taxa, and similarities with faunas from Lake Ngapakaldi in Central Australia, Tedford tentatively assigned the outcrops to the late Oligocene. He identified the basic elements
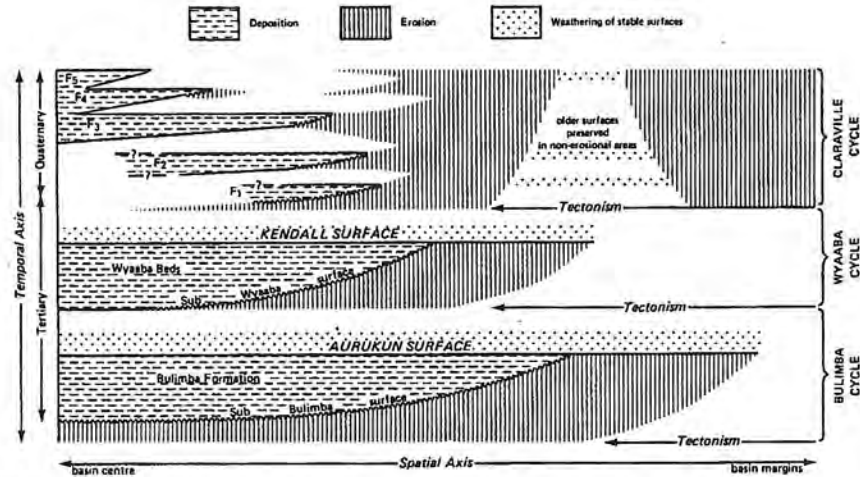
Figure 2.8: Tertiary geological cycles of northern Australia, from Smart *et al.* (1980).

Legend

Early Cainozoic basin margin, pre-Pine Creek Upwarp

Miocene basin margin, post-Pine Creek Upwarp
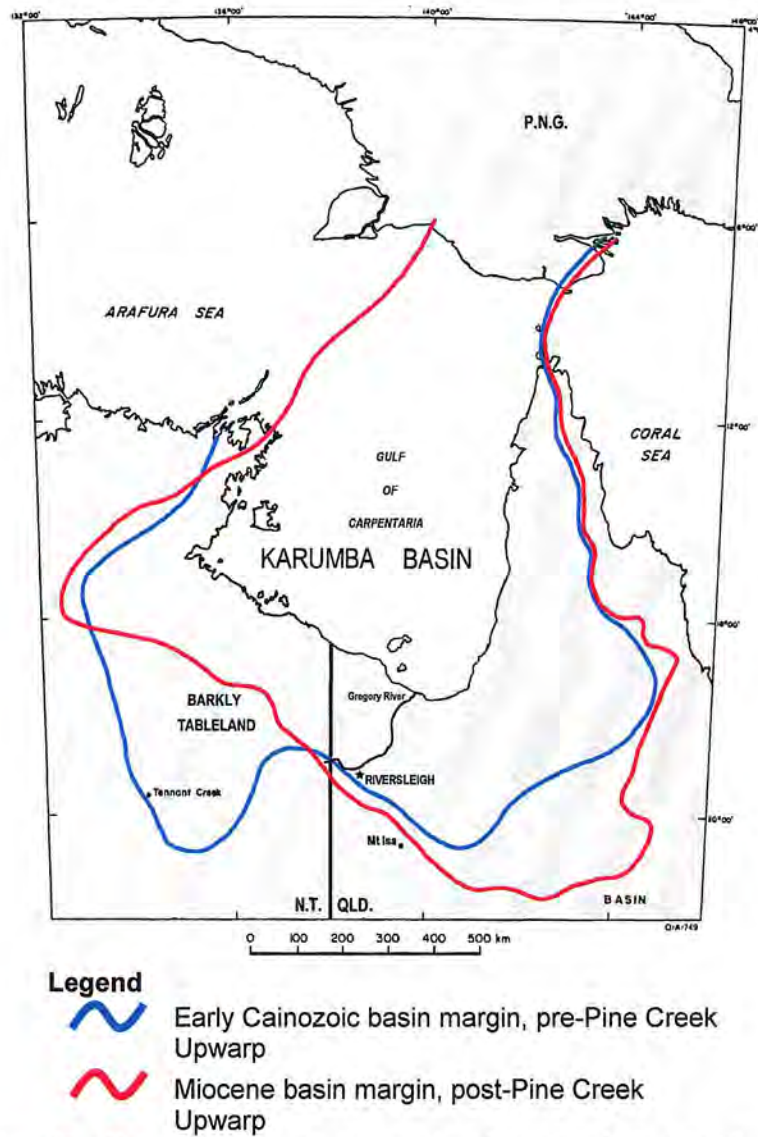
Figure 2.9: Margins of the Karumba Basin, note the margins of the basin before the Pine Creek Upwarp with respect to the position of Riversleigh. After Smart *et al.* (1980).

of facies in that area: the 'basal conglomerate' comprising carbonate and chert fragments in a carbonate matrix, and the overlying heterogeneous limestone. Other relevant key observations included recognition of the undulating basement contact, variable thickness of outcrops of the deposit and random distribution of isolated occurrences and higher concentrations of fossil bone throughout the exposure. The geology was tentatively interpreted as indicative of a clastic lacustrine depositional environment.

The Cambrian karst and associated Tertiary landforms at Riversleigh were subsequently described by Williams (1978). The Cambrian karst was compared to similar terrain in the Limestone Ranges, Western Australia, which is dominated by large joint-controlled grike systems, expanding box-valleys producing low-relief residual towers and a denudation pattern characterised by a planation surface at the top of the profile (Jennings and Sweeting 1963). By analogy with processes occurring in that system, Williams (1978) modelled a depositional process responsible for the formation of the vertebrate-rich Carl Creek Limestone, involving seasonal infusion of unconsolidated alluvial sediment during the wet season with calcium carbonate-rich water, and consolidation during the dry season to produce a 'tufaceous alluvium' valley-fill containing preserved vertebrate and invertebrate material (Figure 2.10).

Further extensive exploration and collection of fossil vertebrate material at Riversleigh expanded both the age range of the deposits and the scope of the depositional history. Archer *et al.* (1989, 1994) recognised a complex combination of Tertiary lithologies from at least three time periods during the middle Tertiary: late Oligocene, early Miocene and middle to late Miocene. Pliocene and Pleistocene fossil deposits in the area were also recognised. Ages of deposits were determined by stage of evolution comparison and biocorrelation of taxa with faunas at Riversleigh and from other Australian fossil localities. They recognised the occurrence of different kinds of depositional environments in which vertebrate remains may have accumulated including lacustrine ('pool') conditions and cave environments. Archer *et al.* (1989) introduced the 'Systems' concept of stratigraphy for use when discussing localities and their faunas of late Oligocene, early Miocene and middle to late Miocene age; this is discussed in more detail below. The stratigraphic record at Riversleigh was considered to have been

A) A GENERAL SITUATION FAVOURING DEPOSITION OF CALCAREOUS TUFACEOUS ALLUVIUM IN A TROPICAL SEASONALLY WET REGIME

B) SEASONAL PATTERN IN THE DEPOSITION OF CALCAREOUS TUFACEOUS ALLUVIUM

1) WET SEASON

2) END OF WET SEASON

3) END OF DRY SEASON
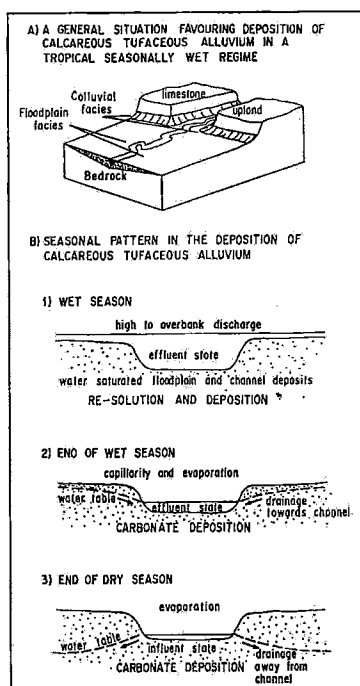
Figure 2.10: The tufaceous alluvium model of Williams (1978) showing infusion of alluvial sediments with calcium-carbonate-rich waters during spate and net deposition of carbonate during dry times.
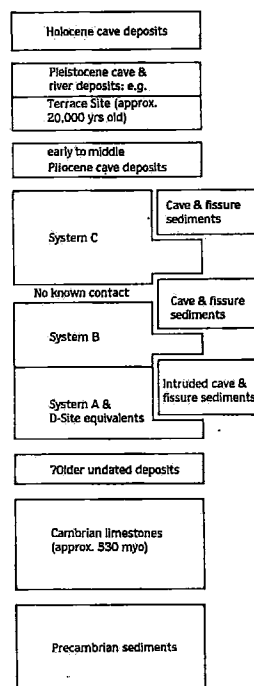
Figure 2.11: Lithostratigraphic sequence of Archer *et al.* (1994, 1997). From Archer *et al.* (1994).
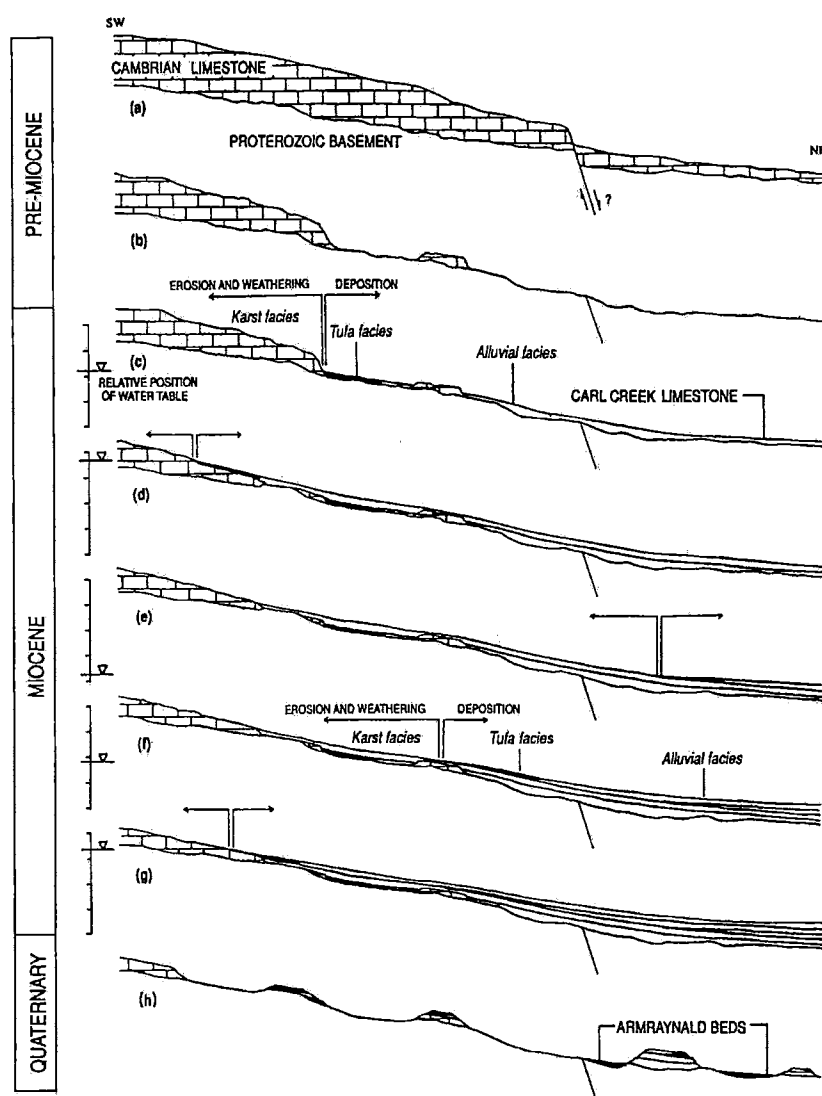
Figure 2.12: The Riversleigh arid alluvial fan model of Megirian (1992). In this model, a depositional basin is formed in the Riversleigh area by movement of a hypothetical slip fault prior to deposition of Riversleigh carbonates.

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divided into at least three discrete stages of deposition, cave formation and infill throughout this period (Figure 2.11).

Megirian (1992) offered the first complete description of the Riversleigh Tertiary geology, identifying key facies and their distributions at Riversleigh. While many of his observations of the geology are valid and useful, there are several problems with the work, among the most significant being misinterpretation of the age-range of the deposit and assimilation of distinct facies from different time periods. Alternative interpretations of lithofacies and depositional environments were not addressed. As a result, aspects of the observations and depositional model must be reassessed. The model, which focuses mainly on the primary depositional phase, describes the deposition of clastic carbonates in an alluvial fan system in a dry to arid climate (Figure 2.12). One of the significant contributions of Megirian's work was the recognition of the role of tufa in the Tertiary geological development of Riversleigh, in this case as the source of clastic sedimentary components. Alternatives to and reinterpretations of aspects of the work of Megirian (1992) are a primary focus of this work. Megirian's model and interpretations are described in greater detail below where relevant. Price (2002) also recognised there were some similarities between some Riversleigh Tertiary carbonates and tufa.

Creaser (1997) provided further clarity of the age relationships of various fossil localities at Riversleigh, and highlighted the potential significance of topographic and spatial relationships to interpretation. He identified and named as 'Sequences' key outcrops at Riversleigh that were considered representative of different stages of deposition. He compared the heterogeneous carbonates at Riversleigh to calc-lithites, and considered their deposition at Riversleigh throughout the middle Tertiary to have been cyclic, involving subsidence, deposition, karst development and erosion that repeated at least three times during the middle Tertiary, corresponding to the three 'Systems' A, B and C of Archer *et al.* (1989, 1994, 1997). The primary depositional process was considered to be a braided alluvial environment (*sensu* the alluvial fan model of Megirian 1992) with a probable northeasterly flow direction, although Creaser did consider the palaeoclimate as necessarily arid because calc-lithites can accumulate

in humid environments with high rainfall such as the Huon peninsula in Papua New Guinea.

Archer *et al.* (1997) provided further correlation between faunas from Riversleigh and from other parts of Australia and discussed of the potential influence of regional climatic processes on Riversleigh faunas during the Tertiary. More precise dates were established for the time spans to which faunas from Riversleigh were assigned and key aspects of these faunas were outlined.

2.3 Tertiary global and regional processes: climatic cycles and the northward drift of the Australian continent

Processes at regional or global scale that influenced the development of climate and environments in Australia during the Tertiary include the northward drift of the Australian continent from temperate to tropical latitudes and the oscillation of climatic conditions between periods of relatively warm and wet conditions and periods of relatively cool and dry conditions.

2.3.1 Northward drift of the Australian continent and Riversleigh palaeolatitudes

Palaeogeographic reconstructions of the Australian continent throughout the Phanerozoic were provided by Veevers (1984) and Li and Powell (2001), timing of seafloor spreading was provided by Müller *et al.* (2000) and the convergence of the northern Australian margin was summarised by Veevers (2000).

Seafloor spreading between Australia and Antarctica was initiated in the late Cretaceous (67.7 Ma; Müller *et al.* 2000), final separation was achieved by 40.1 Ma (Müller *et al.* 2000) when Antarctica became completely surrounded by ocean (Li and Powell 2001).

Positions of the Australian continent (and Riversleigh) throughout the Tertiary are illustrated in Figure 2.13. During the Oligo-Miocene the Australian continent drifted northward, and the Riversleigh area moved through the (modern) subtropical latitudes. In the late Oligocene (approximately 30 Ma) Riversleigh was situated at about 33-34°S,

by the late Miocene (approximately 10 Ma) Riversleigh had reached about 23-25°S, and is now at 19°S (see table 2.1). Climatic conditions at certain latitudes may not necessarily be comparable to those in modern climatic zones, although modern climatic conditions at those latitudes can be taken into account when modelling palaeoclimate.

Epoch		Time (Ma)	Palaeolatitude (°S)
Late Miocene	L	10	23-25
	E	11.2	(25-26)
Middle Miocene	L	14.8	
	E	16.4	(26-27)
Early Miocene	L	20.6	27-28
	E	23.8	(28-30)
Late Oligocene	L	25	(31-32)
		30	33-34

Table 2.1: Approximate palaeolatitudes of Riversleigh during the Oligo-Miocene. Palaeolatitudes are as figured in Veevers (1984; see Figure 2.13), intermediate palaeolatitudes inferred from figures in Veevers (1984) are in brackets.

2.3.2 Global climatic cycles and the southern greenhouse/icehouse oscillations

McGowran and Li (1994) combined information from the geological record, fossil records of marine foraminifera and molluscs, eustatic curves and oxygen isotope data to identify fluctuations in climate in Australia during the Oligo-Miocene. Climate during this period fluctuated between cooler and drier 'icehouse' conditions and warmer, wetter 'greenhouse' conditions, including a period in the middle Miocene at about 15-16 Ma (Miocene climatic optimum) during which relatively extreme greenhouse conditions prevailed. The 'greenhouse' type conditions of the early and middle Miocene are considered to have been more favourable to the regional proliferation of vegetation comparable to modern closed forests or rainforest and relatively high faunal diversity. The 'icehouse' type conditions of the late Oligocene and late Miocene are considered to have caused relatively decreased diversity and drier environments.

Late Mesozoic and Cainozoic global temperatures inferred from modelling of atmospheric CO_2 concentrations conform to this pattern (Crowley and Kim 1995), and the development of permanent Antarctic ice-sheets associated with global cooling in the late Miocene has been related to this curve (Barrett 2003; see Figure 2.14).
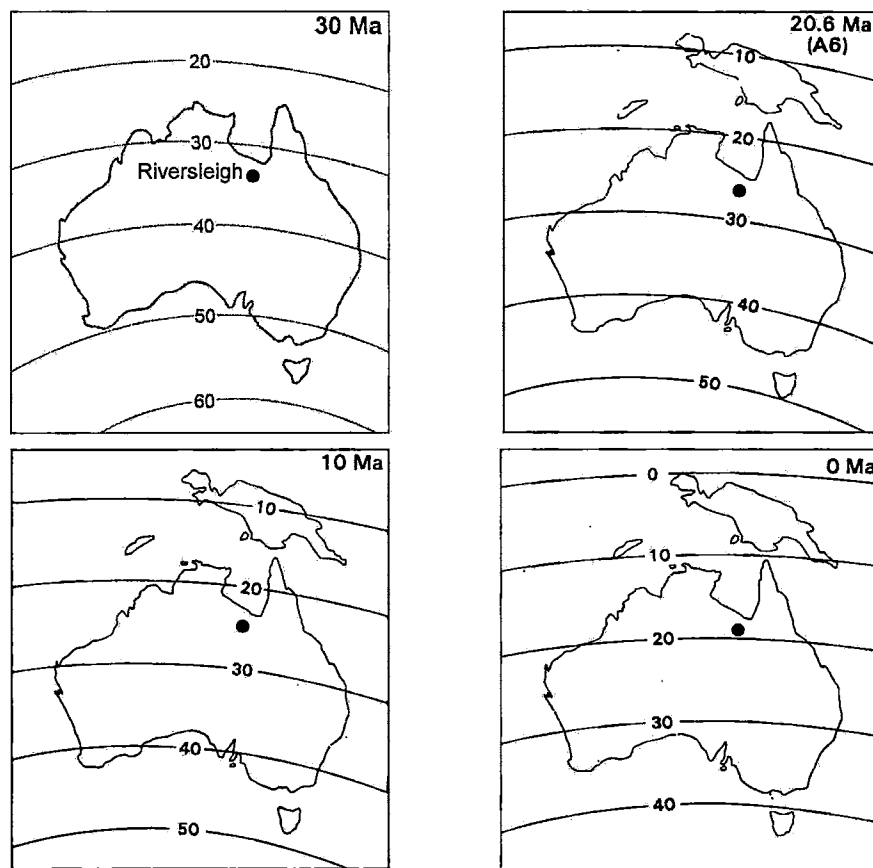
Figure 2.13: Palaeolatitudes of Australia (with position of Riversleigh marked) during the middle to late Tertiary from Veevers (1984), map of late Oligocene (30 Ma) is modified from a different figure in that work. Palaeolatitudes inferred from these positions are used in the text. After Veevers (1984).
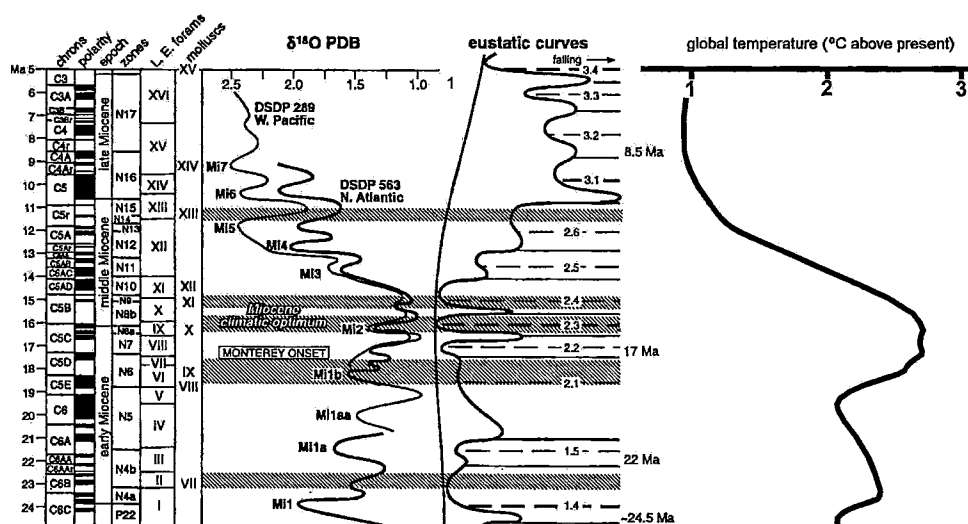
Figure 2.14: Oligo-Miocene greenhouse/icehouse climatic cycles of McGowran and Li (1994) showing the middle Miocene optimum, matched with the corresponding part of the Cainozoic temperature curve of Barrett (2003). After McGowran and Li (1994) and Barrett (2003).

Chapter 3

Materials and methods used in research undertaken during this project

Extensive fieldwork was conducted at Riversleigh on annual expeditions from 1995 to 2003. This fieldwork included exploration; excavation of fossil localities and retrieval of fossil specimens; observation of local geology, landforms and processes from the ground and air; interpretation of aerial photographs; collection of rock samples; and detailed investigation of individual fossil deposits involving mapping, photography, sampling and observation and recording of lithology and depositional structure.

Rock samples were sectioned for petrographic analysis. Specimens with the prefix 'RA' were collected by the author between 1995 and 2002. Specimens with the prefix 'R' were collected by M. Archer and P. Creaser and the author in 1998. Specimens with the prefix 'EP' were collected by E. Price in 2001, thin sectioned on her behalf and originally used to provide data for her Honours Thesis (Price 2002). Notation in captions is of the format (PP/XP; specimen number; locality name) or (PP/XP; specimen number) when locality is the same for all figured specimens, where PP denotes plane polarised light and XP denotes cross-polarised light.

X-Ray diffraction (XRD) technique involved grinding of samples to a fine powder using a tungsten carbide mill and agate mortar and pestle. Samples were pressed into separate aluminium holders using a glass slide. X-ray diffraction traces were recorded onto a Philips X'Pert system using monochromatised Cu radiation (40 kV, 30 mA) over a two-theta angular range of 2-60 degrees at approximately 1 degree per minute.

Vertebrate bones were etched from carbonate matrix using 5-10% acetic acid. Invertebrate material was etched from phosphate matrix using 5% hydrochloric acid. The prefix QMF refers to specimens held in the fossil collections of the Queensland Museum.

Positions of fossil localities were mapped using differential GPS in conjunction with F. Nissen of the Queensland Parks and Wildlife Service as part of the Riversleigh Fossil Site Register and Geographic Information System Project, completed by the author in November 2001. Locality positions were reconciled with a rectified mosaic of high-detail aerial photographs and digitised topographic data to produce an accurate reconstruction of the terrain in the study area, for use in interpreting landforms and geographic relationships of localities. Literature was reviewed to retrieve all published references to fossil taxa known from Riversleigh which were entered into a database with a hierarchical tree structure to allow searching and retrieval of taxonomic data at all levels of taxonomic grouping. Locality data and faunal lists were cross-referenced to generate faunal lists from individual localities. These lists have been supplemented in this work by additional unpublished data from Myers (2002) and Crosby (2002a). In faunal lists in this work, known occurrences of taxa that are not published, including unpublished names, appear in square brackets.

Dunsinane Site was mapped by the author using a Seikkosha TM20E theodolite and staff. AL90 site was mapped using laser surveying equipment by F. Nissen. Mapping data was used by the author to generate those locality reconstructions. Regional terrain reconstruction was based on data from Royal Australian Survey Corps Series R631 1:100 000 Topographic Map Sheets 6659 (Riversleigh) and 6660 (Lawn Hill).

Chapter 4

Review of concepts, processes and geology

4.1 Terminology and definitions

Definitions and terms used in this work are defined here. Some of these terms and definitions could be considered as standard for ongoing work at Riversleigh.

Carbonate rocks and limestone

There is extensive literature on carbonate rocks. Leighton and Pendexter (1962) define carbonate rocks as those that contain at least 50% carbonate minerals, and limestones as carbonate rocks in which the primary carbonate mineral is calcium carbonate (as opposed to dolomites which are primarily composed of calcium magnesium carbonate). In terms of mineral composition the range of facies present at Riversleigh (as described in greater detail below) classify as limestone. The terms limestone and carbonate are used interchangeably here in accordance with this definition to refer to Riversleigh lithologies rich in calcium carbonate.

Limestone classification systems

There are several limestone classification systems, summarised and compared by Flügel (1978). Limestones may be classified according to their parallels with siliclastic sediments (Folk 1962), by aspects of particle fabrics (Dunham 1962), the proportions of grains to micritic material (Leighton and Pendexter 1962) and effect of water agitation on structure and texture (Plumley *et al.* 1962). All of these classification systems share implicit assumptions related to their primary role in the classification of marine limestones. This should be acknowledged when classifying terrestrial carbonates using any of these systems. The terminology of Dunham (1962) is used here where necessary to describe limestone texture.

Time scale

The time scale used here for the Oligo-Miocene is that of Berggren *et al.* (1995). According to this scheme the Oligo-Miocene (Chattian/Aquitanian) boundary is at 23.8 Ma. In the early Miocene the early-early Miocene/late-early Miocene

(Aquitanian/Burdigalian) boundary is at approximately 20.55 Ma, and the early/middle Miocene (Burdigalian/Langhian) boundary is at 16.4 Ma. The middle/late Miocene (Serravallian/Tortonian) boundary is at 11.2 Ma.

Carl Creek Limestone

Carl Creek Limestone is the name given by Jack (1896) to limestone outcrops in the area near the O'Shanassy River reported to contain the fossil mollusc *Tellina*. This usage has since been revised by authors after Paten (1960) to apply to the terrestrial limestone outcrops containing fossil molluscs and bones in the Riversleigh area that are distinct from the Cambrian Thorntonia Limestone. Outcrops considered representative of the Carl Creek Limestone were dated as late Oligocene by Tedford (1967) and as Miocene by Megirian (1992). However, Archer *et al.* (1989, 1994, 1997) showed that the Riversleigh Tertiary limestone deposits actually consist of different carbonate facies from different time periods spanning the late Oligocene to late Miocene. The depositional history of these facies and their relationships are discussed in further detail below. The definition of the Carl Creek Limestone is revised at the end of this work.

Because the term Carl Creek Limestone encompasses several facies of different ages that are the subject of interpretation and discussion below, the name will not be used in this work except where reference is made to the work of previous authors. A revised interpretation of the Carl Creek Limestone is supplied at the end of this work in Chapter 10.

Terrestrial carbonate terminology

There is considerable confusion regarding terminology referring to terrestrial carbonates both in the literature and in common usage. There is no widely accepted standard for terminology relating to tufaceous lithologies. A standard terminology for use in the context of Riversleigh research is proposed below.

Tufaceous lithologies: tufa and travertine

The variety of terminology referring to tufaceous lithologies was reviewed by Viles and Goudie (1990a), and the terminology referring specifically to tufa was reviewed by Pedley (1990) and Drysdale (1995). Definitions often overlap, and use of colloquial

terms from different languages in the literature further complicates standardisation of terminology.

Tufaceous lithologies are considered here to be a group comprised of tufa and travertine sharing the distinction that both are precipitated from supersaturated waters primarily by biological mediation, as well as physico-chemical mediation, usually in a surface (i.e. sub-aerial) environment.

Distinctions between travertine and tufa have been clarified by Ford and Pedley (1996:118). The term *travertine* refers to "all 'freshwater' thermal and hydrothermal calcium carbonate deposits dominated by physico-chemical and microbial precipitation [that] invariably lack *in situ* macrophyte and animal remains". Travertine is usually more dense, hard and crystalline. The primary mediators of precipitation are bacteria able to withstand conditions that are hostile to other potential organic mediators (such as those that form tufa), physical precipitation by turbulence and agitation, and evaporation to a degree greater than that of tufa (Chafetz and Folk 1984).

The term *tufa* refers to "the product of calcium carbonate precipitation under a cool water (near ambient temperature) regime and typically contains the remains of micro- and macrophytes, invertebrates and bacteria" (Ford and Pedley 1996:117). The primary mediators of precipitation are photosynthetic organisms (plants and algae), physical precipitation by turbulence and agitation, and by evaporation. Pedley (1990), Drysdale (1995) and Ford and Pedley (1996) provide examples of different tufa facies and the environments in which they form, described below. While most tufa deposits are lithified, some tufa deposits may be poorly consolidated or friable.

Speleothem

The term *speleothem* refers to the mode of occurrence of minerals precipitated in caves, rather than their chemical composition (Hill and Forti 1997a). While speleothem can be comprised of many different types of minerals, including gypsum, ice, halite, phosphates and sulfates, they are usually formed from carbonates. In this work, the term speleothem refers to carbonate speleothems, unless otherwise specified. Carbonate speleothem is here considered distinct from tufaceous lithologies because the primary

means of precipitation is physico-chemical mediation from supersaturated waters in cave environments (as defined below).

Hard calcite speleothems are deposited as syntaxial overgrowths on previous crystals with the c-axis usually oriented perpendicular to the growth surface (Ford 1988). They include dripstones (i.e. stalactites and stalagmites that can exceed 30m in height and girth), flowstones that may extend for hundreds of metres and accumulate thicknesses that can exceed 2-3 metres, and euhedral spar coatings that may occur on passage surfaces and are usually formed under phreatic influence (*ibid.*).

Karst

Historically, understanding of karst systems focussed primarily on landscape processes with distinctive hydrology and landforms Klimchouk and Ford (2000a). The concept of karst is best described as encompassing the net processes (both destructive and constructive) that occur in soluble rock systems. Klimchouk and Ford (2000a:46) define the concept of karst as follows: "The karst system is an integrated mass-transfer system within soluble rocks with a permeability structure dominated by conduits dissolved from the rock and organised to facilitate the circulation of fluid."

Thus the key components of a karst system include a soluble rock type, dissolutional fluid and a drainage system formed by dissolution within that rock. Karst processes often occur in carbonate rocks, where water is the dissolutional fluid. The water table in a carbonate terrain usually plays a key role in the development of karst.

The profile of karst systems can be divided into the vadose zone above the level of the water table and the phreatic zone below the level of the water table. The epikarstic (subcutaneous) zone is the uppermost zone of karst rock where the degree of permeability and fissuring is relatively greater than the rock below and which functions primarily as a zone of storage and concentration of flow into the vadose zone (Klimchouk 2000).

Karst terrain

Karst processes can (but do not always) result in the formation of distinctive landform patterns at the surface, which are termed *karst terrains*. A karst terrain can be defined as "terrain with distinctive characteristics of relief and drainage arising primarily from a higher degree of rock solubility in natural waters than is found elsewhere" (Jennings 1971:1). These characteristic landforms include: "closed depressions of various size and arrangement" and "disrupted surface drainage" (White 1988:3). Closed depressions include solution dolines, blind valleys and similar landforms resulting from the abandonment of surface drainage systems. Because solution plays a greater role in the development of surface landform in karst than in non-karst terrains, landform development in karst can follow distinctive sequential patterns.

Karst stratigraphy

Bosák *et al.* (1989) defined the karst stratigraphic term *karst period* as a temporal span characterised by long-lasting conditions during which a karst system may develop. A karst period can be divided into *karst phases*, during which different types or generations of karst forms may be generated because of "...geodynamic or major climatic change, e.g. uplift or downwarping, a phase of permafreezing, etc." (Bosák *et al.* 1989:32).

Using this karst stratigraphic concept, Osborne (2000:115) defined *paleokarst* as "karst developed largely or entirely during past karst periods".

Karst dissolutional drainage systems: speleogenesis and caves

Klimchouk and Ford (2000a) recognised a dimensional hierarchy of four types of water-containing spaces that contribute to the development of dissolutional drainage systems in karst. In order of increasing dimension these voids are pores, fissures which are planar and the width of the structure is negligible compared to length, conduits which are elongated openings in which width is a significant proportion of the length and vugs and caverns which may be several orders of magnitude larger than matrix pores.

Speleogenesis is the term given to the organisation of combinations of these types of voids, usually by dissolutional enlargement to form organised subsurface drainage

systems and the bodies of groundwater thus formed and controlled by these systems are termed aquifers (Klimchouk and Ford 2000a).

In addition to the drainage and containment of water, subsurface voids (usually at the larger end of the scale) can also provide depositional environments in which speleothem and sediments can accumulate.

Although the term *cave* is found widely both in the literature and in common usage, reconciliation of the term with the concepts of dissolutional spaces is not simple. Ford and Williams (1989:242) define a karst cave as "a solutional opening that is greater than 5-15mm in diameter or width. This is the effective minimum aperture for turbulent flow". Other authors (i.e. White 1988:60) regard proper caves as "large enough to admit a human being", and refer to smaller solutional openings that play a part in the development of these proper caves as 'conduits'.

The anthropocentric view of caves is not necessarily relevant to the interpretation or modelling of subsurface environments in karst, where dissolution and deposition can occur in spaces that would not normally be enterable by living beings within the size range of any type of human.

In the context of this work, subsurface karst dissolutional spaces where characteristic processes including dissolution and the formation of subsurface deposits such as speleothem and clastic sediments may form are considered caves, regardless of their physical size. Speleothem and clastic cave sediments are referred to here as cave facies.

Biostratigraphy

When confronted with the diversity of faunas and the complex Tertiary depositional history of Riversleigh, which was not yet fully understood, Archer *et al.* (1989) introduced unconventional biostratigraphic nomenclature for Riversleigh faunas and fossil localities. Because physical stratigraphic relationships often did not exist between localities containing faunas of similar age, and localities yielding faunas of different age often occurred in the same place and/or at the same level in the topographic profile, it

was considered both inaccurate and unwise to attempt to apply traditional stratigraphic terminology.

Both faunas and the deposits from which they were collected were placed in 'Systems'. This term came into use in the context of Riversleigh because it alluded to the complex relationships of faunas and geology that were not adequately addressed by existing terminology.

According to conventional nomenclature (i.e. Hedberg 1976, Holland *et al.* 1978), the chronostratigraphic term 'System' corresponds to a span of time equivalent to a geological period. Megirian (1994) suggested that the usage of the 'System' terminology should be abandoned because of this semantic incompatibility that contravened the conventional use of terminology and because of the inherent lack of distinction between faunas and rock units in the 'System' concept.

In contrast to this view, the implementation of the 'System' concept has made it possible to better understand and eventually attempt to interpret the Tertiary geological history of Riversleigh. This is achieved by combining aspects of faunas and geology, rather than their separation.

In this work the Tertiary geological history of Riversleigh is divided into *depositional phases*, which are diagnosed by both geological and faunal criteria and dated by biocorrelation of their contained faunas according to Archer et al. (1989, 1994, 1997). The karst stratigraphic term *phase* was used by Bosák *et al.* (1989) to describe a period of time during which a certain form of karst may develop due to prevailing conditions (see above).

In this work Riversleigh faunas are placed into *faunal zones*, which is a term compatible with the conventions of biostratigraphic nomenclature. These faunal zones are comprised of discrete local faunas (collected from individual localities) that are considered to belong to the same span of time. Spans of time to which specific faunas are considered to belong in this work follow Archer *et al.* (1989, 1994, 1997). As such, Riversleigh faunal zones as defined here are best considered as assemblage biozones
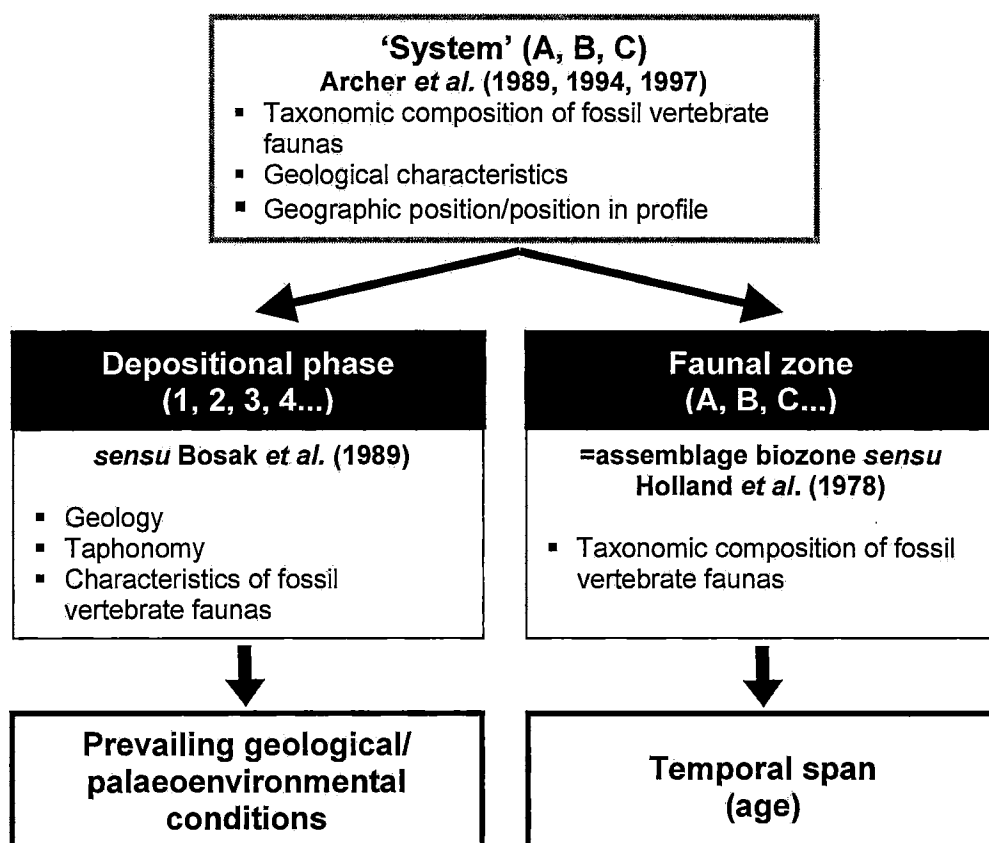
Figure 4.1: Revision of the 'System' bio/lithostratigraphic concept of Archer *et al.* (1989, 1994, 1997) with stratigraphic concepts and terminology introduced in this work.
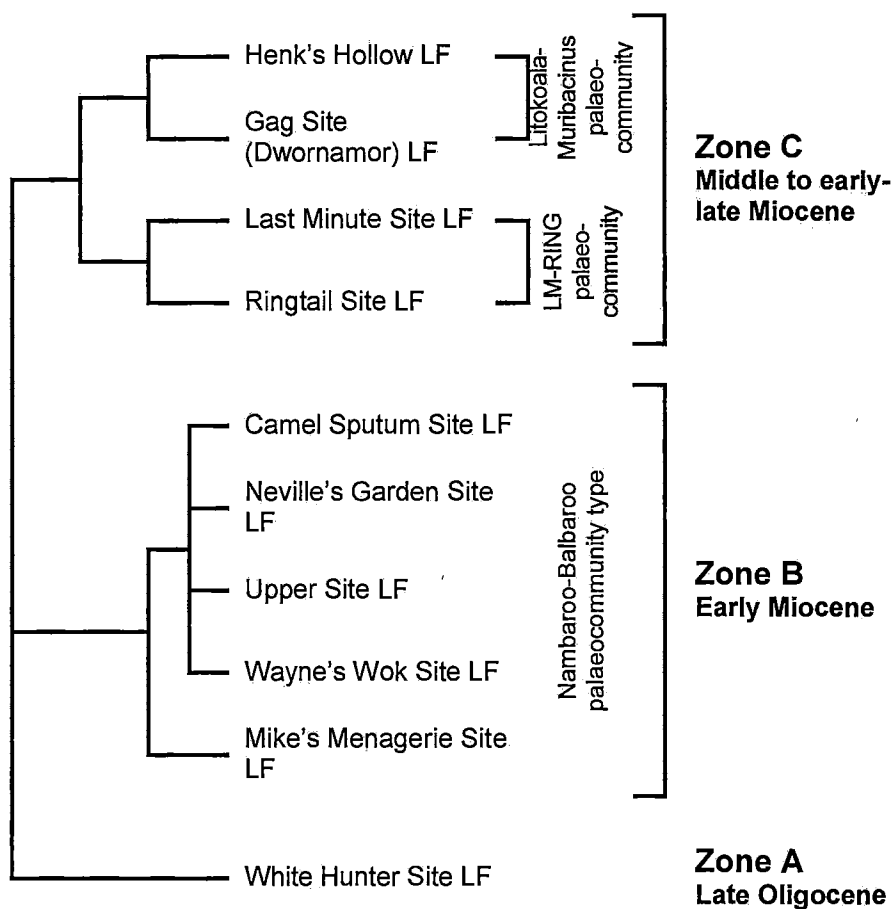
Fig 4.2: Palaeocommunity groupings of Myers (2002) used as faunal zones used in this work based on assigned ages of contained faunas from Archer *et al.* (1997).

Age-range (Archer *et al.* 1989, 1994, 1997)	Bio/lithostratigraphic nomenclature of Archer *et al.* (1989)	Revised biostratigraphic nomenclature	
Middle to early-late Miocene	Riversleigh System C	Riversleigh Faunal Zone C	**Depositional phases occur throughout this period**
Early Miocene	Riversleigh System B	Riversleigh Faunal Zone B	
Late Oligocene	Riversleigh System A	Riversleigh Faunal Zone A	

Table 4.1: Riversleigh faunal zones A, B and C and corresponding time periods of 'Systems' A, B and C of Archer *et al.* (1989, 1994, 1997).
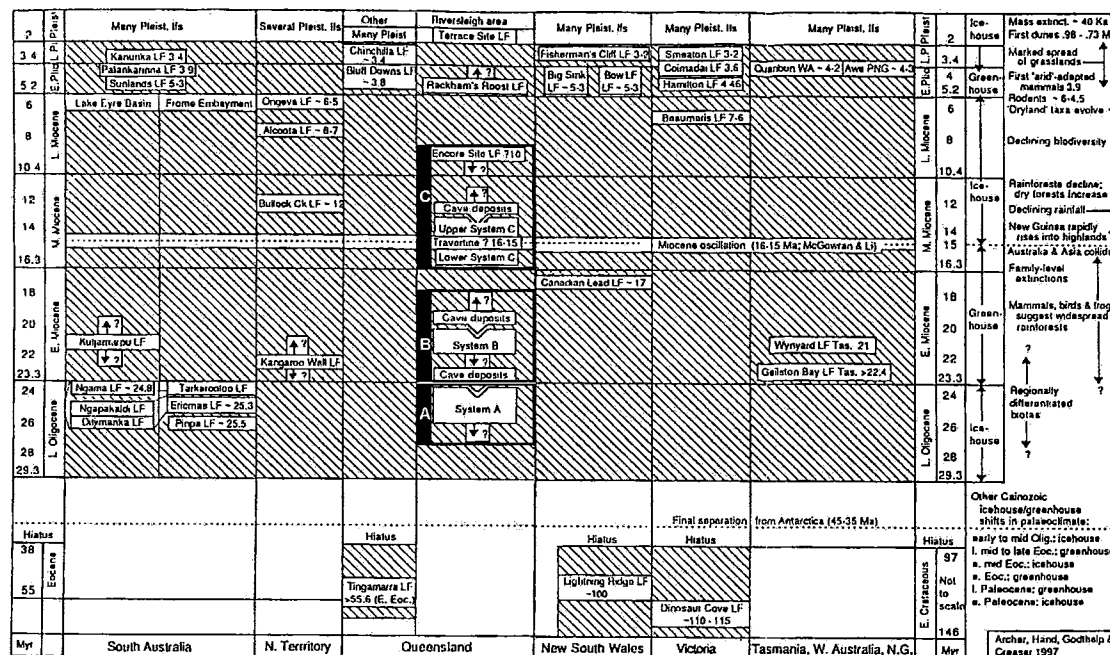
Figure 4.3: Correlation of Riversleigh Faunal Zones A, B and C (='Systems' A, B and C) with other Australian Tertiary mammal faunas. After Archer *et al.* (1999).

sensu Holland *et al.* (1978). Unlike depositional phases (and 'Systems'), faunal zones are distinguished only by the taxonomic composition of vertebrate faunas and are not diagnosed using geological criteria.

Both of the concepts of 'phase' and 'faunal zone' replace complimentary aspects of the 'System' terminology because phases are events characterised by a combination of geological and faunal features, and zones are time periods defined by faunal biocorrelation without the use of geological characters. These relationships are illustrated in Figure 4.1.

Distinction of faunal zones from depositional phases is important because a depositional phase may contain more than one faunal zone or a faunal zone could transcend more than one depositional phase. The term *zone* in this biostratigraphic context does not denote a physical or stratigraphic distribution in a geological section, but rather a *temporal* one only.

Myers (2002) used classification and ordination analyses to resolve distinct groups within a number of representative local faunas from Riversleigh. These groups were defined primarily by the presence/absence of particular taxa and suites of characteristic species, and indicated possible temporal and/or ecological affinities between related faunas. These groups generally conform to the 3-stage 'Systems' concept of Archer *et al.* (1989, 1994, 1997) and can be interpreted as palaeocommunities of penecontemporaneous local faunas that form a robust basis for the concept of temporally distinct faunal zones at Riversleigh (Figure 4.2). Patterns that might be related to evolutionary and/or environmental changes over time have also been recognised in certain groups of middle Tertiary mammalian taxa from Riversleigh including diprotodontids (Black 1997a, Murray *et al.* 2000), balbarid and macropodid kangaroos (Cooke 1997a) and phalangerids (Crosby 2002a).

The relationships of Riversleigh faunal zones with 'Systems' are illustrated in Table 4.1, and the correlation of Riversleigh faunal zones (following 'Systems') with other Australian Tertiary mammal faunas is illustrated in figure 4.3.

4.1.1 Proposed new terms referring to tufa and travertine formation and their depositional environments

There is currently no term in use that refers to the processes and environments that form tufaceous lithologies. The terms *tufagenic* and *tufagenesis* are proposed to refer to environments and processes (tufagenic) that form tufaceous lithologies (tufagenesis) as defined above and described below.

The term tufagenic is not diagnostic, but descriptive, and may be used broadly to refer to the processes and environments related to the formation of tufaceous lithologies, in the same way as other descriptive terms; for example 'pedogenic' refers broadly to certain geological processes related to the surficial environment, including formation of surficial deposits and soil. The term is intended to replace cumbersome phrases such as 'tufa and travertine forming environment' and 'tufaceous deposit forming'. Similarly, the term tufagenesis replaces phrases such as 'tufa and travertine formation' and 'tufaceous deposition'.

4.2 Terrestrial carbonates: origins and diagnosis

Gierlowski-Kordesch (1998) recognised seven sedimentary origins for non-marine carbonates:

1. Clastic fluvial/lacustrine (transported) carbonates (also including some forms of tufa).
2. Carbonate deposits formed by localised springs (i.e. tufa and travertine).
3. Carbonate deposits formed from groundwater (i.e. hydrothermal) discharge (i.e. travertine).
4. Pedogenesis in dry environments and by processes associated with movement of groundwater (i.e. calcrete).
5. Biochemical precipitation in undersaturated aqueous environments due to fluctuating conditions (i.e. varves).
6. Cave deposits (i.e. speleothem).
7. Eolian deposits.

Freytet (1973) established idealised diagnostic sequences for clastic carbonates and carbonate alluvial fan deposits were classified by Nickel (1985; see Figure 4.4). Characteristics, facies distributions and origins of certain fluvio-lacustrine deposits were described by Freytet (1973), Nickel (1982, 1985), Ordóñez and Garcia del Cura (1983) and Gierlowski-Kordesch (1998). Lacustrine carbonate facies and depositional settings were recognised and classified by Platt and Wright (1991).

Clastic fluvio-lacustrine (including alluvial) carbonates are the most common terrestrial carbonates and can be characterised by the following:

1. The presence of cross-beds, ripple-marks and other bedding and depositional structures that provide diagnostic proof of energetic flow (Freytet 1973, Nickel 1985, Gierlowski-Kordesch 1998).

2. The presence of facies and combinations of facies with distinctive lithologies representing channels, levees, beaches, bars, floodplains and fan environments including conglomerates, gravels, sands, muds, silts, clays and evaporites (Freytet 1973, Nickel 1982, Nickel 1985). Facies changes are usually abrupt (Freytet 1973).

3. These facies are often truncated by unconformities, exposure surfaces (i.e. oxidised, desiccated), and evidence of bioturbation from roots and/or burrowing (Freytet 1973, Nickel 1982).

4. Facies comprised of varying particle size (i.e. poorly sorted), particularly channel deposits, usually exhibiting normal grading (Nickel 1985).

5. The presence of oncoids, oncoidal tufa and stromatolitic microphytic tufa that indicate energetic flow (Freytet 1973, Ordóñez and Garcia del Cura 1983, Nickel 1982, Nickel 1985).

6. In the case of fluvial systems including alluvial fans: areal distribution of clastic material with coarser material proximal to the source and finer material distal from the source (Nickel 1985).

7. In the case of lacustrine settings: a characteristic areal distribution of high/low energy marginal and high/low energy basinal facies that reflects lake basin morphology (Platt and Wright 1991).
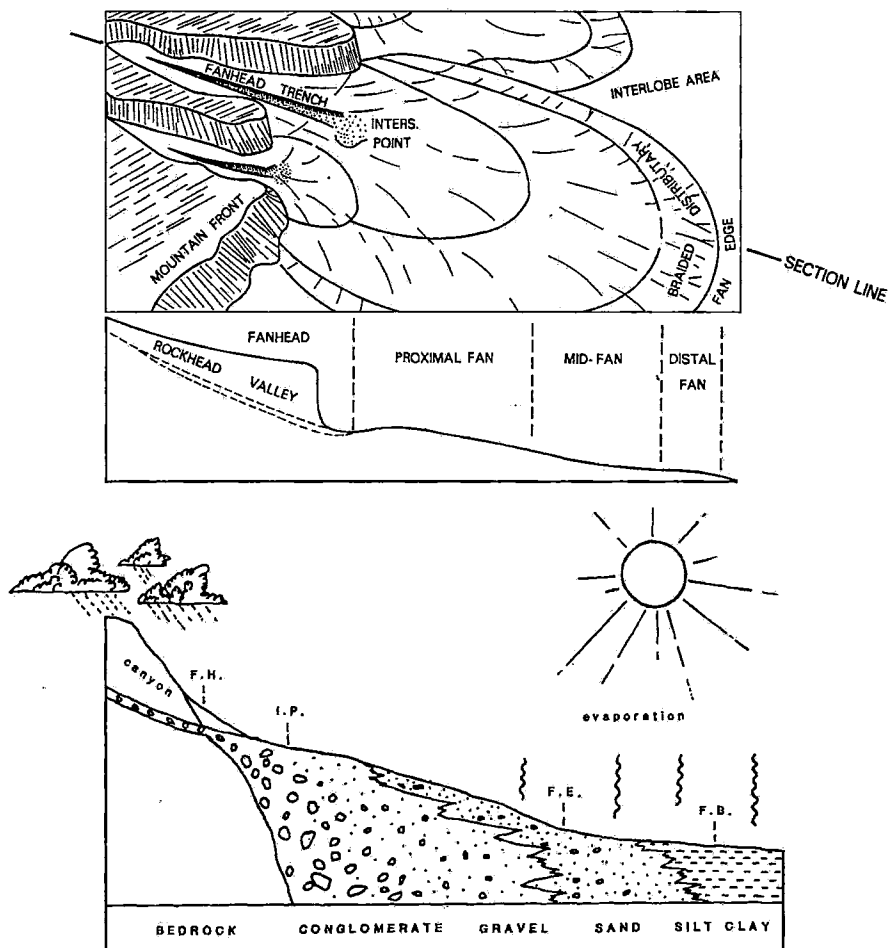
Figure 4.4: Alluvial fan model, showing distribution of major structural elements and lithofacies. Flow energy and clastic particle size decreases distally from the fan head. Conglomeratic deposits are proximal to the fan head. The alluvial fan model of Megirian (1992) is based on this type of depositional system. From Nickel (1985).
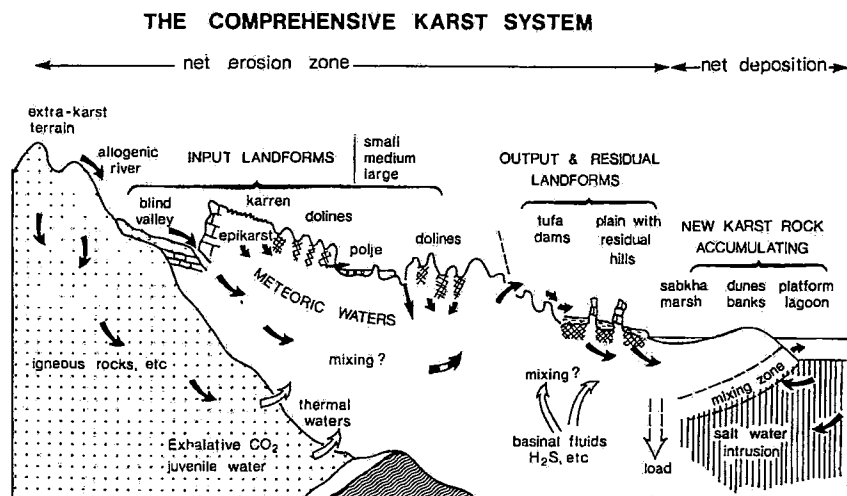
Figure 4.5: Summary of processes and features occurring in karst systems. From Ford and Williams (1989).

35

8. In smaller basins with high carbonate source content, carbonate can occur throughout the system (Gierlowski-Kordesch 1998) whereas in larger systems carbonate increases in concentration toward distal areas (Nickel 1985, Gierlowski-Kordesch 1998).

9. The lithology of the source area is represented throughout the system. A change in the proportion of carbonate to non-carbonate composition of deposits reflects a change to the source of clastic material (Gierlowski-Kordesch 1998).

10. Evidence of pedogenic processes influencing the diagenesis of sediments (Freytet 1973, Nickel 1985, Drysdale 1995, Gierlowski-Kordesch 1998).

While they usually occur in fluvio-clastic environments, tufagenic systems can exert considerable influence over flow and depositional processes and can produce characteristic lithologies and facies distributions. Because of their relevance to the interpretation of the Riversleigh Tertiary geology, tufagenic processes are discussed in more detail below in Section 4.4. Similarly, cave deposits are also discussed in more detail below Section 4.3.

Calcretes (caliche) are powdery to nodular to highly indurated carbonates formed by the displacive and/or replacive introduction of carbonates into soil, rock or sediment primarily in the vadose zone, and are found mainly in arid or semi-arid regions (Flügel 1982, Goudie 1983). Hardpan is a particularly dense form of laminar calcrete. Characteristic features that distinguish calcrete from other terrestrial carbonates include authigenic laminar and concentric structures, brecciated and corroded grains, replacement of original fabric - including quartz - with massive micrite and calcite, casts of roots and burrows and characteristic vertical profile patterns (Read 1976, Flügel 1982, Goudie 1983). Because pedogenic processes contributing to calcrete formation alter sedimentary carbonate deposits by modifying or destroying primary structures, sedimentological diagnosis of primary deposits may be hindered (Nickel 1985, Gierlowski-Kordesch 1998).

Eolianites are composed of windblown particles, usually ooids and skeletal grains, bonded by calcitic granular cement that can exhibit structure related to particle sorting, cross-bedding and may contain palaeosols and fossils (Flügel 1982).

4.3 Karst systems: development, depositional processes and environments, landforms and terrain evolution

Karst processes, including speleogenesis, hydrogeology, terrain development and depositional processes have been covered by extensive literature. Aspects of karst systems (Figure 4.5) that are significant with regard to this work are:

1. Processes that generate depositional environments and generate characteristic facies in which fossils may be preserved. These processes include speleogenesis, cave deposition and tufagenesis.

2. Processes of landscape evolution that generate patterns of landform development and characteristic surface features. These processes include denudation, sequential landform development, disruption of surface drainage and exposure of cave deposits.

The distribution of these processes (and their output products) in the karst profile is related to the position of the vadose and phreatic zones. Karst systems developing as a result of these processes can be complex, and interpretation of stratigraphic relationships difficult. In a karst profile, dissolution and deposition can occur simultaneously at different levels, or at the same level at different times. Traditional concepts and approaches to interpretation and stratigraphy such as the principles of superposition and basin infill should be applied with caution to the interpretation of karst systems.

4.3.1 Speleogenesis and cave depositional processes

Because the development of dissolutional drainage systems is a key process in karst, Klimchouk and Ford (2000a:47) regarded karst as "... a function of speleogenesis". Aspects of dissolutional drainage systems in karst that are relevant to this work include:

1. Processes and patterns of cave formation
2. Depositional processes in caves

An understanding of these processes is significant to the interpretation of processes and palaeoenvironmental conditions (and changes in those conditions) involved in cave formation and infill, including fossilisation of vertebrate material, in the past at Riversleigh.

4.3.1.1 Speleogenesis: cave formation

Cave formation results from a complex combination of processes and characteristics of a karst system including host rock lithology, depositional history and structure; tectonic activity including faulting and formation of fissures and joints; chemistry and mode of supply of dissolutional fluids. Aspects of speleogenesis and resulting patterns of cave development were modelled and discussed by a number of authors including White (1988), Ford and Williams (1989), Klimchouk (2000), Klimchouk and Ford (2000a, 2000b), Lowe (2000), Osborne (2000), Palmer (2000, 2002).

Klimchouk and Ford (2000b) recognised a number of lithologic and structural factors affecting speleogenesis including the proportion of soluble mineral comprising the host rock (rock purity), the presence of adjacent and/or interbedded deposits with different solubility/hydrogeological properties, the porosity of the host rock, and the presence of structural features including fissures, joints, bedding planes and faults. Variations in these characteristics of host rock can affect the morphology and the distribution of caves formed by dissolution. Generally, cave formation favours lithologies and structures, or a convergence of lithological and structural factors, within host rock where flow of water and rock solubility is relatively high. The inception of speleogenesis can be considered to have occurred when organised laminar flow becomes established locally within carbonate rock, rather than migrational seepage (Lowe 2000).

Klimchouk and Ford (2000b) summarised the typical sequence of diagenetic stages (i.e. in marine carbonates) in the development of karst. The mineralogy and porosity of the host rock are characteristics developed during the formation of the sediment in the *eogenetic* stage. Dynamic depositional conditions producing exposure surfaces and vertical facies changes contribute to structural characteristics (i.e. bedding planes), and subsurface dissolution may occur in relatively susceptible layers. Dissolutional processes occurring at this stage are termed *syngenetic*. The *mesogenetic* stage involves burial of the sediment (i.e. in most cases to great depth for millions of years), resulting in decrease in porosity, dewatering, changes to mineralogical composition and the development of patterns of structural weakness related to the primary structure of the sediment (i.e. fissures). Exposure of the sediment by uplift or removal of overlying rock

occurs in the *telogenetic* stage, resulting in increasing circulation of meteoric water and changes to the composition of fluids within the rock; unloading and stress release affecting patterns of structural weakness; and exposure to weathering. Fissures, joints, faults, fractures and folding developed during mesogenesis and telogenesis contribute to the pattern of dissolutional processes at this time.

Palmer (2000) summarised modes of supply of dissolutional fluid to carbonate host rock (recharge) that can control patterns of cave development. Modes of recharge that are relevant to this work include:

1. Epikarstic recharge by direct meteoric input at the surface.
2. Dispersed recharge by diffuse flow through porous host rock.
3. Point source recharge related to surface drainage systems.

Epikarstic speleogenesis can occur when flow of meteoric water from the surface causes dissolutional widening of fissures or other vertically-oriented structural weaknesses, contributing to the development of solution dolines and caves (Lowe 2000, see Figure 4.7). Klimchouk (2000) modelled the formation of deep vertical shafts without associated solution dolines by epikarstic drainage in karst systems in Central Asia and the Italian Pre-Alps. These shafts exhibit ovate, elongate or complex plan patterns metres or tens of metres in dimension, and can penetrate to depths measuring tens of metres (Figure 4.8). Epikarstic speleogenesis is a vadose process.

Dispersed recharge is more characteristic of young, texturally immature limestone, in which diffuse flow becomes reorganised along major flow paths due to relative differences in solubility of sediment layers, structural weaknesses, and ongoing cementation of surrounding host rock (Lowe 2000). Syngenetic caves may form by this process during eogenesis. Jennings (1968) and White (1994, 2000) described syngenetic cave systems in late Pleistocene sand dunes in which patterns of cave development were controlled by bedding planes, ongoing cementation of the poorly lithified matrix, and the presence of an indurated layer that provided structural support. Caves thus formed tended to be low and horizontally extensive. The vertical distribution of caves in the profile was controlled by the position of the water table.
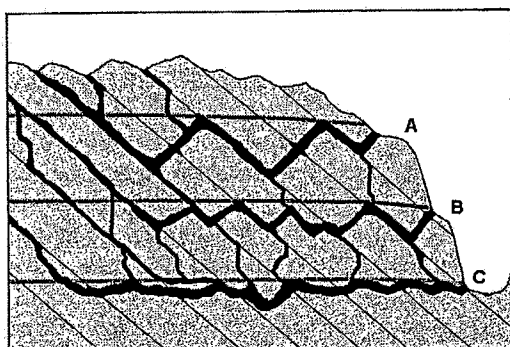
Figure 4.6: Pattern of development of caves in phreatic/lower vadose zones by flow fed by point recharge based on the phreatic cave model of Ford and Williams (1989). Development is associated with the level of the water table and host rock structure. Successive cave systems develop lower in the profile as the water table drops (A, B and C) and each system develops within increasingly restricted spans of relief as the frequency of vertical fissures increases over time and diminishes the effect of structure on morphology. From Palmer (2002).
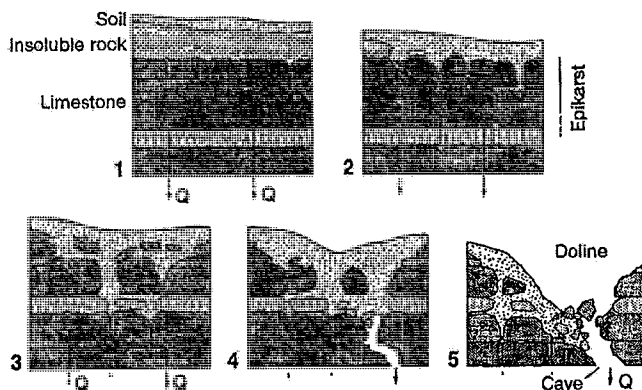
Figure 4.7: Model of epikarstic speleogenesis and associated doline formation. From Palmer (2000).

↓ shaft flow
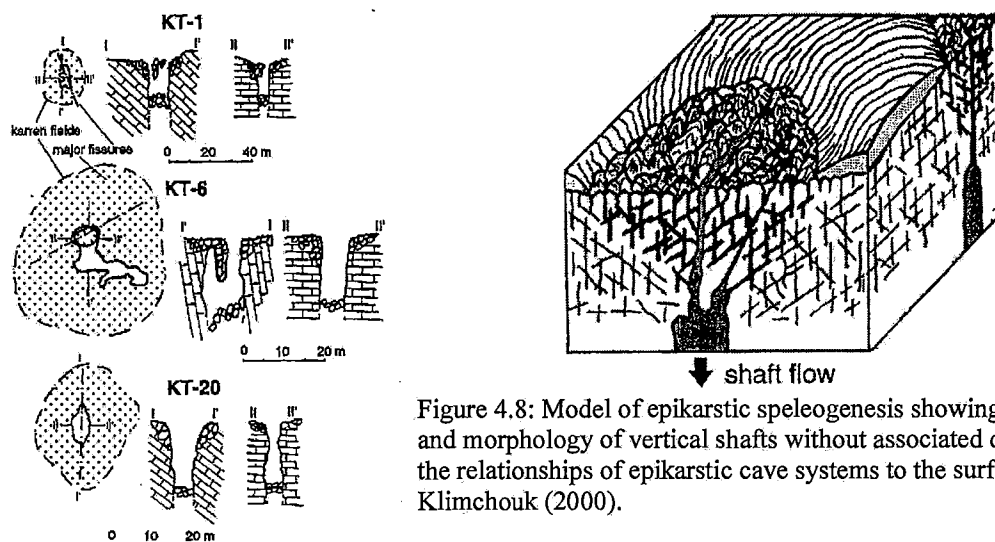
Figure 4.8: Model of epikarstic speleogenesis showing formation of and morphology of vertical shafts without associated dolines, and the relationships of epikarstic cave systems to the surface. From Klimchouk (2000).

CAVE PATTERN		curvilinear branchwork	rectilinear branchwork	anastomotic maze	network maze	spongework maze	ramiform pattern
SOURCE OF AGGRESSIVE WATER	dolines	●	●	●			
	sinking streams	●	●	●	●	•	
	uniform seepage				●	●	
	mixing of 2 sources				•	●	●
	hypogenic		•		●	•	●
DOMINANT STRUCTURES	bedding-plane partings	●		●		•	●
	fractures		●		●		●
	matrix porosity					●	•

Figure 4.9: Generalised relationships between host rock structure, recharge mode and patterns of cave development. Dolines are sinking streams are sources of point recharge. Uniform seepage (diffuse recharge) and porous matrix result in sponge work patterns. From Palmer (2002).

Ford and Williams (1989) described the typical pattern of cave development by underground drainage systems in which phreatic and/or vadose flow contributes to the development and widening of conduits and passages. This pattern of development is typical of point recharge systems where surface drainage flow is captures and develops underground. There is a tendency for speleogenesis to occur at the vadose/phreatic interface (i.e. the level of the water table). This may be reflected in the vertical profiles of cave systems that have developed at different levels as the water table has gradually lowered (Figure 4.6).

Different modes of recharge and their related flow patterns can, in conjunction with the host rock structure, produce different morphologies and patterns of caves. Generalised relationships between host rock, recharge type and cave patterns were summarised by Palmer (2002) and are illustrated in Figure 4.9. Caves developed by point source recharge (i.e. vadose and phreatic flow) can have a tendency to develop long, sinuous patterns of isolated caves or passages forming branching or maze patterns. Sponge work patterns can tend to develop as a result of diffuse flow and epikarstic processes.

4.3.1.2 Cave depositional processes

The stratigraphy of cave deposits can be very complex, because cave environments are dynamic and the occurrence and distribution of depositional and dissolutional processes in caves is related to the internal morphology of the cave, proximity to the external environment, climatic conditions affecting throughput and mineral content of permeating fluids, presence of ponds of water and the position of the water table (i.e. distribution of phreatic and vadose conditions).

Osborne (1984) recognised 3 key features of cave deposits that are significant to interpretation:

1. Primary unconformities between the host rock and cave deposits, which may be complicated by cave morphology, host rock structure and the position of the water table during speleogenesis and subsequent depositional events.

2. Secondary unconformities, which occur between different deposits within the cave may be caused by depositional hiatuses, changes in cave morphology, changes in the input of source material (clastic or as a solute in permeating fluid)

and by dissolution and infill. Different types of deposits may form simultaneously, or at different times, within the same cave environment, depending on prevailing conditions.

3. The subsequent pattern of exposure of such unconformable deposits can produce a variety of complex patterns of vertical and lateral facies changes, including reverse stratigraphy, which may not be readily related to the true chronological sequence of depositional events.

Examples of complexities of the stratigraphy of cave deposits are illustrated in Figures 4.12, 4.13, 4.14.

Cave deposits can be generated within the cave environment, or be derived from an external source. Speleothem, precipitated sediments and sediments formed by breakdown of internal cave structures and materials are generated within cave environments. Material of external origin that enters cave environments under the influence of gravity or water can form clastic sediments. Different types of cave deposits include flow-deposited clastic sediments, turbidites, laminated clays, speleothem, phosphates (derived from guano), talus cones and breakdown deposits (Osborne 1984, 1986, see Figure 4.10).

Osborne (1986) summarised five major depositional environments in which these characteristic deposits tend to form in caves:

1. The upper vadose entrance environment is the dry environment most proximal to the surface in which debris deposits may accumulate under the influence of gravity and of meteoric water wash. Depending on the morphology of the cave entrance, these deposits can form inclined piles or cones with complex bedding and lateral facies changes. These deposits are rich in debris derived from the surface environment including rock fragments, mud, soil and organic debris snails and vertebrate bones. Speleothems are usually poorly developed or absent from this environment.

2. The upper vadose interior environment is further from the entrance environment, which mediates the influence of surface processes in the formation of deposits. Clastic debris deposits can contain a higher proportion of fine sediment and

coarse fragments derived from breakdown of cave interior deposits than those formed nearer to the cave exterior. Speleothems, particularly flowstone and dripstones are a key component of deposits formed in this environment, as are phosphates formed from guano. Pooling of water can occur in this environment, in which localised nothephreatic processes can occur (see below).

3. The lower vadose environment is close to the level of the water table, and may be characterised by intermittent flooding producing laminated deposits and the action of flowing streams which may either erode dissolutional passages or form flow-deposited sediments.

4. Dynamic phreatic environment is characterised by high-energy flow below the level of the water table which may develop and enlarge passages or form coarse deposits with flow-deposited structures.

5. The nothephreatic environment is characteristic of low-energy subaqueous conditions below water table level in which laminated fine sediment and certain forms of speleothem including spar deposits and calcite rafts characteristically form. Occasional influxes of sediment into this environment (i.e. by mass-movement) can form turbidites. Processes occurring in this environment are analogous to those occurring in perched pools in the vadose zone.

Hill and Forti (1997a) provided a classification system based on gross morphology of deposits, although they recognised that petrographic methods provided the best criteria for the classification of speleothems,. Speleothems with very different morphologies can form by processes that are closely related, and thus exhibit similarities in crystal structure. For example, different morphological classes of speleothems that form by physico-chemical precipitation of carbonate caused by the degassing of saturated water (usually as it runs in thin films over a surface) that exhibit similar crystalline form include flowstone, stalactites, stalagmites, oncolites and cave popcorn (White 1988, Ford and Williams 1989, Hill and Forti 1997a). These speleothems usually consist of layers of crystals which share aligned axial orientation (Ford 1988, Onac 1997). This produces a characteristic pattern that is usually clearly recognisable using cross-polarised light (Thrailkill 1976, Figure 4.15).
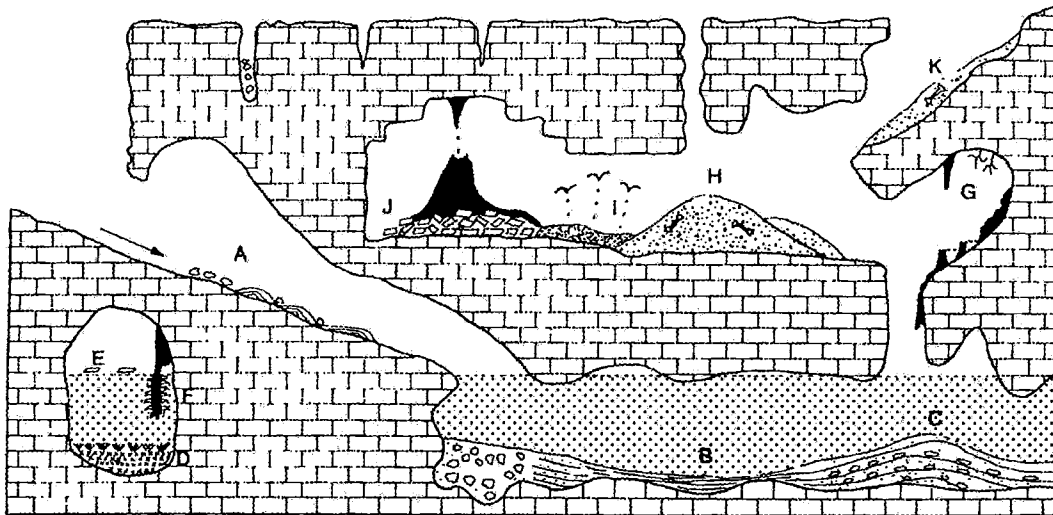
Figure 4.10: Some typical kinds of cave deposits and associated depositional environments. A) Stream deposits can occur in the dynamic phreatic zone and lower vadose zone where dissolutional drainage systems are well-developed. Laminated clays (B), turbidite fans (C), subaqueous deposits (D), calcite rafts (E) and calcite spar deposits (F) are typical of low energy aqueous conditions in the nothephreatic zone and localised pooled water in the interior vadose zone. Speleothem (G), clastic debris deposits (H), phosphates derived from guano and detrital deposits formed by degradation of interior cave deposits and host rock (J) characterise interior environments in the upper vadose zone, with coarse entrance facies (K) being more typical of the entrance environment, which is directly proximal to the exterior. From Osborne (1986).
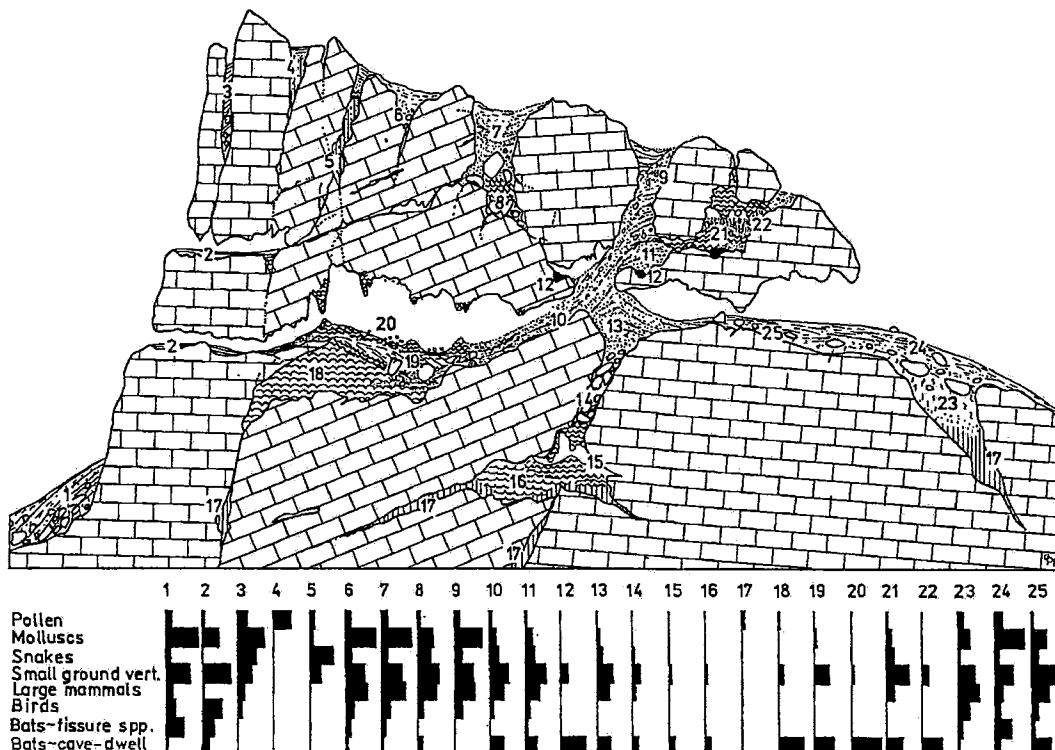
Figure 4.11: Typical distribution of fossil faunal elements in vadose cave deposits. Note that large mammals and birds are best represented in entrance facies and in deposits with direct vertical access to the surface (numbers). Faunas from locations 10 and 13 in particular are examples of diverse faunas found further within the interior environment that, while directly related to a vertical entrance, are likely to outlast those closer to the exterior as denudation progresses. Deposits with higher abundance of cave-dwelling bats and relatively few terrestrial mammals are typical of caves deeper in the interior with restricted vertical access. From Horáček and Kordos (1989).

Clastic cave sediments may be derived from an external source and from the breakdown of cave interiors. Flow deposited sediments (i.e. subsurface drainage system transporting clastics from the surface) can exhibit textural and structural features including cross beds, facies transitions and fining upwards sequences that are typical of fluvio-clastic deposits on the surface (Ford and Williams 1989, Osborne 1986). Turbidites may form when mass movement (i.e. talus cone collapse) distributes material into a subaqueous environment (Osborne 1984). Gravity plays a dominant role in the formation of talus cones, breakdown piles and entrance facies, and can be characterised by complex bedding and lateral facies changes, particularly when the depositional environment is vertical or inclined. Mud in detrital talus sediment can be gradually replaced with spar by seeping water, producing a characteristic texture comprised spherical masses of relatively resilient sediment in a clear spar matrix referred to as 'porous cavity fill' (Osborne 1986). Examples of such complex fossiliferous interior vadose cave deposits in Australia include those at Wellington Caves in New South Wales (Osborne 1983) and Naracoorte Caves in South Australia (Wells et al.1984). Dissolved carbonate in permeating fluid usually supplies cement that lithifies these deposits (Osborne 1986, Hill and Forti 1997a).

Frank (1975) discussed palaeoenvironmental implications of the occurrence of different types of clastic cave sediments that are often associated with speleothem. Entrance facies, collapse breccias, and other gravity-accumulated deposits that usually form without the involvement of water as the depositional medium, can indicate relatively dry conditions. If there is an influx of water into a cave environment, due to relatively wet conditions, ponds may form in which subaqueous sediments may accumulate. Fluvial deposition can occur in cave systems under phreatic conditions.

Because the presence of speleothem in cave deposits indicates that water was present in the system, the implications for palaeoenvironmental conditions are dependent upon the other types of deposits that are associated with the speleothem. If flowstone is associated with deposits formed by a lack of water (i.e. entrance facies) then the presence of flowstone could indicate relatively wet conditions when it was formed. If flowstone is associated with deposits formed by excess of water (i.e. ponds, phreatic
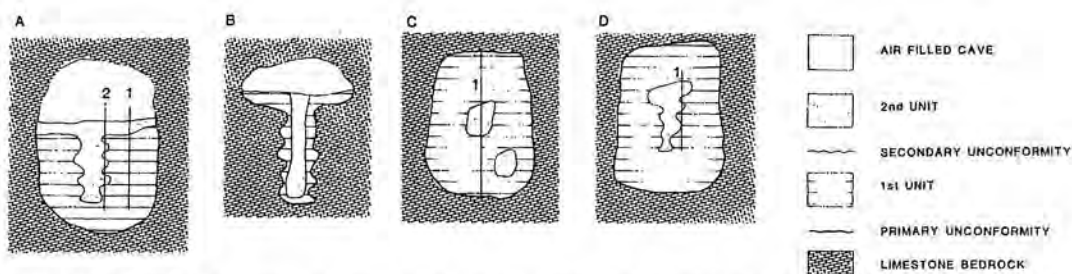
Figure 4.12: Examples of secondary unconformities in cave deposits producing complex vertical sections. From Osborne (1984).
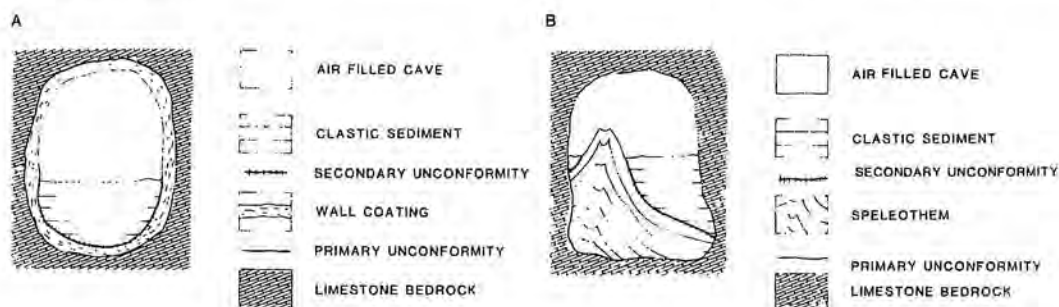
Figure 4.13: Examples of secondary unconformities in cave deposits caused by inclined depositional surfaces and complex morphology of deposits. From Osborne (1984).
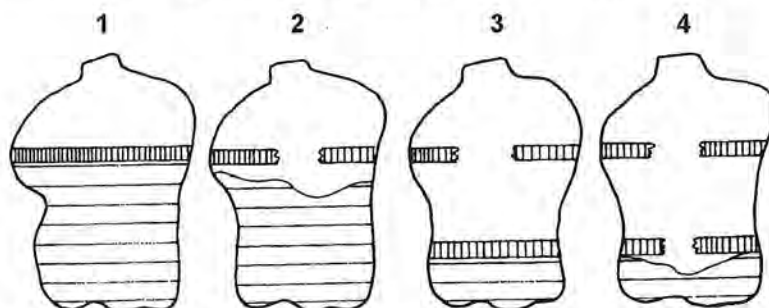
Figure 4.14: Example of 'reverse stratigraphy' caused by successive episodes of dissolution subsequent deposition at lower levels in the profile, producing a vertical sequence to which the principle of superposition does not apply. From Osborne (1984).
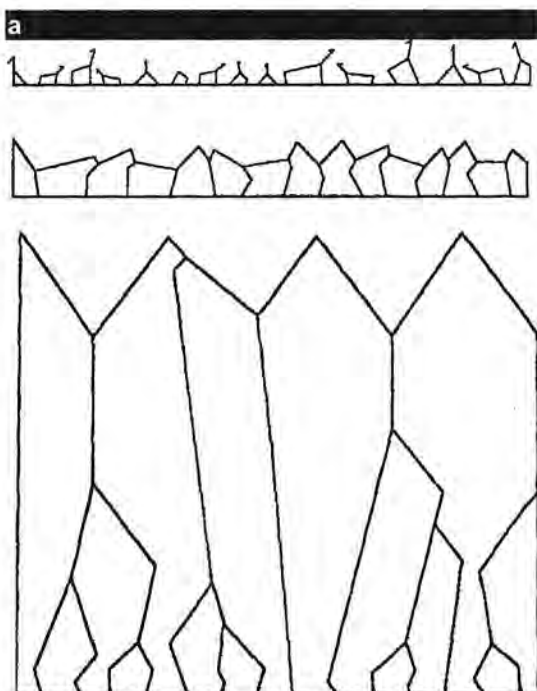
Figure 4.15: Characteristic crystal pattern of calcite speleothems. a) Model of pattern of laminar development giving rise to syntaxial 'palisades' of aligned crystals. From Onac (1997). b) Typical appearance of aligned crystals in calcite speleothem when viewed using cross-polarised light (section normal to axis of stalactite from Colorado, USA, Thrailkill 1976).

sediments) then the presence of flowstone could indicate relatively dry conditions when it was formed.

Depositional environments in caves can favour the preservation of vertebrate fossils, depending on interior and exterior conditions in much the same way as different types of cave deposits. While taxa that inhabit caves (i.e. bats) can tend to be relatively well-represented in some cave fossil assemblages, the representation of other taxa may vary with the cave morphology and proximity of the cave to the surface. Cave deposits formed deeper within caves tend to contain fewer fossils (Bosák 2002). Horáček and Kordos (1989) showed that under typical circumstances (presumably based on sampling of European cave deposits) small terrestrial vertebrates and large mammals tend to be better represented in deposits formed by direct input from the surface (i.e. fissure-fills, talus cones and entrance facies) whereas inner cave deposits tended to be characterised by relatively few vertebrate fossils and higher proportions of cave-dwelling bats (Figure 4.11).

4.3.2 Karst terrains

The formation of dissolutional drainage systems in soluble rocks can influence the development of characteristic landforms at the surface. Processes involved in the formation and development of karst terrains and their characteristics have been discussed in detail by a number of authors including Jennings (1971), and White (1988) and Ford and Williams (1989).

In brief, key aspects of karst terrain development that are relevant to this work include:

1. Karst terrain development is a natural outcome of weathering of carbonate terrains that exposed to the sub-aerial environment because they are relatively more susceptible to chemical weathering and speleogenesis.

2. Because chemical rather than physical weathering is dominant, the entire exposed surface of a karst terrain is subject to corrosion by the processes of sub-aerial exposure (i.e. meteoric water). This process, called denudation, results in gradual attrition of the entire terrain surface. The susceptibility of the host rock to can also accelerate erosional processes, such as valley development.

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3. The chemical weathering process produces characteristic solution features including sculpting of surface features (i.e. rillenkarren, kamenitza), surface fissuring (i.e. grikes, kleftkarren) and closed depressions (i.e. solution dolines). In conjunction with dissolutional drainage systems, these features can play an important role in the processes that shape karst landscapes.

4. Parts of the surface environment in karst terrains can become relatively dry as the terrain matures because the epikarst keeps the surface well-drained of meteoric water and watercourses can flow through dissolutional drainage systems under the ground. Features related to this that are common in karst terrains include lack of running surface water and dry valleys, blind valleys and draw downs.

5. The basement of the karst terrain may be either the water table or an underlying layer of less-soluble rock. The position of the water table in karst is thus significant, since the majority of weathering processes and related landform development occur in the vadose zone and epikarst, where meteoric water draining down to the phreatic zone transports dissolved carbonate away from the surface.

4.3.3 Patterns of development of karst terrains

The concept of sequential patterns of karst terrain development was first recognised by early workers including Grund (1914, in Ford and Williams 1989, Ahnert and Williams 1997). The role of topographic variation at the surface caused by preferential dissolution of the host rock was recognised as a 'template' that controlled dissolution and drainage, resulting in the development of characteristic landforms (Figure 4.16).

Kaufmann (2002) used topographic modelling to show that denudation plays a key role in carbonate attrition which occurs at twice the rate of non-carbonates in terrain dominated by a fluvial system, resulting in a characteristic pattern of landform development in carbonate (Figure 4.17). Rapid deepening and widening of valleys results in the generation of complex highly-variable terrain patterns characterised by sinuous gorges, residual outliers and there is a significant overall loss in surface elevation due to denudation. This pattern of development was compared to the
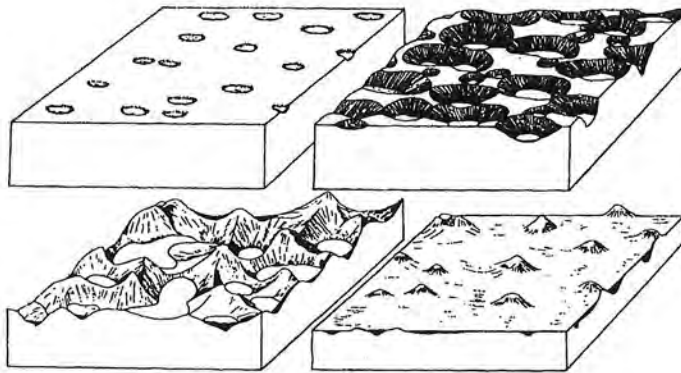
Figure 4.16: Sequential model of the evolution of karst terrain by the development and expansion of dolines by Grund (1914), reproduced from Ahnert and Williams (1997).
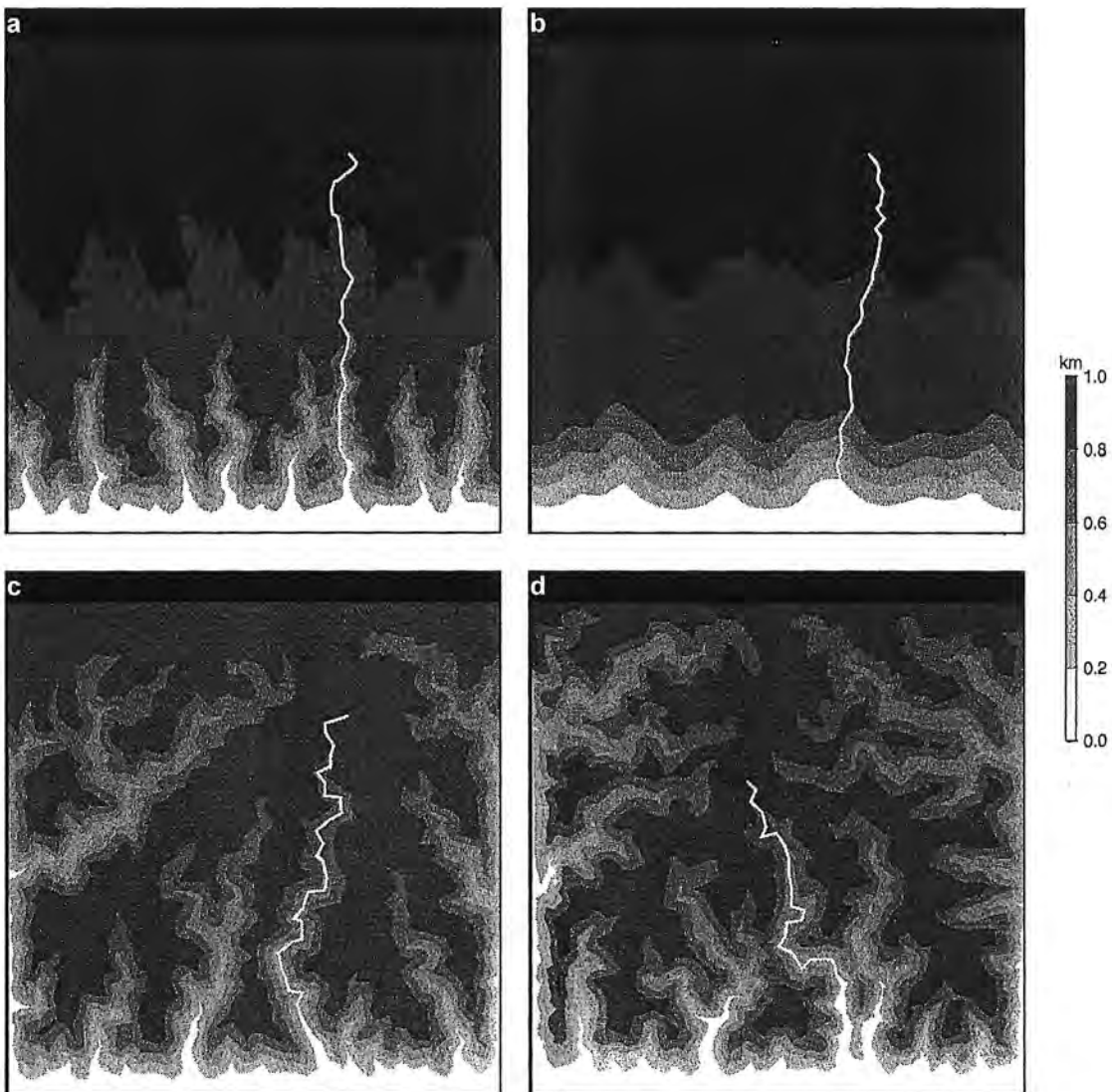
Figure 4.17: Models of patterns of landscape development controlled by a fluvial system. a and b show pattern of landform development in sandstone. c and d show pattern of landform development in carbonate. Note development of topographically variable terrain with residual outcrops and the lower overall relief due to denudation. The deepening of gorges is also much more rapid than in sandstone. The landform development pattern in carbonate has similar morphology to carbonate terrains in France. From Kaufmann (2002).

topography of the Grandes Causses in France, which is characterised by rivers running through sinuous gorges between plateaux undergoing lowering by denudation.

Williams (1983) showed that in young karst landscapes, differences in surface drainage through the epikarst and the position of the vadose/phreatic boundary cause differential corrosion that result in the formation and widening of solution dolines (Figure 4.18). Solution dolines other topographic low-points can exert considerable control over the distribution of the effects of chemical weathering because the interior downslope provides focus for runoff, while areas between depressions experience relatively less corrosion and attrition. As a result, basement level tends to be reached first within depression interiors that subsequently expand laterally.

Williams (1970, 1971) considered how these processes of doline development and expansion contributed to the evolution of topographically variable (polygonal) karst patterns in New Guinea (Figure 4.19) and showed how these patterns could evolve either from a pattern of solution points that is randomly distributed, or related to the form of an initial surface drainage system (Figure 4.20).

In the early stages of karst terrain development, landform patterns can be influenced by capture of overland flow by subsurface drainage and the resulting domination of solution processes at the surface. Varieties of topographically variable karst landscapes resulting from these processes are known as cockpit, honeycomb or polygonal karst. Sequential evolution of a polygonal karst profile by doline development is illustrated in Figure 4.19. In the later stages of development karst terrains can become dominated by the basement-level corrosion plain, on which inter-doline remnants form hill, tower or cone karst outliers.

Using mathematical modelling of landscape development, Ahnert and Williams (1997) showed that solution doline development can predictably occur during the early stages of karst terrain evolution, resulting in the formation of deep dolines that produce a topographically variable polygonal-type karst landscape. They showed how certain parameters such as surface runoff processes and basement level affect the morphology and development of dolines and inter-doline areas to eventually produce a variety of
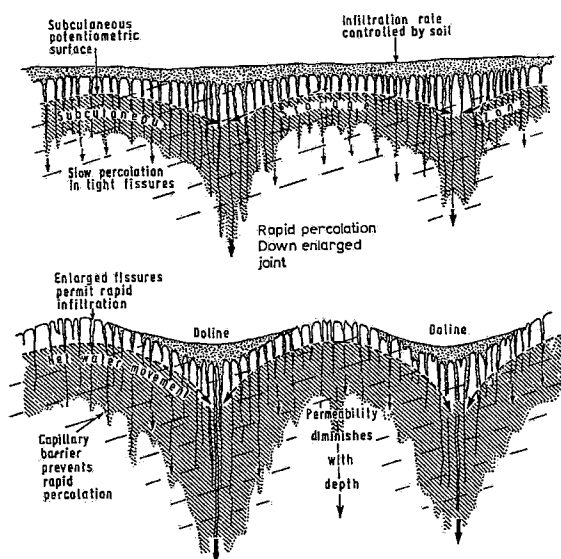
Figure 4.18: The role of vadose and phreatic processes in the development of solution dolines in the epikarst. Surface water flows vertically from the surface to the water table and then moves laterally to zones of high permeability. From Williams (1983).
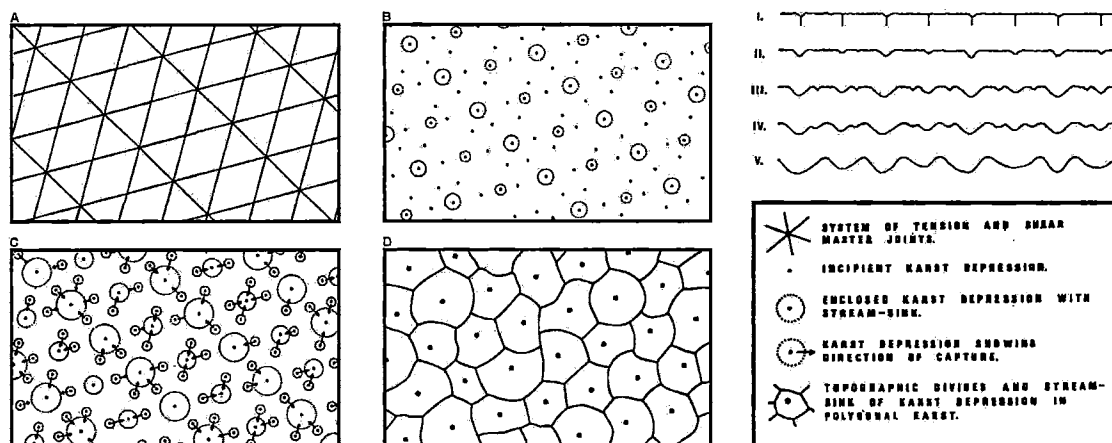
Figure 4.19: Stages in the evolution of polygonal karst terrains by development and expansion of solution dolines in a young karst terrain. A complex topographically-variable terrain results from the initial state of a regular joint pattern. From Williams (1971).
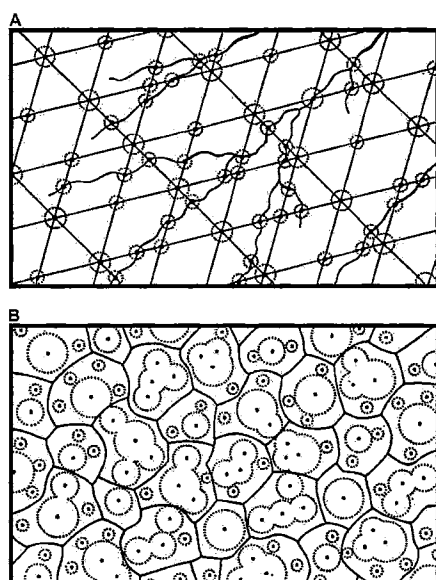
Figure 4.20: Model of polygonal karst terrain development influenced by captured surface drainage pattern. From Williams (1971).
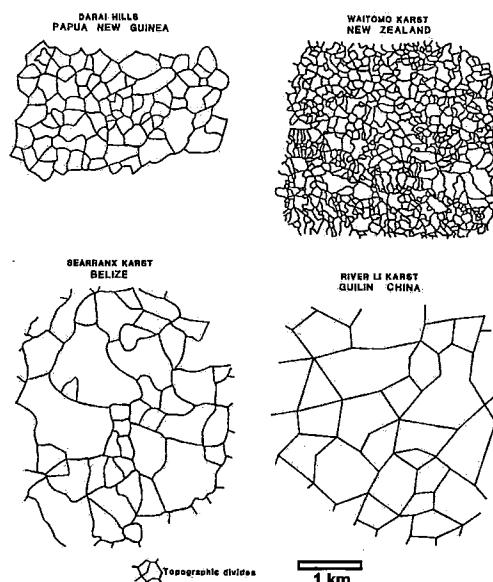
Figure 4.21: Patterns of polygonal karst terrains from Belize, China, New Zealand and Papua New Guinea. Topographic divide = inter-doline crest, from Ford and Williams (1989).

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mature karst landforms that occur in modern karst landscapes including hills, cones and towers (see Figure 4.22). There are several key issues clearly illustrated by this work:

1. While different parameters can produce different landform morphologies in mature karst terrains, the resulting sequence and morphology of karst development tends to be generally similar, especially in the early stages.

2. The development of high relief (i.e. solution doline-dominated) polygonal-type karst can characterise the early stages of karst development, during which deep dolines that reach basement level form.

3. As these karst terrains evolve, the low points are corroded more than the high points. In other words the high-points remain high, while the low-points experience greater degrees of corrosion and erosion and remain low.

4. Denudation plays a significant role in lowering the entire landscape surface at all stages of karst development.

5. Structural parameters (i.e. geological properties, particularly differences in solubility that can be distributed according to joint patterns, or by random variability) and topographic parameters (i.e. existing surface landform) are more important than climate (principally rainfall) in determining the pattern of doline development and the types of landforms produced at maturity (such as cone, tower, etc).

6. Climate (principally rainfall) is more important in determining the rate of karst development.

Polygonal karst is often associated with young carbonate terrains in humid climates, particularly sub-tropical or tropical climates, because precipitation and warm temperatures are important factors that affect the rate of corrosion and doline formation (Ford and Williams 1989, Ahnert and Williams 1997). Polygonal and cockpit karst occurs in many areas around the world including the Darai Hills in Papua New Guinea; the Waitomo karst in New Zealand, Guilin in China, the Malaysian Peninsula in Southeast Asia, the Serranx Karst in Central America and in Jamaica in the Caribbean (Williams, 1971, 1972, Crowther 1982, Ford and Williams 1989, Ahnert and Williams 1997). Examples of patterns of polygonal karst terrain patterns are illustrated in Figure 4.21. Mature karst terrains with characteristic residual tower and cone landforms include the Guizhou Plateau and Guangxi in southern China, the Gort Lowland in

Model KARST1

Model KARST2

Model KARST3

KARST1, T=0

T=9

T=27

T=45

T=69

T=99

KARST2, T=20

T=50

T=74

T=98

KARST3, T=6

T=9

T=45

T=90
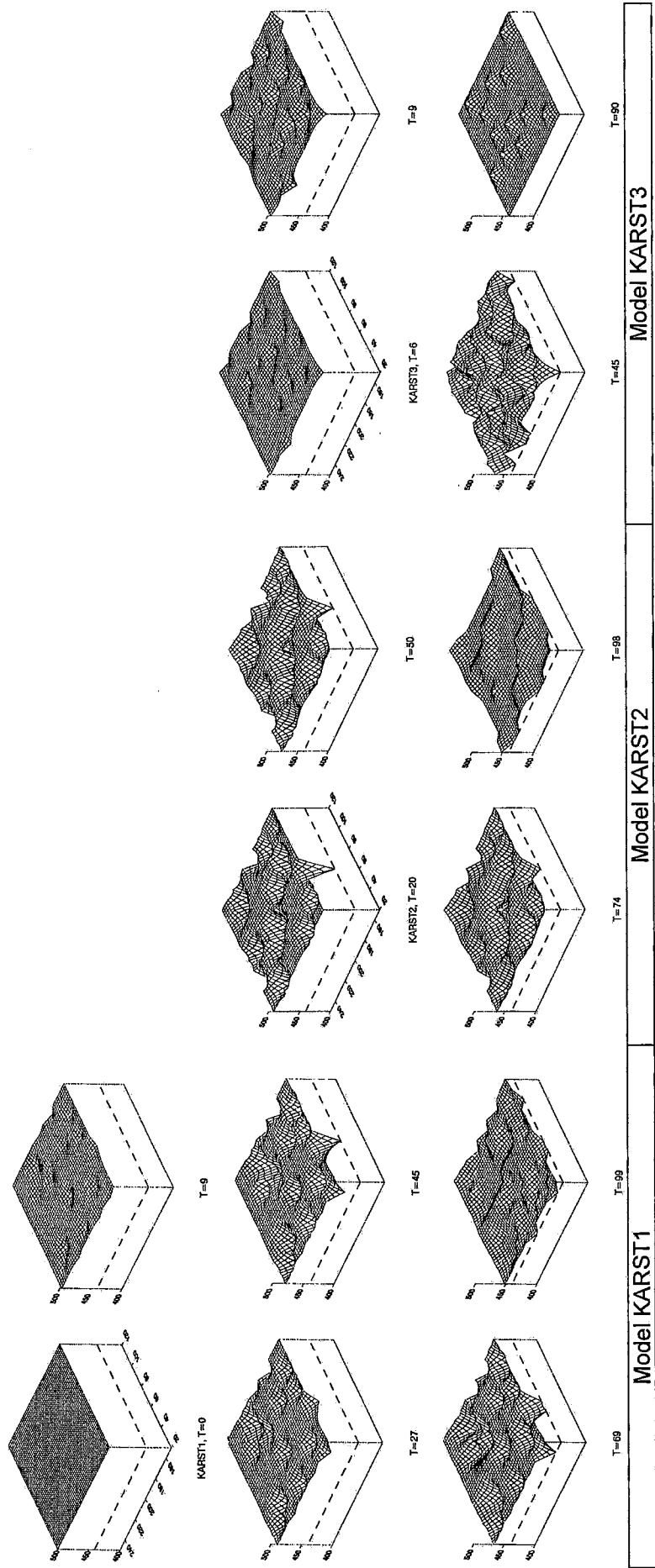
Figure 4.22: Selected models of patterns of karst terrain development showing effects of variation of different parameters in resultant residual landform morphology from Ahnert and Williams (1997). Dispersed residual landforms are generated from a once continuous deposit by differential corrosion and denudation controlled primarily by the development and expansion of solution dolines. Model KARST1 depicts polygonal karst development and residual landforms from the initial state of a sub-level surface with the principal controlling factor being initial random variations in topography. Model KARST2 shows resultant development pattern and residual landforms when the principal controlling factor is initial random variations in solubility of the deposit (primary states similar to KARST1 are not shown). Model KARST3 shows combinations of the effects in the first models with the additional effect of variations in corrosion by differential affects of divergence and convergence of runoff controlled by developing high and low points in the topography, producing residual landforms analogous to cone karst. Residual landforms in these models are comparable to those present in mature karst terrains today, and can be compared to those at Riversleigh. These models demonstrate common sequential patterns of karst terrain development that include the formation of highly variable topography in the early stages of development, the effect of denudation in lowering the entire surface and the manner in which high-points remain high and low-points remain low such that at maturity, residual landforms represent remnants of the previous high-points in the terrain. These models are useful for modelling earlier stages of the development of the terrain at Riversleigh. Horizontal, vertical and time scales (T) are nominal.

Ireland, and the Thousand Hills in Bohal Island in the Philippines (Ford and Williams 1989, Ahnert and Williams 1997).

Application of concepts of sequential patterns of topographic development of karst can be used to model the changes that have taken place during the evolution of the landscape at Riversleigh during the middle Tertiary and the effect of these changes on depositional environments and topography during that time.

4.3.4 Variations in environmental conditions in karst terrains

Karst terrains are often characterised by complex topography and landform morphology that produces a high degree of variation in vegetation and habitat supporting distinctive floras (Crowther 1982, Whitmore 1984). These variations are related to the distribution of drainage processes and surface water, soil types and soil thickness, the distribution of soil cover and exposed rock and types of vegetation in karst. This is relevant to the consideration of processes in karst at Riversleigh during the middle Tertiary and their effects on palaeoenvironments.

Drainage and surface water

Most of the habitats of inter-doline areas, interfluves and other high-points are drier than within dolines, valleys and other depressions (Whitmore 1984), because of the function of the epikarst in draining surface water into the phreatic zone below. As a result, surface water may be absent from karst terrains, or restricted to low points such as doline bases and drainage channels that are at water table or basement level.

Soil type

Soil type has been found to vary directly with topography. Gillieson (1997) recognised three distinct soil types from polygonal karst of the Lelet Plateau in New Ireland: clay in doline bases and lower slopes, clay loam on upper slopes and crests, and mull rendzina in crevices on rocky crests; the latter two were also characterised by the presence of thick root mats also noted by Whitmore (1984) as present in crest environments in Sarawak. Occurrence of clay in doline bases was also noted by Williams (1972) in the Darai karst of New Guinea (Figure 6.7). Crowther (1982) recognised two soil types in karst terrains in West Malaysia, the soil of doline bases and lower slopes being more

acidic than the soil type from upper slopes and crests and noted that these soil types
reacted differently to the effect of precipitation.

Soil thickness and distribution of soil cover and exposed rock

Crowther (1982) found that in West Malaysian karst soil was thicker in doline base and
lower slope areas (>68cm) and achieved minimum surface coverage of 60%, soil in the
upper parts of the topography was thinner (<32cm) and usually achieved less than 50%
coverage, with fissured bare rock exposed on crest-tops and steep slopes. This is similar
to the distribution of soil thickness and coverage in the Lelet Plateau karst, where soil
was thinner (<40cm) and bare rock occurred on occasional exposed crests and on mid-
slope cliffs on longer slopes that can act as a boundary between upper and lower parts of
the profile where soil was thicker (<150cm) (Gillieson 1997).

Vegetation types and variation

Karst terrains support rich floras, including distinctive taxa with a high degree of
endemicity and some taxa may be restricted to limestone terrains (Crowther 1982,
Whitmore 1984). Compared to forest on non-carbonate terrains rainforest in karst may
be less luxuriant (Crowther 1982).

Topography and soil thickness and cover are directly related to the distribution and type
of vegetation. Shrubs and herbs (including crevice plants) inhabit areas of exposed rock
and cliffs (Crowther 1982, Whitmore 1984, Gillieson 1997). Crowther (1982) found
that rocky crests in West Malaysian karst were inhabited by stunted forms of particular
species including *Vitex, Memecyclon* and *Garcinia* that formed a near continuous
canopy, whereas deeper soils of lower parts of the terrain were also vegetated by taxa
including *Hopea, Pentacme* and *Shorea.*

This type of differentiation related to topography and soil was also described by
Gillieson (1997) in New Ireland, where crests and upper slopes, which were
occasionally bare, were dominated by 'oak' (*Castanopsis*) forest and species of
Elaeocarpus, Sloanea and *Cryptocarya*, and doline bases and lower slopes were
characterised by fewer oaks, plus *Pometia, Celtis, Ficus, Psyloxylum, Cyathea* and

Pandanus, as well as the other non-'oak' tree genera above, resulting in a canopy cover of approximately 80%.

Crest environments can provide refuges and conditions that favour certain taxa. In New Guinea, *Nothofagus* forest can occur below the typical montane range on doline crests and karst towers, and species of *Casuarina* can dominate doline crests and upland limestone terrain in Sarawak and New Guinea (Whitmore 1984).

4.3.4.1 Distinction of 'upper' and 'lower' environments

Variations in the distribution of water, soil and vegetation patterns in karst terrains appear to be consistent in different areas. Because differences are directly related to topography, environments occurring in topographically variable karst terrains could be divided into at least two general types: 'upper' crest and upper slope environments, and 'lower' base and lower slope environments. Some characteristics of these environments described above are summarised in Table 4.2.

	'Upper' environment	'Lower' environment
Topography	Crests and steeper upper slopes	Doline bases and gentler lower slopes
Drainage and water	Well drained by solution fissure systems and slopes, relatively dry.	More humid and relatively wet. Runoff and/or surface flow tends to be directed to these environments.
Soil type	More basic, rendzinas in crevices, relatively lower clay content, root mats.	Higher clay content, more acidic.
Soil thickness	Thinner	Thicker
Soil coverage and bare rock	Less soil coverage, exposed rock common on crests, steep slopes and mid-slope cliffs	More complete soil coverage
Vegetation distribution	Exposed rock outcrops dominated inhabited by herbs, shrubs and crevice dwelling plants, vegetation thinner on crests and slopes with scree and exposures, discontinuous canopy.	Vegetation distribution related to more complete soil cover and greater thickness, canopy more continuous compared to crests.
Vegetation types	Certain tree taxa may dominate crests, basal area of trees smaller	Different taxa and may dominate bases and lower slopes, greater diversity of plant taxa

Table 4.2: Comparison of 'upper' and 'lower' environments in topographically variable karst terrains.

'Upper' environments are characterised by relative dryness, thinner soil cover and greater occurrence of exposed rock outcrops. Crests and upper slopes are inhabited by relatively fewer plant taxa that may be better adapted to dryness, and because of the greater occurrence of exposed rock, herbs, shrubs and crevice dwellers may be more abundant and the canopy thinner or more disrupted.

'Lower' environments, including doline base and lower slope landforms, are characterised by relatively higher humidity and wetness and thicker soil with different properties to soil from upper environments. These conditions support a higher diversity of plant taxa, many of which may not be represented in upper environments, and may exclude some taxa that dominate upper environments.

In karst terrains with highly variable topography, complex patterns of adjacent environments may thus occur. The division of environments recognised here, is relevant to the consideration of palaeoenvironmental implications of these patterns discussed later in the text.

4.4 Tufagenic systems: formation and diagnosis of tufa and travertine

Viles and Goudie (1990a) described broad categories of tufa facies and processes contributing to tufagenesis. Pedley (1990) introduced a comprehensive classification of tufa facies and provided models depicting depositional environments in which different tufa facies, combinations of facies and morphologies form. The depositional models were updated by Ford and Pedley (1996), with references to the occurrences of modern and fossil tufas from around the world.

Chafetz and Folk (1984) provided comprehensive description and diagnosis of processes related to the deposition of travertine deposits. For comprehensive examples and references to different forms of modern and fossil tufagenic systems refer to Viles and Goudie (1990a) and Ford and Pedley (1996).

Tufa deposits may be classified according to botanical associations that recognise the macrophytic or microphytic organisms (i.e. algae) contributing to tufa formation and distinguishing them from inorganically precipitated forms of tufa (Viles and Goudie 1990a); geomorphological and hydrological criteria that indicate the effect of flow regime and the morphology of the depositional environment on the morphology of tufa deposition (i.e. cascade, barrage, lacustrine; Viles and Goudie 1990a, Pedley 1990, Ford and Pedley 1996); or by petrological classification by identifying the texture and lithological components of tufa (Pedley 1990, Drysdale 1995, Ford and Pedley 1996).

4.4.1 Diagnosing travertine

Travertine is more commonly associated with thermal springs. Because temperature plays an important role travertine is usually restricted in distribution proximally to the source. The primary mediators of precipitation are bacteria able to withstand conditions that are hostile to other potential organic mediators (i.e. those that form tufa), physical precipitation by turbulence and agitation, and evaporation to a degree greater than that of tufa.

Travertine can be characterised by:

1. Greater homogeneity of texture and composition because of more stable conditions in the depositional environment; a more limited degree of contamination by other lithologies or organic matter because of proximity to the source; a greater degree of purity of the precipitate; a more well-developed crystalline texture and resulting greater density and hardness; the presence of textures formed by bacterial processes (i.e. bacterial 'shrubs' are distinctive).

2. Bacterially-influenced textures are the dominant recognisable organic type rather than algal or macrophytic.

3. Because travertine is usually more dense and resilient, and depositional environments often tend to be more continually constructive than constructive/destructive compared to those forming tufa, travertine deposits tend to build up rapidly over shorter periods of time. They are more likely to show a clear, unbroken depositional sequence in section compared to tufa. Travertine formation tends to be restricted proximally to the source, whereas tufa deposition can be more widespread throughout a tufagenic system.

While a clear distinction can often be made between tufa and travertine, their occurrence or formation is not mutually exclusive because many similar processes are involved. Either may form under similar environmental conditions. While travertine formation can occur in waters up to 90° C, most travertine formation occurs in waters between 5 ° C and 30° C (Chafetz and Folk 1984), which overlaps the water temperature in the majority of tufagenic systems.

4.4.2 Diagnosing tufa

The majority of tufa is formed from water with high dissolved carbonate content in fluvial environments. The primary mediators are photosynthetic organisms (plants and algae), physico-chemical precipitation by turbulence and evaporation. Tufagenesis can occur at any point in a hydrological system when the mineral saturation in the water and the effects of mediating processes are favourable. Examples of petrography of tufaceous lithologies are shown in Figures 4.24, 5.14, 5.15.

Tufa can be characterised by:

1. Heterogeneity of texture and composition because of the presence of varieties of organic and inorganic matter in the (usually fluvial) depositional system that can include mud (micritic or otherwise), sand, rock fragments, lumps of unlithified sediment, calcite rafts, calcite crystals, biologically precipitated carbonate textures and fragments of these, opaque indistinguishable organic matter or precipitate formed under the influence of the presence of organic matter, iron oxides, bone fragments, mollusc shell fragments, irregular voids, air/water bubbles and moulds of macrophytic tissues including roots and stems (see Pedley 1990, Viles and Goudie 1990a, Drysdale 1995). Some forms of tufa can exhibit greater homogeneity, particularly those deposited in low energy conditions (Pedley 1990, 1993, Ford and Pedley 1996)

2. Textures influenced by algae and macrophytes are the dominant recognisable organic textures (see Pedley 1987, 1990, Drysdale 1995).

3. Some forms of tufa are highly porous (open-fabric) and susceptible to induration and infill by calcite either during the tufagenic phase or as part of subsequent processes (see Drysdale 1995, Ford and Pedley 1996).

4. Other forms of tufa can be dense and/or rich in algally-precipitated textures or mud with a high organic and/or iron-oxide content (Pedley 1990, Ford and Pedley 1996).

5. Tufa is susceptible to weathering and reworking because it usually occurs in systems with high destructive potential. Tufa forms in the presence of, and directly influences, dynamic flow and ponding regimes. Tufa may be broken down and reworked due to exposure to the sub-aerial environment, flow erosion and also by processes associated with macrophytic bioturbation and the presence of acidic humus (see Golubić 1969, Pedley 1987, 1990, 1993).

6. Tufa deposits can exhibit characteristic facies distribution indicating tufagenic conditions in settings that may be lacustrine, high-energy flow, or barrage systems (Pedley 1990, Drysdale 1995, Ford and Pedley 1996).

4.4.3 Tufa facies

Pedley (1990) described and classified the principal types of tufa facies. A revised classification of facies based on Pedley (1990) and Drysdale (1995) is provided here.

Viles and Goudie (1990a) found that classifications of tufa facies can be site specific. This was recognised by Drysdale (1995) who devised a revised classification for use at Louie Creek in Queensland by distinguishing intraformational tufa containing a high proportion of reworked tufa ('detrital tufa') from tufa with a high proportion of non-carbonate (i.e. siliclastic) components of external origin ('lithoclastic tufa'). This is significant because the presence of reworked tufa and non-carbonate 'contaminants' have implications for the interpretation of the processes in a tufagenic system and the nature of the depositional environment.

The revised system and nomenclature for use in this work (below) consists of an alternative organisation of classes of tufa facies-types (as described by other authors previously) and alternative (arguably more meaningful) names for some of these classes. This system has been devised for description of facies present at Riversleigh and may not necessarily be compatible with other tufaceous deposits.
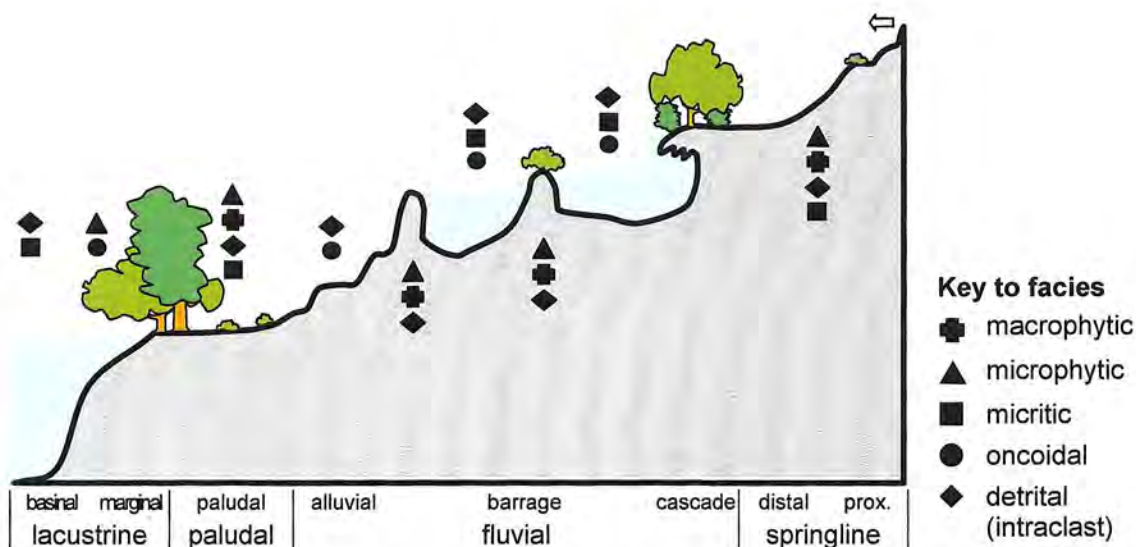
Figure 4.23: Depositional environments of tufa and facies associations.
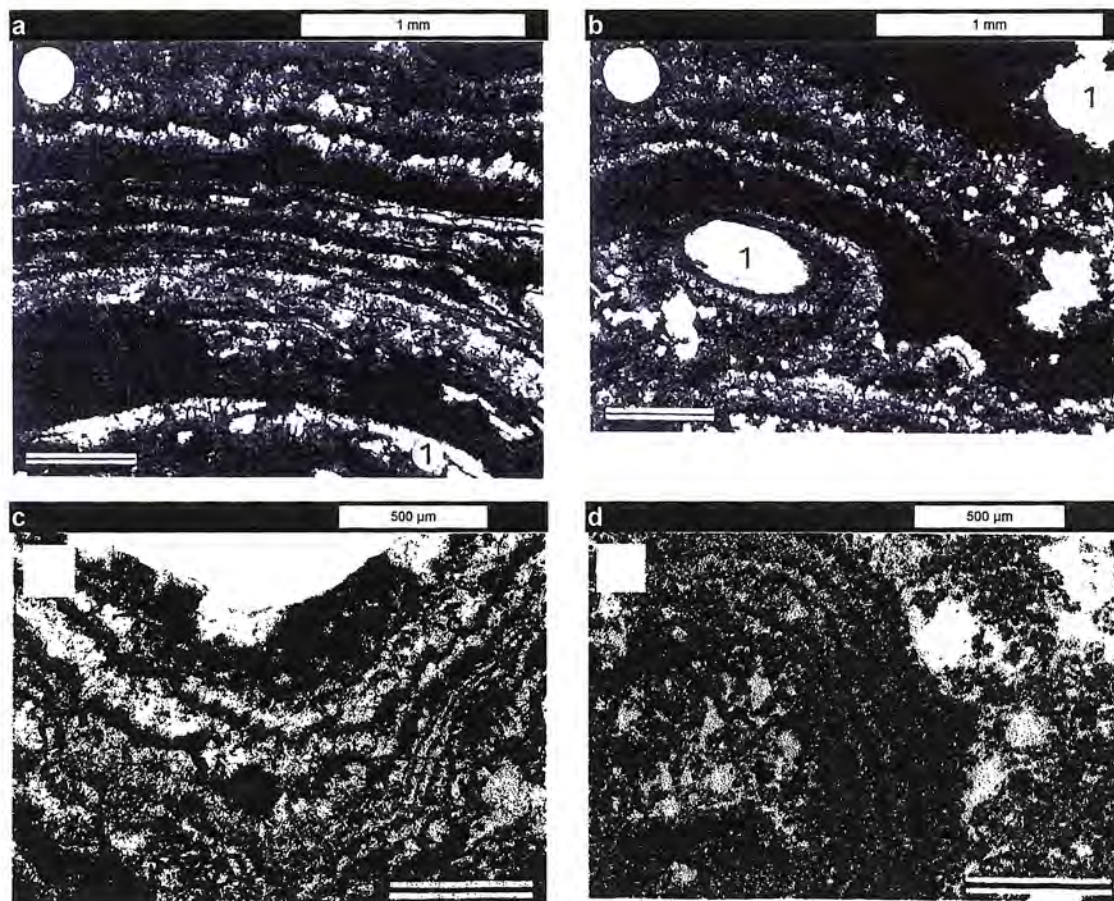
Figure 4.24: Petrography of tufaceous lithologies showing some key lithotextures. a) Isopachous fringe cement encrusting macrophyte tissue structure comprised of alternating layers of calcite and micrite forming a characteristic laminated pattern (Caerwys tufa, Wales, Pedley 1987). b) Chironmyid tube holes with isopachous fringe cements (Caerwys tufa, Wales, Pedley 1987). c) Laminar cement and micrite surrounding an open void at top (Alport Quarry, Lathkill Dale, England, Pedley 1993). d) Laminated cement with clotted micrite textures and open fabric at right of field (Monsal Dale, Wye Valley, England, Pedley 1993).

4.4.3.1 Autochthonous tufa facies

Autochthonous tufa facies are composed primarily of precipitate that has formed *in situ*.

Microphytic tufa

Tufa with texture controlled primarily by algal growth that usually (but not always) exhibits stromatolitic laminated banding or bedding (Pedley 1990, Drysdale 1995) which often reflects environmental or biological changes, such as changes in hydrological setting, physiological growth patterns (Drysdale 1995). This is considered equivalent to phytoherm boundstone of Pedley (1990) and microphytic tufa of Drysdale (1995).

Macrophytic tufa

Tufa comprised of carbonate encrustations around roots, stems, leaves, branches and/or trunks of macrophytes that may be living or dead (Pedley 1990, Drysdale 1995). The fabric is characteristically highly porous and often contains infills of micritic, peloidal or fine intraclast tufa (Pedley 1990). This facies can contain diverse faunas of annelids, gastropods, ostracods and insect larvae (*ibid.*). This is considered equivalent to phytoherm framestone of Pedley (1990) and macrophytic tufa of Drysdale (1995).

Larval tufa

Tufa comprised of encrusted cases, retreats and nets constructed by insect larvae and sometimes pupae, including larval burrow- and cocoon-dominated facies (Drysdale 1995). Larval activity in some instances reworks the original (usually microphytic) facies (*ibid.*)

4.4.3.2 Allochthonous (clastic) tufa facies

Autochthonous tufa facies are composed primarily of components that have not formed *in situ*, however lithification (by ongoing tufagenesis) of the individual allochthonous components does occur *in situ*.

Oncoidal tufa

Tufa fabric comprised of individual and/or cemented oncoids, in which gastropods often form nuclei (Pedley 1990, Drysdale 1995). This facies is often associated with higher

energy-flow in fluvial channels (Ordóñez and Garcia del Cura 1983) and in high-energy marginal lacustrine facies (Platt and Wright 1991).

Micritic tufa

Fine-grained tufa usually formed in low energy environments, is usually structureless in thin section but may exhibit clotted texture and is generally associated with freshwater and terrestrial gastropods, charophytes and ostracods and may fill voids in open-framed tufas (Pedley 1990). Tufa comprised of peloids consisting of polynucleate masses 10-70um in diameter that can grow or compact to form clotted textures (Pedley 1990).

Intraclast tufa

Heterogeneous tufa with fabric composition dominated by reworked tufa fragments (Pedley 1990). Molluscan faunas are common and there may be inter-bedded microphytic tufa (Drysdale 1995). This facies may accumulate in fluvial channels or in low energy environments (Pedley 1990). Intraclast tufa composed primarily of reworked macrophytic tufa has been classified as phytoclast tufa by Pedley (1990).

Extraclast tufa

Heterogeneous tufa with fabric composition dominated by non-tufaceous sand- to cobble-sized lithoclasts, typically transported rock fragments that are not products of the tufagenic regime (extraformational). Drysdale (1995) distinguished this facies from calcrete on the basis of environmental setting, colour and petrography (i.e. presence of algal laminae, casts left by decay of plant material in tufa). This facies type often contains molluscan fauna (*ibid.*) and is otherwise considered petrologically and depositionally equivalent to lithoclast tufa of Drysdale (1995) and, aside from the presence of lithoclasts, to detrital tufa of Pedley (1990).

Tufaceous palaeosols

Soil horizons may be preserved within tufaceous deposits because of the dynamic conditions of the tufagenic depositional environments and thus may be considered tufa facies (Pedley 1990). These palaeosols often contain fragments of tufa (*ibid.*).

Intraclast and extraclast tufa may be referred to collectively as detrital tufa.

4.4.4 Tufa depositional morphology and tufagenic environments

Although they usually form in clastic systems, tufa deposits can differ fundamentally from fluvio-lacustrine clastic carbonates. Tufagenic systems are self-regulating, can generate lithified carbonates *in situ*, accumulation can exceed destruction even under conditions of high-energy flow that would erode and transport non-carbonate sediment, precipitated clast size can vary inversely to flow rate, and siliclastics may be excluded from flow systems and deposits (Ford and Pedley 1996).

Tufagenesis can therefore occur in locations that are not restricted by basin morphology and would otherwise not support clastic sedimentation. Cascade tufas, which can form spectacular deposits at waterfalls and cliff edges, illustrate how tufa can form in environments in which other forms of deposition do not occur (see Viles and Goudie 1990b). The influence of water flow in encouraging degassing and precipitation is a primary factor in the formation of these deposits and tufa barrages (Viles and Goudie 1990a, Pedley 1990, Drysdale 1995).

Figure 4.23 outlines the major morphological types of tufaceous facies and the environments in which they form.

Ford and Pedley (1996) described 5 types of tufagenic environments:

1. Fluvial environments that are divided into two categories:
   a. Braided fluvial systems dominated by oncoidal tufa, microphytic tufa also with detrital lime muds.
   b. Barrage systems are characterised by dams that obstruct flow and form lake and pond environments immediately upstream in which low-energy depositional conditions occur. The barrages may often be formed of microphytic or macrophytic tufa and barrage basins fill with micritic and detrital tufa (Figure 4.26, 4.27, 4.29). These systems are usually incised and reworked, often when the upstream barrage basins are filled with deposits (see the cycle of Golubić (1969), Figure 4.25). A basal facies comprised of preserved surface material may occur at the base of barrage infill deposits, see Figures 4.27, 4.29.
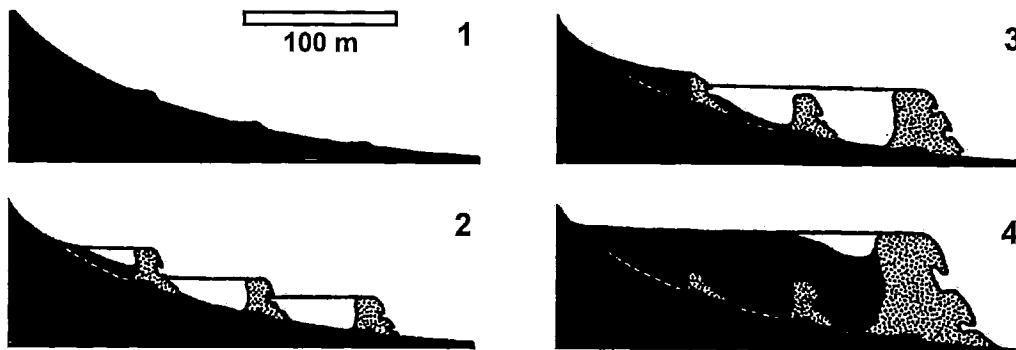
Figure 4.25: Model of cyclic processes of formation and infill of fluvial barrage systems. Incision follows infill of the terminal barrage basin after stage 4. From Golubić (1969).
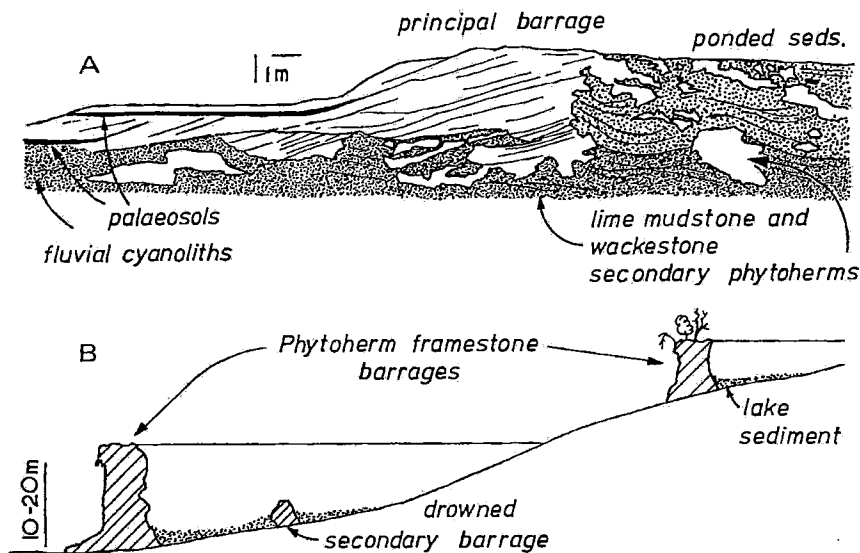
Figure 4.26: Profiles of fluvial tufa barrage systems. A) Section through the late Quaternary system at Caerwys in Wales showing the structure of the main barrage (macrophytic tufa) and the pond fill comprised of lime mudstone and wackestone rich in oncoids, gastropods, and drowned smaller barrage structures. The deposits downstream of the main barrage are rich in detrital tufa and oncoids. B) Section through the recent barrage system at Plitvice in Croatia. Large barrages form rapidly generating deep lake environments in which lacustrine sediments slowly accumulate. From Pedley (1990).
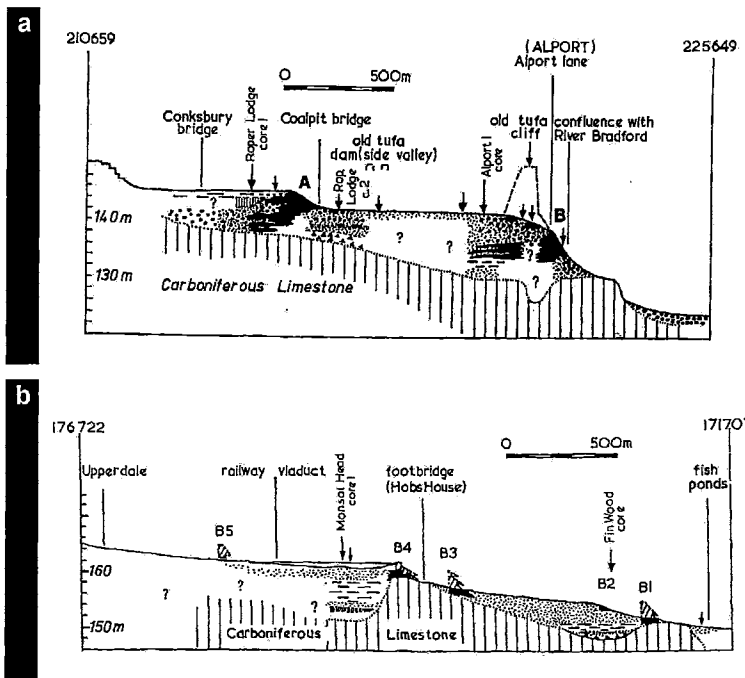
Figure 4.27: Profiles showing stratigraphy of fluvial barrage systems in Eastern England. a) Lathkill Valley system, showing barrage pond deposits comprised of micritic, detrital and oncoidal tufa. Note the basal facies comprised of in situ reworked basement material comprised of carboniferous limestone breccia in a clay matrix (triangles). b) Wye Valley system showing micritic and intraclast tufa barrage pond infill (stippled) with interbedded peaty micrite (dashed lines) The upstream barrage infill has a basal peat deposit (vertical bars) and the lower infill deposit also has a basal facies of limestone breccia in clay (triangles). From Pedley (1993).

2. Perched spring-line (slope) deposits are associated with exsurgences at high points in the landscape.

    a. Proximal deposits may be characterised by lobate flat or convex deposits consisting of macrophytic and microphytic tufa formed on the steeper slopes with occasional paludal conditions and ponding immediately proximal to the source.

    b. Distal deposits downslope are typically fine low-angle sheet-like deposits of fine detrital tufa that may preserve palaeosols.

3. Lacustrine tufa deposits are characterised by stromatolitic microphytic formations, micritic tufa and lime muds. Oncoidal tufa may form in high-energy lacustrine margins.

4. Paludal (marsh) tufas are characterised by a mixture different types of tufa formed in different microenvironments including micritic tufa, macrophytic and microphytic growths and unlithified tufa (spring chalk). These deposits can also include lithoclastic and organic debris, palaeosols and exposure surfaces.

5. Subaerial tufas can form on exposed carbonate screes in high-altitude areas.

4.4.5 Depositional rates of tufa

A summary of depositional rates of tufa reported by various authors has been provided by Viles and Goudie (1990a: 32) showing that in central and northern European systems tufa deposits can grow at rates between .01 and 10 mm per year. Drysdale and Gale (1997) found that accumulation rates varied between localities and within localities along Louie Creek in Queensland, with medium to higher energy flow regimes exhibiting the highest depositional rates (averaging up to 6.98mm a^{-1} with a maximum of 30.36mm a^{-1}) and still water zones exhibiting the lowest rate (averaging .36mm a^{-1} with a maximum of 4.84mm a^{-1}), contributing to an overall mean rate of 4.15 mm for the entire system. Changing flow regimes and seasonal climate changes influenced deposition and erosion rates (*ibid.*).

It is difficult to attempt to make long-term projections of tufa deposition based on computed annual rates of deposition because of the uncertainties caused by dynamic flow conditions and changing climate.

To attempt to establish possible deposition rates over longer time scales, approximate estimates of accumulation rates of two ancient tufa deposits are computed here.

4.4.5.1 Louie Creek, Queensland

The distribution of modern and ancient tufa deposits along Louie Creek in Queensland (Drysdale and Head 1994, Drysdale 1995) is illustrated in Figure 4.28. From this map a surface coverage of $294400m^2$ (29.44ha) has been calculated for the fossil tufa outcrops that have been dated within an age range from the Holocene to approximately 300ka (revised U/Th dating, R. Drysdale, personal communication, 2004), and achieving total thicknesses exceeding 7m.

This figure is an estimate because the extent of occurrence of modern tufa along Louie Creek has not been included in the areal calculation, some areas mapped as tufa may not have complete coverage, exposed deposits may have been reduced in thickness and lateral extent by erosion and denudation and it is likely that there are additional tufa deposits that are buried and have not been observed in outcrop, and so have not been mapped.

Given these inherent uncertainties, it is fair to conclude that over a period of about 300ka, tufa deposition up to and exceeding 7m in thickness covering approximately $29440m^2$ of terrain has occurred through 10m of relief in a drainage system fed by a single source within a $36000000m^2$ (3600ha) area. Given that these deposits represent different stages from at least one complete cycle of deposition, hiatus and erosion, fluctuations in flow regimes and depositional conditions could be considered to have been averaged, and that if this process continues, that this could translate to a net coverage of approximately $97152m^2$ (9.7 ha or approximately $.3km^2$) over a 1Ma period.

4.4.5.2 Caerwys, Wales

The Caerwys tufa deposit in Wales (Figure 4.29) is deltaic (triangular) in shape, is approximately 1km in length, up to 350m in width, achieves a maximum thickness exceeding 12m and extends through 46m of relief (Pedley 1987). Because a humus layer within the tufa has been dated at approximately 8ka and the deposit lies upon an *in*
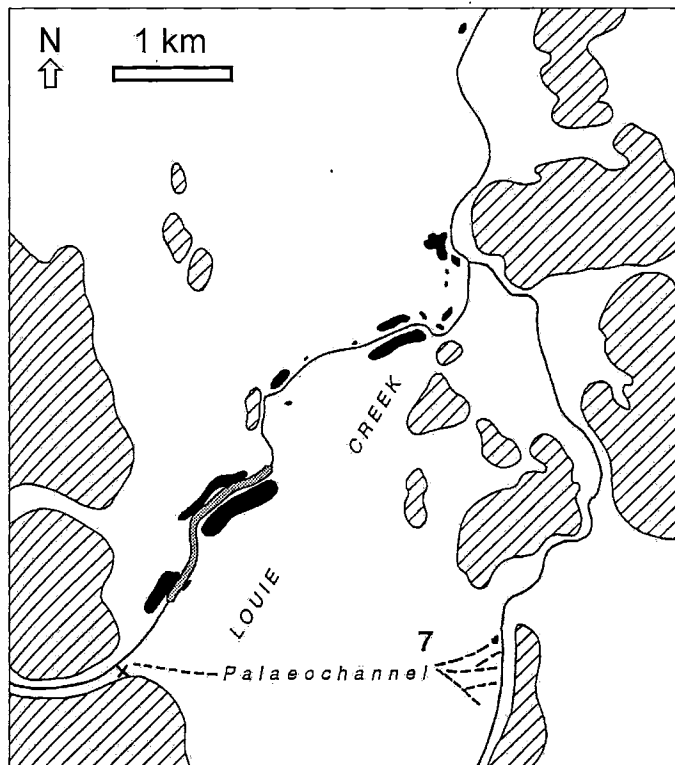
Figure 4.28: Tufa deposits at Louie Creek, Queensland, 30 km north of Riversleigh. Pleistocene and Holocene tufa deposits are marked in black, the zone in which modern fluvial barrage deposits is currently occurring is stippled, outcrops of Cambrian limestone are hatched. The areal distribution of Pleistocene and Holocene tufa deposits was used for approximate calculation of depositional rate in the text. After Drysdale and Head (1994).
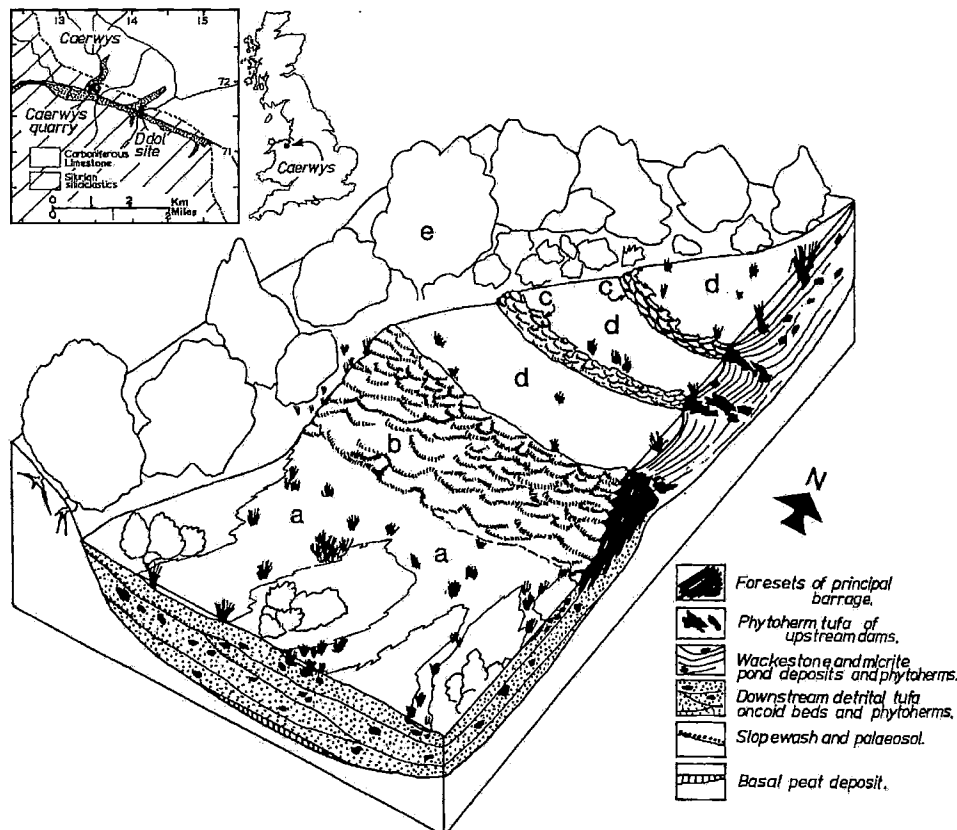
Figure 4.29: Reconstruction of the Holocene tufagenic fluvial barrage system at Caerwys, Wales. Inset is the location of the deposit. The barrage pond deposits are comprised of micritic and detrital tufa, braided stream deposits below the barrages are dominated by detrital tufa. Captions for original labels in figure: a) Stream-dominated areas downstream of the barrage. b) Principal tufa barrage. c) Smaller upstream barriers. d) Ponds upstream of the main barrage. e) Regional palaeo-slope of the wooded valley site. Note the basal facies comprised of Late Devensian peat. This model is comparable to the basic tufagenic depositional unit at Riversleigh (see Section 5.2.4). After Pedley (1987).

situ peat deposit that is considered Late Devensian (i.e. >12ka) the formation of the deposit is considered to be a Holocene event (*ibid.*). This indicates that deposition along this single distributary has covered an area of approximately 175000m² (17.5ha) during the last 10-12ka. If tufagenesis continued at this rate, depositional coverage could achieve approximately 1750000m² (175ha) over 100ka and approximately 17500000m² (1750ha or approximately 300km²) over 1Ma.

4.4.6 Tufa in the geological record

Tufa tends to be poorly represented in the pre-Pleistocene geological record (Pedley 1990, Drysdale 1995, Ford and Pedley 1996). Some possible factors contributing to this under-representation of fossil or ancient tufa are:

1. Definitions of tufa and travertine vary in the literature.

2. Literature that recognises, describes and diagnoses tufa of pre-Holocene age is rare. Most literature focuses on active or recently active systems. This appears to have led to a prevailing notion that tufa formation is a Holocene phenomenon. In some traditional texts (i.e. Pettijohn 1957, Termier and Termier 1963) karst systems and tufagenic processes and deposits are regarded as miscellaneous peculiarities.

3. Tufa is usually formed in dynamic environments subject to fluvial conditions in which the balance between accumulation and erosion often changes and tufa deposits are reworked. This is considered the natural outcome of tufagenesis in barrage systems (Golubić 1969). Under these conditions, primary geomorphic structures (i.e. barrages) are unlikely to remain intact, and thus deposits may not be recognised and interpreted as tufagenic.

4. The often highly porous open fabric of tufa facies is very susceptible to induration and infill, so that this characteristic texture of fresh tufa may be obscured or lost in older tufagenic deposits. Ongoing post-diagenetic processes can result not only in further infill of characteristic voids, but also dissolution and destruction of diagnostic textures (i.e. macrophyte tissue moulds, burrows, voids, etc), particularly if tufa deposits are exposed to weathering and dissolved minerals move through the deposit.

5. Fossil tufa may be easily misdiagnosed because of strict usage, and the inherent assumptions of, carbonate classification systems that are designed primarily for

interpretation of clastic marine carbonates; and by the interpretation of carbonate deposits using direct analogy with siliclastic (or otherwise non-carbonate) systems.

Chapter 5

Riversleigh middle Tertiary lithotypes,
facies and assemblages

The location and geology of the Riversleigh area is described and illustrated in Chapter 3. Reconstructions of the main study area at Riversleigh terrain showing the distribution of Tertiary deposits and the location of geographic features and key localities are illustrated in Figures 2.1, 2.2, 2.3, 2.4, 2.5, 2.6. Localities and geology of the study area are shown in figure 5.3.

Description of aspects of some lithotypes and facies distributions discussed below were provided by Megirian (1992). The majority of those descriptions and observations are valid and are upheld here, however differences in diagnosis and interpretation are noted where necessary. Some specific problems with aspects of previous work are discussed in more detail below.

Interpretation and description here is necessarily restricted to representative localities and fossil faunas (Figure 5.3). Individual deposits at Riversleigh can exhibit a great variety of lithological characteristics. Further detailed investigation of the complex lithologies at individual deposits is necessary to provide better understanding of the depositional histories of individual localities and to test and expand the scope of the interpretations and models presented here. The diagnoses and interpretations here can provide a basis for methods of interpretation of other localities at Riversleigh.

5.1 Broad divisions of facies

Petrological analysis alone is not sufficient to distinguish or interpret facies and depositional environments at Riversleigh because similar geological features can occur in different deposits that are considered to have formed under different depositional conditions. The following five criteria have been used to establish distinguishing characteristics of Tertiary carbonate facies at Riversleigh and to interpret modes of deposition:

1. Morphology and depositional geometry of deposits.

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2. Presence or absence of key lithological components including speleothem and intraformational or extraformational lithoclasts.

3. Recognition of principal lithotextures (below) and assessment of the relative abundance of these lithotextures.

4. Aspects of taphonomy of vertebrate faunas associated with deposits.

5. Taxonomic composition of these associated vertebrate faunas, particularly relative abundance and diversity of certain types of taxa.

Using these criteria, Tertiary lithofacies at Riversleigh may be divided into two broad categories (Figure 5.1):

1. Primary heterogeneous carbonate 'host' facies.

2. Cave facies, including speleothem and cave sediment.

The primary heterogeneous carbonate facies constitute the majority of Tertiary deposits at Riversleigh, and contain fossil vertebrate faunas. While cave deposits actually comprise a very small proportion of the overall geology, occurring 'within' the heterogeneous host, these volumetrically restricted deposits are numerous and also contain distinctive vertebrate faunas.

Aspects of physical relationships of components of the major lithofacies types at Riversleigh, including relief, distribution and lithological variation are illustrated in the idealised profile, geological and locality map and geological sections in Figures 5.2, 5.3, 5.4.

5.1.1 Principal lithotextures

Petrography can be used in combination with other characteristics of Riversleigh deposits and faunas (as outlined above) to distinguish cave facies from non-cave host facies. There are nine distinctive lithotextures recognised in lithologies from Riversleigh that contribute to the diagnoses of facies and broad divisions of facies. These lithotextures are:

1. Arenaceous lithotexture

2. Intraclasts lithotexture

3. Globular lithotexture
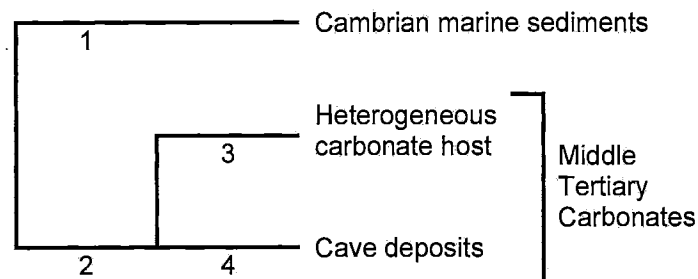
Figure 5.1: Classification of broad divisions of Riversleigh Tertiary lithofacies.
Characters at numbered nodes:

1. Massive limestone, dolomite, chert layers and massive bedded chert.
2. Heterogeneous carbonate, reworked Cambrian chert lithoclasts, abundant Tertiary molluscs and ostracods, Tertiary vertebrate fossils.
3. Abundant reworked tufaceous intraclasts, dominant micritic, intraclast, bio-precipitated, peloidal, arenaceous lithotextures with open fabrics, occasional Cambrian chert lithoclasts (more abundant in basal facies), laterally and vertically extensive geometrically unrestricted deposits, normal grading and lenticular profiles may be observed, relatively greater abundance and diversity of fossil aquatic vertebrates.
4. Presence of flowstone and other speleothem, relatively lower abundance and diversity of aquatic vertebrates, abundant and diverse fossil bat faunas, associated and articulated fossil skeletal parts more common, depositional geometry restricted and clearly delineated by facies change, dominance of crystalline and phosphatic lithotextures.

Figure 5.2: Idealised schematic profile of Riversleigh Tertiary carbonates illustrating relationships of key facies. The Cambrian/Proterozoic basement is undulating and basal facies are discontinuously distributed at the interface with the Tertiary deposits.

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Palaeontology Laboratory, School of Biological,
Earth and Environmental Sciences, UNSW.

Figure 5.3: Topographic and geological map of main study area in the Riversleigh WHA showing
positions of key localities referred to in the text. Distribution of geology is based on field observations and
air photo interpretation. Profiles A, B and C are illustrated in Figure 5.4. Geographic placenames are
indicated in Figure 2.4. Terrain reconstructions generated from this map are illustrated in Figures 2.5 and
2.6. While the distinction between chert-dominated and limestone-dominated Cambrian deposits is not
denoted by a mapped geological boundary, the general distribution of these facies-types may be relevant to
interpretation of the Tertiary karst.

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Figure 5.4: Representative sections of Riversleigh Tertiary carbonates showing relationships between geology and topography. Note the undulating basement contacts and the elevations of Tertiary carbonates that are equal to and exceed local outcrops of Cambrian and Proterozoic rocks. Late Oligocene deposits on Southern Gag Plateau are equivalent in elevation to Middle Miocene deposits on Gag Plateau. Geology as observed at the surface is illustrated only, because underlying relationships and deposit thicknesses have not been observed and cannot be extrapolated. Vertical exaggeration x60.
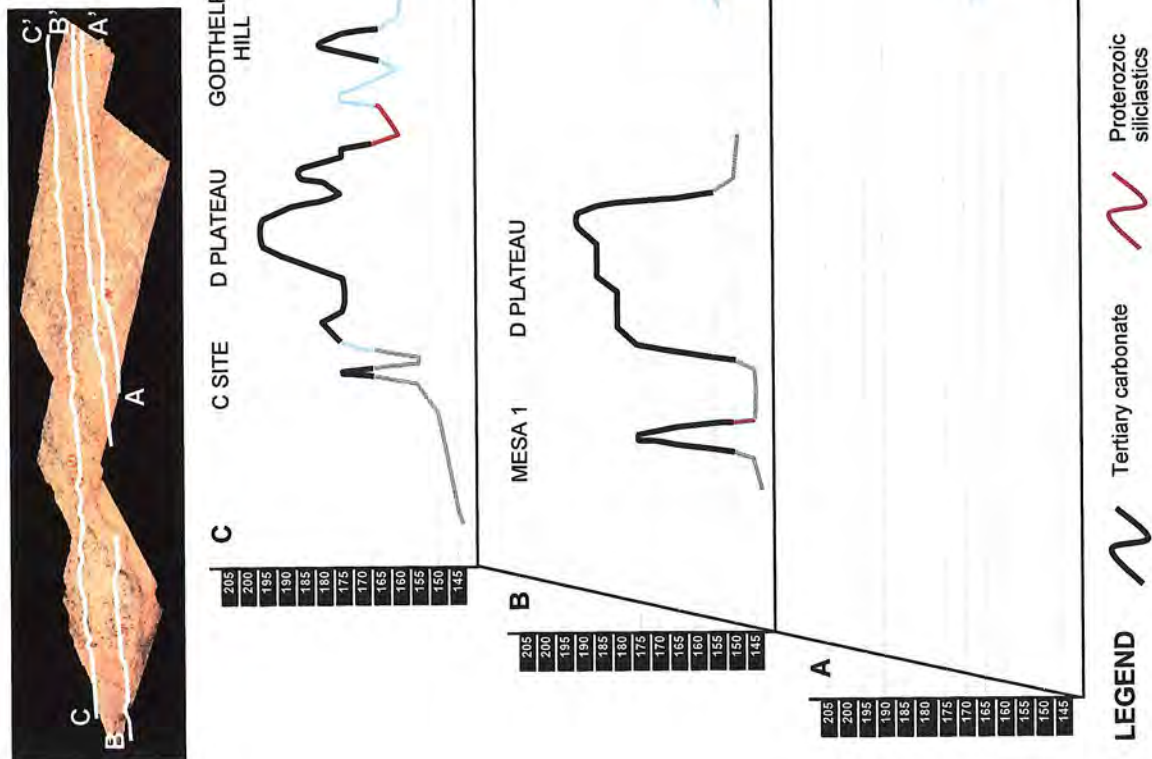
4. Bio-precipitated lithotextures

5. Micritic lithotexture

6. Detrital crystals lithotexture

7. Crystalline lithotexture

8. Phosphatic lithotexture

9. Flowstone/speleothem lithotexture

With the exception of flowstone and speleothem, the individual presence of any of these lithotextures is not necessarily diagnostic of facies-type, however they can be used to interpret certain conditions that existed in depositional environments. Additionally, different combinations of certain lithotextures tend to dominate cave deposits and non-cave deposits. For example, non-cave heterogeneous carbonate host facies are dominated by combinations of the first 6 textures – arenaceous, intraclasts, globular, bio-precipitated, detrital crystals and micritic textures - whereas facies dominated by combinations of crystalline, detrital crystals and phosphatic textures are considered characteristic of cave facies. The presence of speleothem is considered diagnostic of cave deposits.

Although separating textures on the basis of morphology divides natural broader groups of related textures that are formed by similar processes (i.e. different kinds of micritic textures), the division of textures on the basis of appearance is more useful because they are easily recognised and compared, do rely on lithological interpretation of fabrics, and because this allows assessment of the dominance of certain combinations of textures which would not be possible using larger, poorly resolved groups.

Description of lithotextures below has been limited, where possible, to appearance only, and the relevant interpretations of these lithotextures and their occurrence is given in the descriptions of deposit types further below in Sections 5.2 and 5.3. The observed occurrence of these textures in deposits from selected localities at Riversleigh is illustrated in Table 5.1.

Arenaceous lithotexture (Figure 5.5)

This texture is characterised by the abundance of fine sub-angular to rounded siliceous sand grains and/or bone fragments. The fine calcareous matrix is usually iron oxide-rich and brownish or orange in colour.

Intraclasts lithotexture (Figure 5.6)

Intraclasts are usually coated and bound by micrite, which may be laminated. Intraclasts are usually distinguished by slight variations in texture or orientation with respect to the binding matrix, and are usually micritic.

Globular lithotexture (Figure 5.7)

This texture is characterised by masses of ovate to spherical particles of micrite that can exceed 1mm in dimension. Particles that are either amorphous or are otherwise nucleated by small fragments of tufa, shell, calcite crystal or sand coated with micrite. Masses of particles that are not completely bound form an open fabric filled with clear calcite spar.

Bio-precipitated lithotextures (Figure 5.8)

These textures are distinguished by distinctive structures that may be considered indicative of biologically mediated precipitation. These structures include micrite exhibiting 'clotted' texture, isopachous laminar micrite and bacterially precipitated structures (bacterial 'clumps' and 'shrubs'). It is recognised here that weathering and time have reduced the clarity of some of these structures, remains of algal filaments and clearly defined isopachous fringe cements of Pedley (1987) are indistinct. Some laminar structures may be the product of non-biological processes.

Whether 'clotted' micrite is of biological origin is not fully resolved because this type of micrite, which is comprised of peloidal clumps up to 70 μm in diameter may be derived either from invertebrate faecal pellets, micrite affected by water current action, changes in hydrostatic pressure, bacterially mediated precipitation or changes in partial pressure caused by CO_2 removal by macrophytes and cyanobacteria (Pedley 1987; see Figure 4.24d). Because biological influence may be at least partially involved in the formation of 'clotted' micrite and its formation is related to other ongoing biological
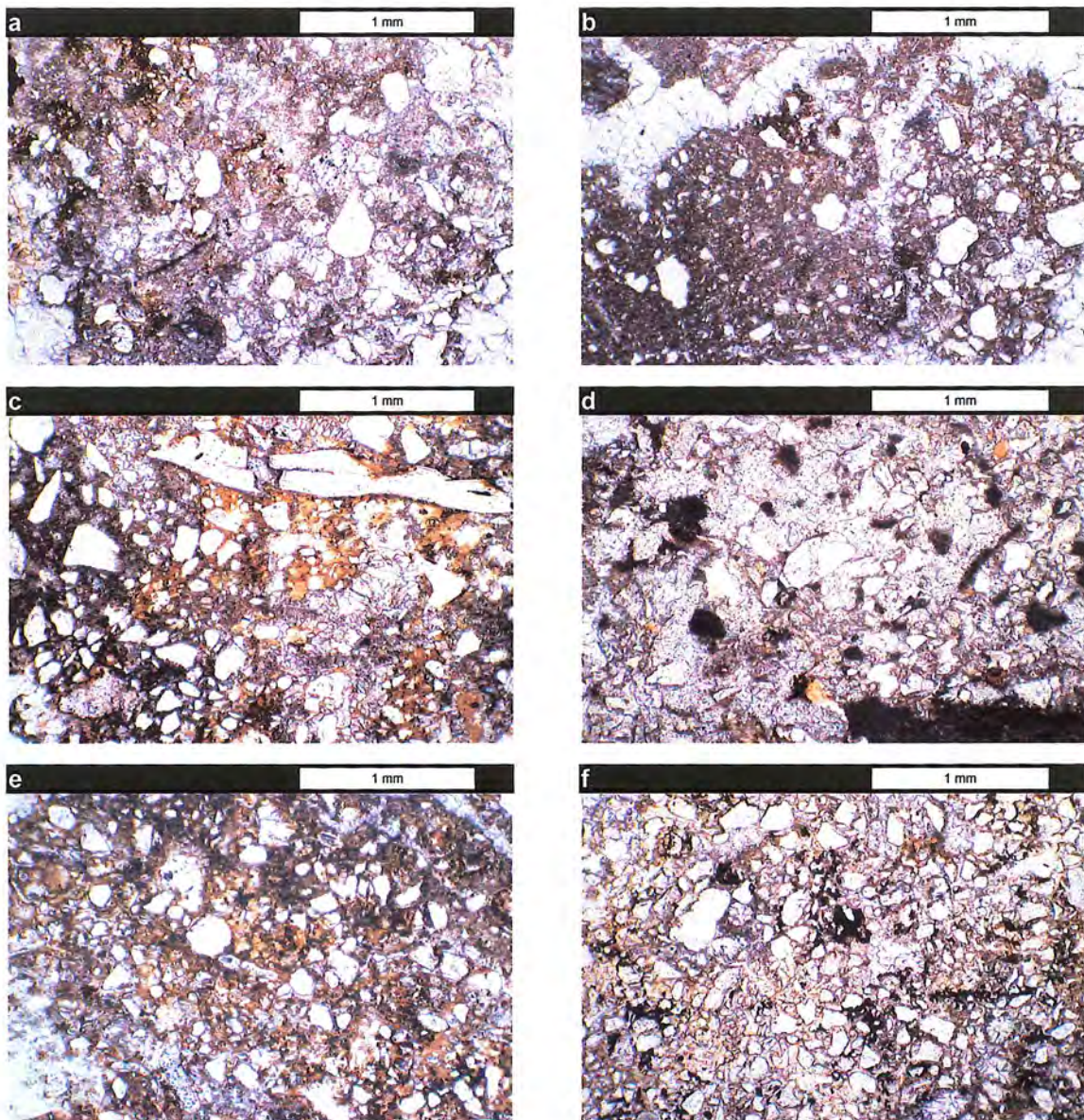
Figure 5.5: Arenaceous lithotextures from various localities at Riversleigh. a,b) White Hunter Site (PP; EP74). c) LD94 Site (PP; R125). d) Ringtail Site (PP; R137). e) Dunsinane Site (PP; RA1995-9). f) Arenaceous matrix of basal facies for comparison (PP; R145A; near Lockwood's Link Site).
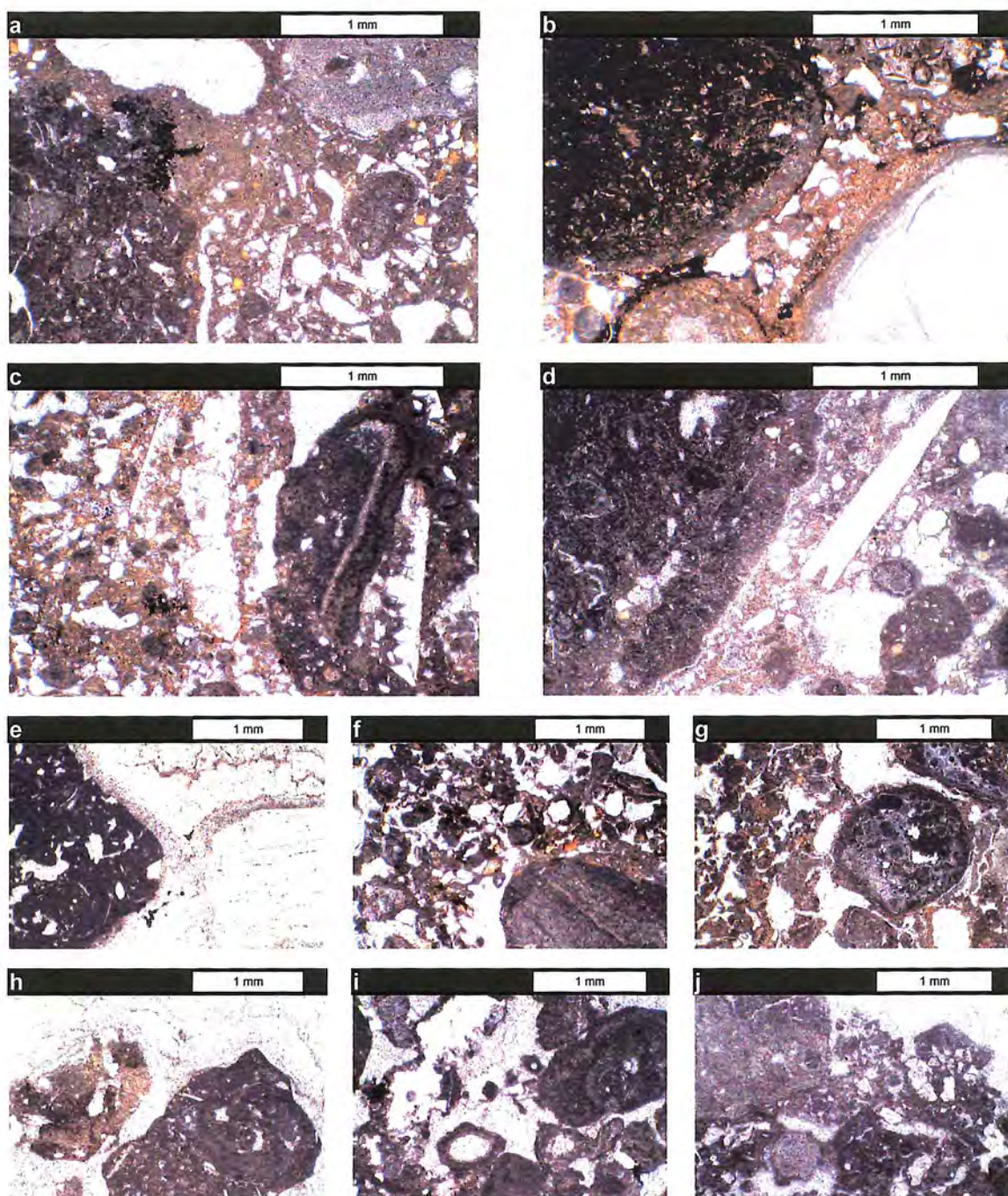
Figure 5.6: Intraclast lithotextures from various localities at Riversleigh. a) Two different kids of intraclast in micritic matrix with detrital crystals (PP; R110; Main Site). b) Tufaceous intraclasts and gastropods with micritic coating in a matrix of coated particles (PP; RA2003-4; Lane's Leap). c) Intraclast in micritic matrix with detrital crystals (PP; R112; Bird Bone Site). d) Intraclasts and coated particles in a bone and detrital crystal-rich micritic matrix (PP; EP24; Gag Site). e) Intraclast and bone in matrix of zoned spar (PP; R117; Don Camillo Site). f) Intraclasts and coated particles, open fabric (PP; R111; Skull Site). g) Intraclasts with micritic coating, ovate voids (PP; R108A; Bob's Boulders Site). h) Intraclasts in sparry matrix (PP; R128; Quentin's Quarry Site). i) Intraclasts and ovate voids with laminar micrite coating in sparry matrix (PP; R137A; Ringtail Site). j) Intraclasts and micrite with spar (PP; R109A/2; Henk's Hollow Site).
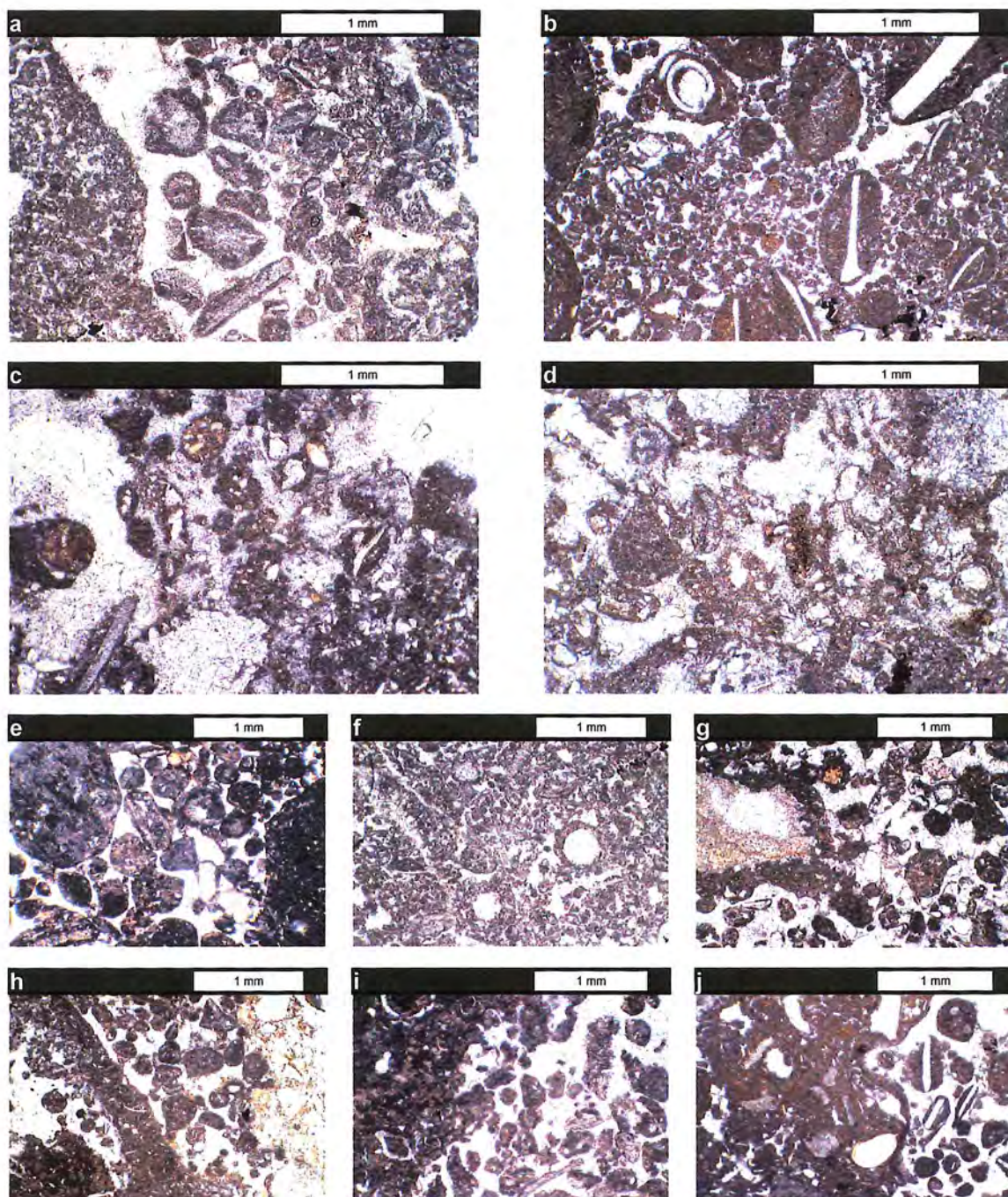
Figure 5.7: Globular lithotextures from various localities at Riversleigh. Similar textures are formed by different processes in cave and non-cave deposits at Riversleigh, this is discussed in more detail in the text. a) Hiatus Site (PP; R147A). b) Ringtail Site (PP; EP23). c) Camel Sputum Site (PP; EP76). d) Inabeyance Site (PP; R158). e) Hal's Hill (PP; RA2003-3B). f) Hiatus Site (PP; R147A). g) White Hunter Site (PP; EP74). h) From above White Hunter Site (PP; R150A). i) Henk's Hollow Site (PP; EP28). j) Jaw Junction Site (PP; R107).

processes during tufagenesis, 'clotted' micrite is included here as a bio-precipitated texture.

Isopachous fringe cements are alternating laminations of (often 'clotted') micrite and spar formed by successive layers of cyanobacterial filaments (Pedley 1987; see Figure 4.24). Similar micritic textures with alternating light and dark layers in samples from Riversleigh are considered comparable to these structures.

The morphology of bacterially precipitated textures, including bacterial 'shrubs' in travertine deposits were described in detail by Chafetz and Folk (1984). Successive layers of these structures may form laminar coatings that can exhibit distinctive patterns. Structures resembling bacterial 'shrubs' were recognised in speleothem from Godthelp Hill by Megirian (1992), and have been recognised here in oncolites from Upper Burnt Offering Site and Bullseye Site and in cave sediment from Mike's Menagerie Site.

Micritic lithotexture (Figure 5.9)

Micritic texture is distinguished by its dense, nearly amorphous appearance in which particles including shell fragments, calcite crystals and sand are conspicuous.

Detrital crystals lithotexture (Figure 5.10)

This highly distinctive texture is characterised by abundant, poorly sorted, randomly oriented calcite crystals in either a micritic or sparry matrix. Some crystals form elongate structures with a distinctive smooth surface and an opposing irregular surface formed by the ends of crystals. These structures have previously been recognised in Riversleigh deposits as calcite rafts (Megirian 1992, Price 2002). Calcite rafts are delicate structures (usually less than 1mm in thickness) with a smooth upper surface and a dogtooth-textured lower surface that also form on the surface of quiet pools of water by degassing of CO_2 (Hill and Forti 1997a).

Crystalline lithotexture (Figure 5.11)

Crystalline texture is distinct from calcite spar that fills voids in all Riversleigh lithologies. This texture is characterised by calcite crystals that are translucent under
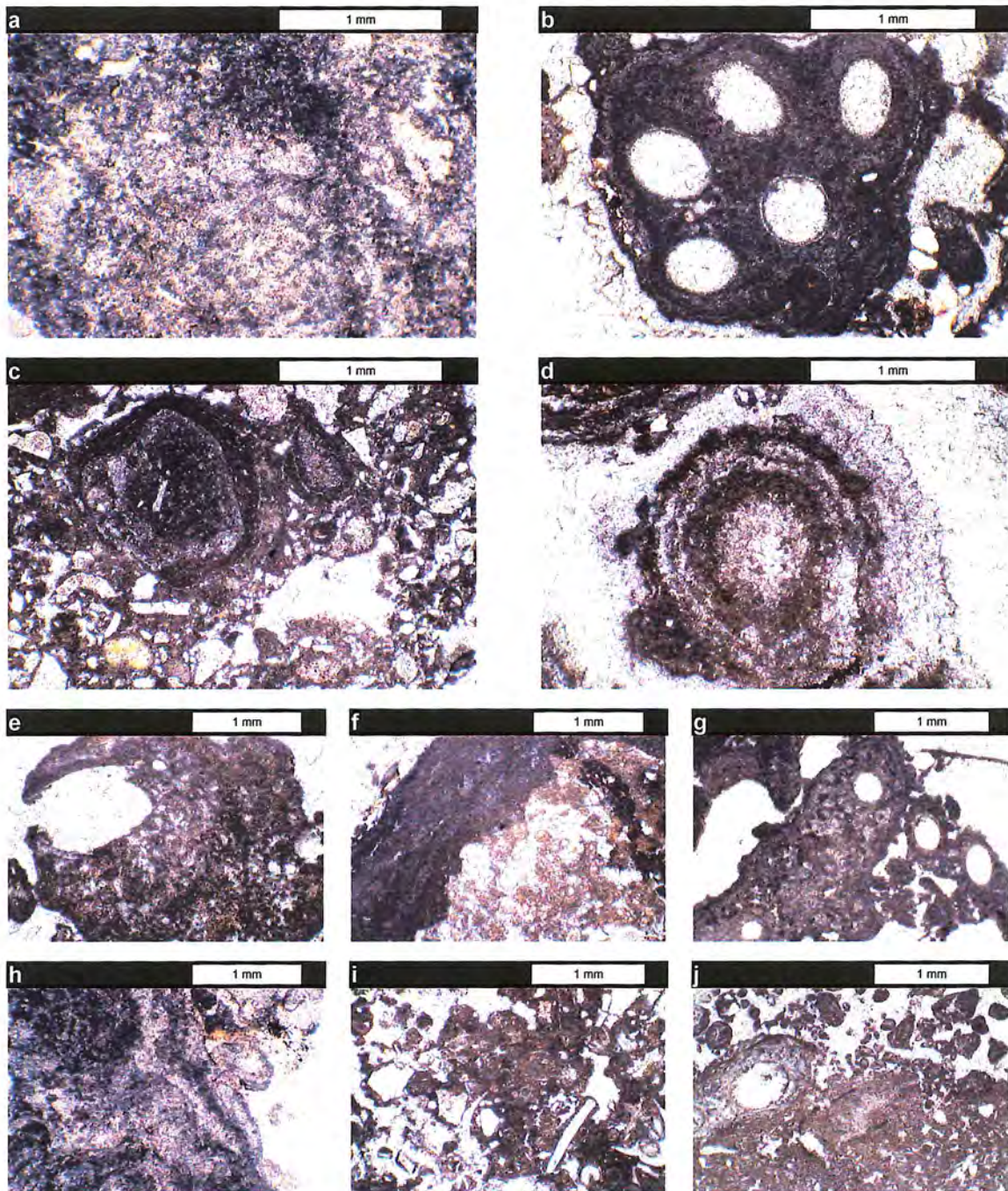
Figure 5.8: Bio-precipitated textures from various localities at Riversleigh. a) 'Clotted' texture (PP; RA2003-1; Mesa 3). b) Laminar micrite precipitated around ovate voids, possibly of macrophytic or insect origin (PP; R137A; Ringtail Site). c) Laminar micrite coating around tufaceous intraclast (PP; R109A/3; Henk's Hollow Site). d) Laminar micritic structure resembling bacterially precipitated texture, see oncolites in Figure X.40 (PP; R154A; Mike's Menagerie Site). e) Micrite with 'clotted' texture surrounding an ovate void of possible biological origin (PP; R137A; Ringtail Site). f) Dense laminated micrite with open matrix (PP; R137; Ringtail Site). g) Laminar micrite with 'clotted'; texture surrounding voids of probable organic origin (PP; R137A; Ringtail Site). h) Laminar micrite with 'clotted' texture (PP; RA2003-1; Mesa 3). i) Micrite-bound particles (PP; EP74; White Hunter Site). j) Laminar micrite-bound particles (PP; R147B; Hiatus Site).
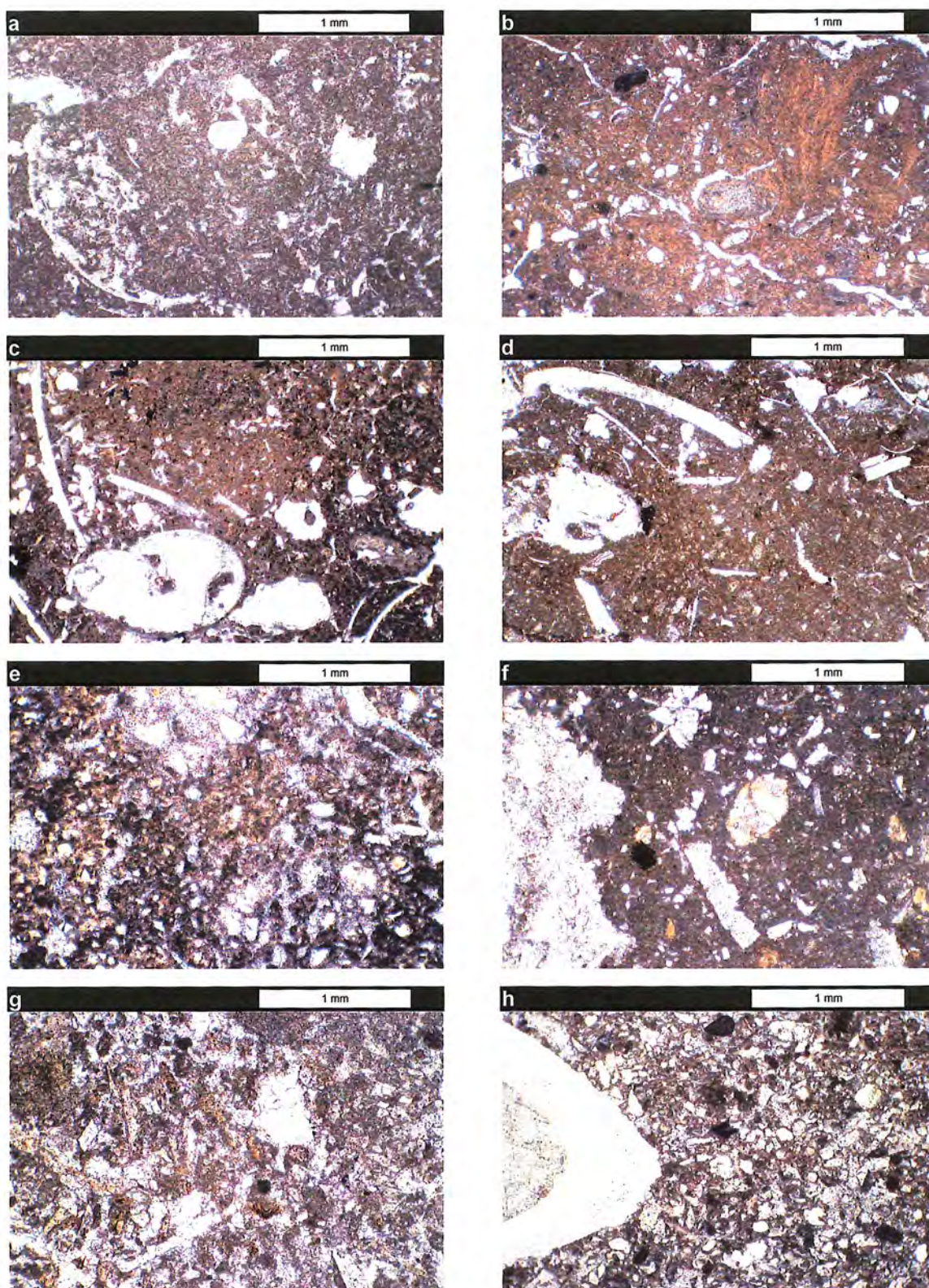
Figure 5.9: Micritic lithotextures from various localities at Riversleigh. a) Hiatus Site (PP; R147B). b) Bob's Boulders Site (PP; R108). c) Jaw Junction Site (PP; R107). d) Above White Hunter Site (PP; R150A). e) Henk's Hollow Site (PP; EP28). f) Camel Sputum Site (PP; EP76). g) Wayne's Wok (PP; R151A). h) RSO Site (PP; R152A).
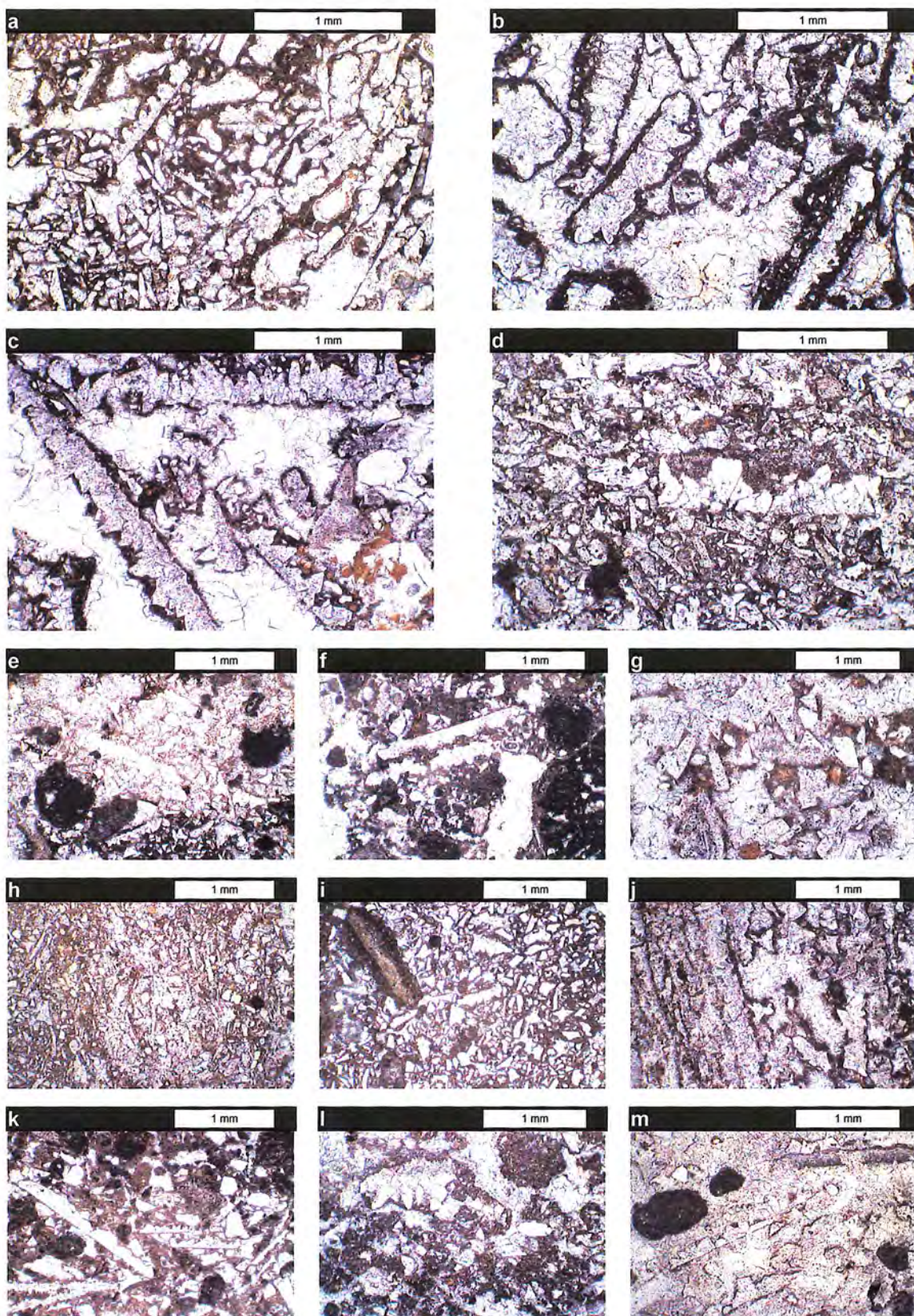
Figure 5.10: Detrital crystals lithotextures from various localities at Riversleigh. a) LD94 Site (PP; R125). b) Mike's Menagerie Site (PP; R154). c) Gag Site (PP; R118A). d) Camel Sputum Site (PP; R155). e) Ringtail Site (PP; R137). f) Henk's Hollow Site (PP; R109). g) Gag Site (PP; R118A). h) Last Minute Site (PP; R140). i) Courtenay's Cache Site (PP; R121). j) Gag Site (PP; EP26). k) Bird Bone Site (PP; R112). l) Inabeyance Site (PP; R158). m) RSO Site (PP; R152A).

plane polars, usually inter-grown, may be coloured by contaminants, often exhibit different patterns (sometime resembling layers) and may be either coarse or fine.

Phosphatic lithotexture (Figure 5.12)

The phosphatic texture was described by Megirian (1992) from the cave deposit at Bitesantenary Site at Riversleigh, and interpreted as altered phosphorite possibly derived from bat droppings. This texture is characterised by the presence of amorphous masses of orange or brown material that appears black under crossed polars.

Flowstone/speleothem lithotexture (Figure 5.13)

This distinctive texture is recognisable by the aligned syntaxial crystal structure which is apparent when viewed using cross-polarised light. The diagnosis of this lithotexture as speleothem is discussed in more detail in Section 5.3.2. The presence of speleothem is considered characteristic of cave deposits.

5.2 Riversleigh primary heterogeneous carbonate host facies

These deposits account for the majority of Tertiary deposits at Riversleigh. Tedford (1967) and Megirian (1992) have both described gross morphology of outcrops of this facies type.

5.2.1 Interpretations by previous workers

Tedford (1967) postulated that the heterogeneous and gastropod–rich micritic carbonates may have been deposited on the margins of a large lake, which is supported by the vertebrate taphonomy and faunal compositions. However, there is little evidence of any lacustrine basin structure and other diagnostic facies and facies distributions do not occur (see Platt and Wright 1991).

The tufaceous alluvium model of Williams (1978) is challenged by a number of factors, including the petrography of the Tertiary carbonates that are rich in well-preserved primary structures which does not conform to the expected petrography of lithotypes formed by what would essentially have been a calcretisation process comparable to that of the arid alluvial fan model of Megirian (1992); the age of fossil vertebrates contained
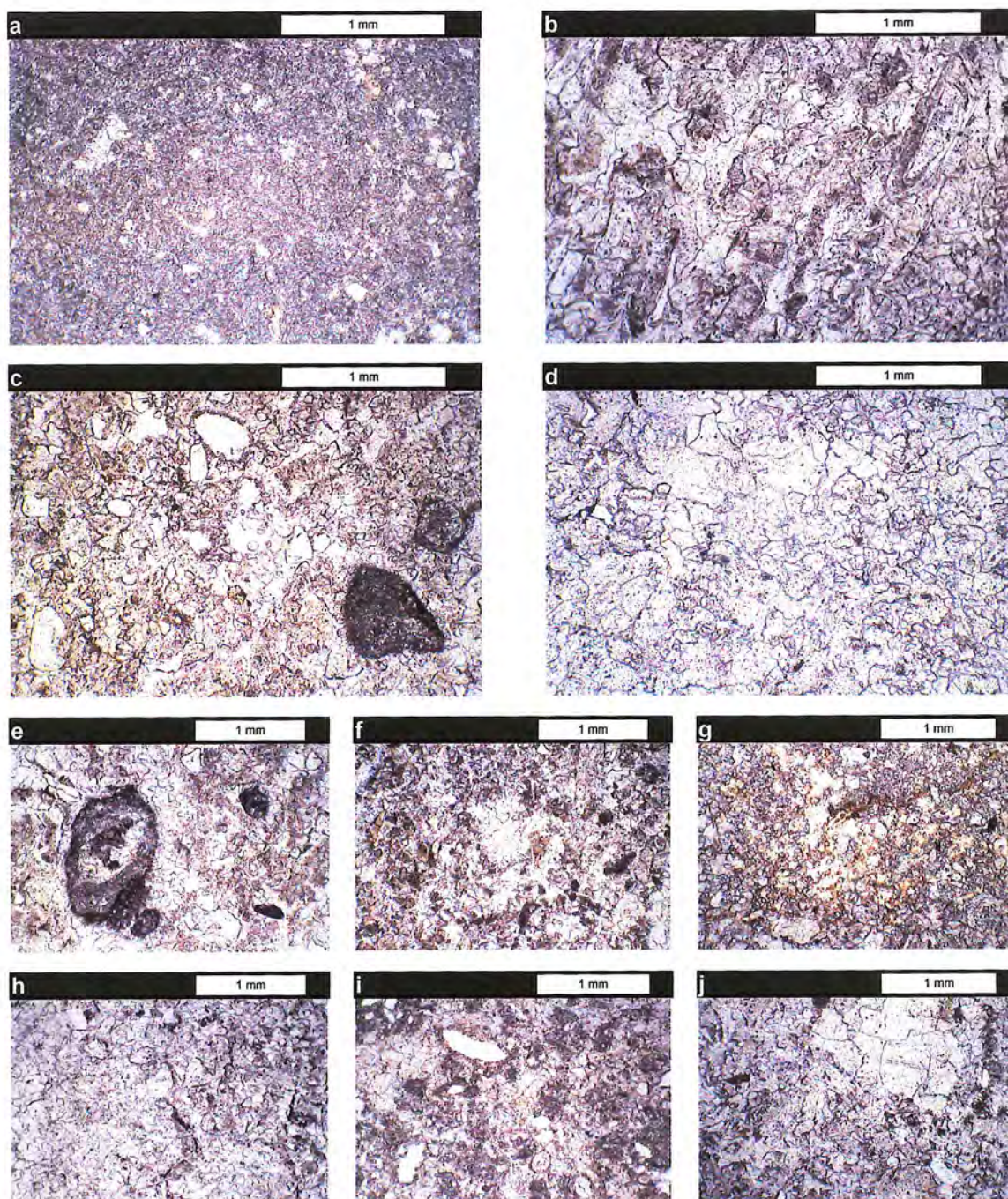
Figure 5.11: Crystalline lithotextures from various localities at Riversleigh. a) Gag Site (PP; EP24). b) Neville's Garden Site (PP; EP14). c) White Hunter Site (PP; R150). d) Upper Site (PP; R156). e) White Hunter Site (PP; R150). f) Wayne's Wok Site (PP; R151C). g) Wayne's Wok Site (PP; R151C). h) Mike's Menagerie Site (PP; R154). i) Camel Sputum Site (PP; EP77). j) Camel Sputum Site (PP; R155).
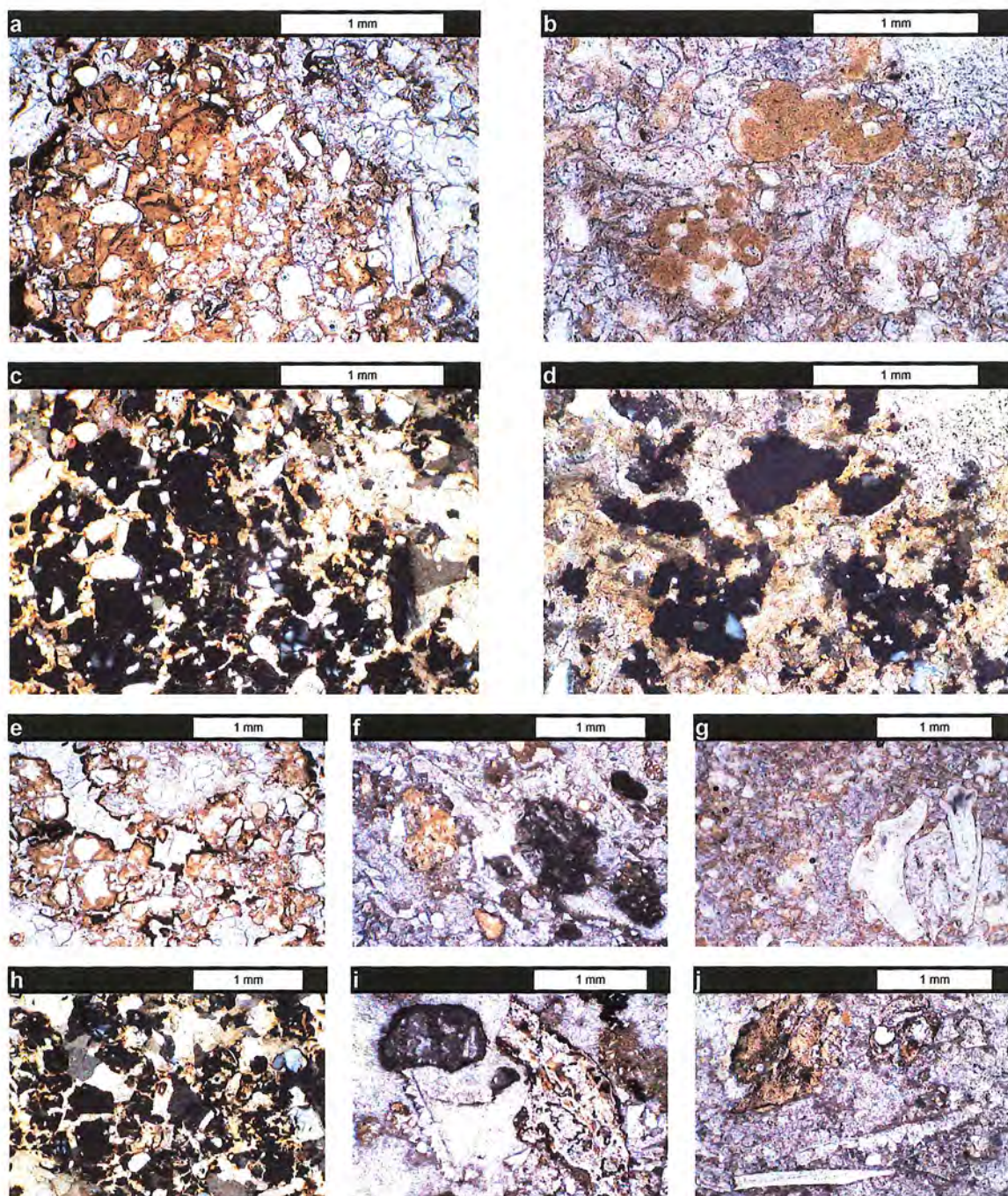
Figure 5.12: Phosphatic lithotextures from various localities at Riversleigh. a/c) Phosphatic lithotexture showing black isotropic appearance of amorphous phosphate under crossed polars (PP/XP; RA2003-6; AL90 Site). b/d) Phosphatic lithotexture showing black isotropic appearance of amorphous phosphate under crossed polars (PP/XP; R138/1; Gotham City Site). e/h) Phosphatic lithotexture showing black isotropic appearance of amorphous phosphate under crossed polars (PP/XP; RA2003-6; AL90 Site). f) Phosphatic lithotexture with crystalline matrix and tufaceous intraclasts (PP; R138/2; Gotham City Site). g) Phosphatic lithotexture showing section through part of the tooth-row of a microchiropteran bat (PP; R138/1; Gotham City Site). i) Phosphatic texture, tufaceous intraclasts, a corroded particle and a detrital calcite raft (PP; R138/2; Gotham City Site). i) Phosphatic texture, bat bone and a detrital calcite raft (PP; R139; Brer Rick's Bat Site).
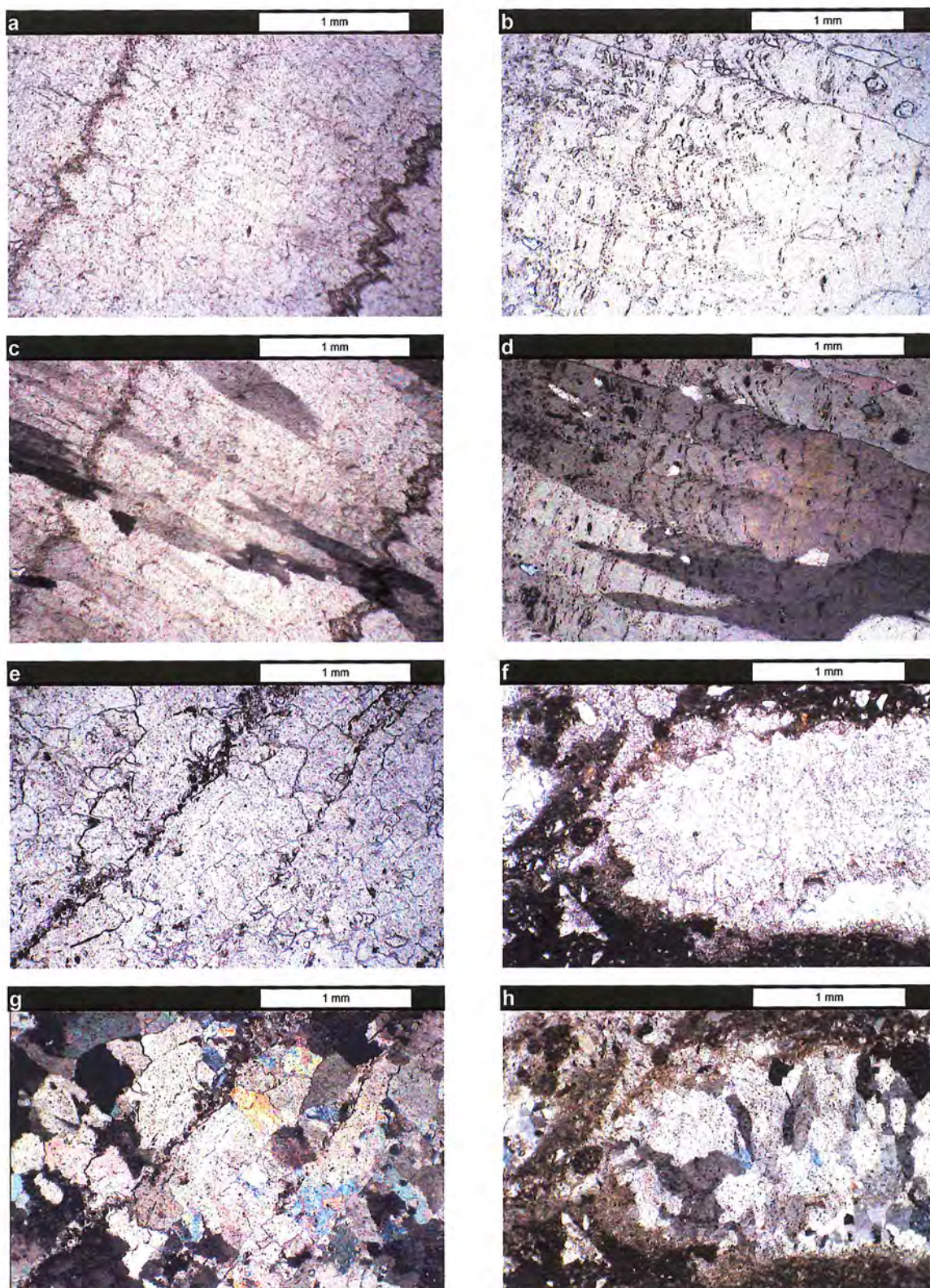
Figure 5.13: Flowstone/speleothem lithotextures from various deposits at Riversleigh. Discussion of diagnosis of flowstone/speleothem is in section X and. a/c) Flowstone (PP/XP; RA2003-9B; AL90 Site). b/d) Flowstone (PP/XP; R153; RSO Site). e/g) Altered flowstone, compare to 5.13a/c and b/d (PP/XP; R156; Upper Site). f/h) Shelfstone tip with micrite matrix (PP/XP; EP76; Camel Sputum Site).

Table 5.1: Lithotextures and diagnostic characteristics among deposits at selected fossil sites at Riversleigh. Although source data is not complete, the general pattern of characteristics of cave deposits and host deposits is apparent. Combinations of arenaceous, intraclasts, globular, bio-precipitated, micritic and detrital crystals lithotextures tend to dominate host facies. Deposits considered to have been formed in cave environments tend to be dominated by combinations of globular, detrital crystals, crystalline, phosphatic and flowstone/speleothem lithotextures. Flowstone and speleothem textures are the only textures regarded as diagnostic by their presence. Other diagnostic characteristics including depositional geometry and aspects of vertebrate faunas are described in more detail in the text.

in the Tertiary deposits is restricted to the middle Tertiary, rather than spanning a continuous period of time from the present into the Tertiary as the model would suggest; the requirement of seasonal wet/dry season weather patterns for which there is no evidence of their occurrence during the Tertiary; and the presence of non-tufaceous alluvial sediments along the Gregory River containing faunas dating from the Pleistocene (i.e. Terrace Site > 20ka, Archer *et al.* 1994, 1997) which are unconsolidated and not carbonate-enriched and have thus not been subject to this tufaceous enrichment process throughout this entire period of time.

Archer *et al.* (1989, 1994) considered fossiliferous deposits of this rock-type to have been formed in low-energy surface 'pool' environments, into which slumped margins supplied reworked clasts. However this was based on limited lithological data, and depositional context accounting for the formation and preservation of these deposits was not supplied. The concept of these 'pool' deposits was developed using aspects of the geology of some deposits that have been subsequently diagnosed here as vadose cave deposits (see Section 5.3 below).

Megirian (1992) interpreted the heterogeneous intraformational tufa facies as clastic fluvial deposits characteristic of a proximal alluvial fan (*sensu* Nickel 1985) that formed under arid conditions because the rate of carbonate accumulation exceeded the rate of dissolution by weathering. According to that model, occasional high-energy flow distributed reworked tufa from a tufagenic source proximal to exsurgences in the Cambrian karst onto the fan. Vertebrate bones were occasionally preserved by localised tufagenesis occurring throughout the fan.

By the application of standard geological interpretation, Riversleigh heterogeneous carbonates, which contain large lithified clasts in normally graded lenticular deposits, would be interpreted as indicative of energetic clastic transport conditions. Texturally they match the distribution of clastics expected from a proximal alluvial fan *sensu* Nickel (1985), which was the basis of the diagnosis of this depositional environment in Megirian (1992). However, a clastic alluvial origin for these facies in a depositional environment in an arid climate is considered unlikely because of the following reasons (also refer to Section 4.2 for diagnostic features of fluvio-lacustrine clastic carbonates):

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1. Absence of flow structures, particularly cross-beds, which are considered diagnostic of fluvio-clastic conditions (Freytet 1973, Nickel 1985, Gierlowski-Kordesch 1998).

2. Although intraformational tufaceous clasts (exceeding cobble-size) are very common, Cambrian limestone and chert clasts of comparable proportions are very rare (except in basal facies). If the depositional flow regime was capable of transporting large tufa fragments onto an alluvial fan, comparably proportioned components from the proximal source area should also be present in fan deposits. This contrasts with the modern surface and fluvial deposits at Riversleigh that are rich in reworked Cambrian chert, as is the system at Louie Creek (Drysdale 1995). Gierlowski-Kordesch (1998) suggested that change in the carbonate composition of fluvio-clastic deposits reflected a change in source area. Because the proximal tufa deposits of this model occur in the same source area as the other potential clastic material, this is considered an unlikely explanation for their absence.

3. If the heterogeneous carbonates had been distributed into the fan by occasional high-energy flow under otherwise dry to arid conditions, then pedogenic processes would have dominated diagenesis (i.e. calcretisation). This is common in fluvio-clastic systems (Freytet 1973, Nickel 1985, Drysdale 1995, Gierlowski-Kordesch 1998). Drysdale (1995) observed calcretes formed from non-tufaceous fluvial sediment in the semi-arid Louie Creek system. The Riversleigh tufaceous carbonates do not exhibit diagnostic characteristics of pedogenic processes, such as degradation, or loss of, primary depositional structures. Calcrete at Riversleigh is considerably different in structure and texture to the heterogeneous carbonates (see Section 5.2.3.3. below).

4. There is an absence of other facies, and combinations of facies, that are characteristic of the distribution of facies in fluvio-clastic and alluvial fan systems. In these systems, facies are usually separated by abrupt contacts that are often clearly delineated by textural change, unconformities and exposure surfaces indicating transitions between different depositional environments (i.e. see Freytet 1973, Nickel 1985), which are not evident. Oncoidal tufa and microphytic tufa, which characterise channel deposits in fluvio-clastic carbonate

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systems, are also absent (deposits interpreted by Megirian (1992) as oncoidal tufa and microphytic tufa are here reinterpreted as spelaean, see below).

5. Taphonomic evidence from vertebrate faunas from these facies indicate minimal transport has occurred (see Myers 2002, Bassarova 2004). Generally, preservation is good, rounding and weathering of fragments is limited, and tiny or fragile vertebrate remains (including those of frogs, small birds, lizards and bats) are preserved. This does not indicate prevailing high-energy conditions.

6. Vertebrate faunas from these facies contain relatively more abundant and diverse aquatic taxa, particularly chelid turtles, crocodilians, fish and lungfish. This suggests that permanently wet conditions prevailed, rather than dryness or aridity.

Subsequent interpretations and modelling of depositional processes at Riversleigh have been based on the arid alluvial fan model of Megirian (1992), and thus inherit the same challenges described above. The 'pool' deposits of Archer *et al.* (1989, 1994), were considered to have occurred in this system (Archer *et al.* 1997, Creaser 1997). Ford and Pedley (1996) considered the alluvial fan model of Megirian to be representative of the alluvial tufa system of Pedley (1990) and Ford and Pedley (1996). Creaser (1997) suggested that cyclic alluvial deposition of this type and intervening tectonic activity occurred more than once at Riversleigh, although not necessarily under dry or arid climatic conditions. Repeated occurrences of subsidence and uplift are not supported by the geological record at Riversleigh or the Karumba Basin (see Day *et al.* 1983).

Thus, the primary issues to be addressed here are:

1. Interpretation of the lithology of the heterogeneous carbonates using diagnostic criteria to provide clarification and alternatives to the facies identifications of Megirian (1992).

2. Identification of depositional mechanisms that can account for this lithology and other distinctive aspects of the deposits including their depositional structure, apparent lack of a confining depositional basin, the abundant intraclasts, rarity of Cambrian chert, and indicators of low-energy conditions.

5.2.2 Petrographic diagnosis and interpretation of middle Tertiary tufaceous lithologies from Riversleigh by comparison with recent tufaceous lithologies

Figure 5.14 illustrates petrography of a sample of recent tufa collected at Indarri Falls, Lawn Hill, in Queensland. Figure 5.15 shows petrography of a sample of recent micritic tufa collected at Bitter Springs, Mataranka, in the Northern Territory. These samples exhibit petrological features that may be considered diagnostic of tufa (see Section 4.4.2). These include:

1. Mineralogical composition is primarily of micrite exhibiting dense, laminar (isopachous) and 'clotted' textures that often form as the result of biological processes.

2. Highly variable texture with open fabric characterised by a matrix comprised of a poorly sorted heterogeneous assortment of particles coated and cemented with micrite, and abundant irregular voids of various shapes and sizes.

3. Heterogeneous particles include gastropod shells and shell fragments, ostracod shells and shell fragments, sand grains, fragments of reworked tufa and lumps of sediment.

4. Abundance of moulds of organic structures (regular ovate voids, usually with laminar micritic coatings) usually formed from macrophyte tissues or insect tubes that have since decayed.

Figure 5.16 illustrates the petrography of representative samples of heterogeneous carbonate from Riversleigh. This lithotype (which is assigned to a facies and described in more detail below) is the most common and widespread at Riversleigh. It is easily recognised as gastropod-rich heterogeneous poorly-sorted carbonate containing reworked sand to gravel-sized clasts of micritic carbonate (i.e. see Figures 5.20 and 5.21). Using the carbonate classification scheme of Dunham (1962), Megirian (1992) described outcrops of this lithotype as clastic limestone comprised of conglomerate, breccia, calcarenite and calcwacke.

Figure 5.17 illustrates the petrography of a representative fossil deposit at Riversleigh, Ringtail Site. It is clearly apparent that these Tertiary lithotypes are both very similar to

each other as well as being very similar to tufa from Indarri and Mataranka (Figures 5.14, 5.15). They all share the same petrological characteristics of tufa including highly variable heterogeneous open fabric comprised of coated and cemented particles, abundant irregular voids, moulds of organic structures (regular ovate voids), micrite with dense, clotted and laminated textures and a variety of poorly sorted particles including gastropod shell fragments, sand and lumps of sediment. There are also fragments of bone and calcite crystals in the Riversleigh specimens.

In contrast to the recent tufa samples, voids in the Tertiary samples are filled with calcite spar, rather than being empty.

These representative Tertiary lithologies can be interpreted as forms of tufa, and so too can other lithologies from deposits at Riversleigh that share similar characteristics. They can be interpreted as having been formed by tufagenesis and to thus comprise tufagenic facies. Analysis of petrography (below) has shows that these tufaceous lithotypes are widespread at Riversleigh. Figure 5.18 illustrates comparative petrography of recent and fossil tufaceous lithologies from a variety of localities at Riversleigh, showing a wide variety of characteristic features that are shared between the two.

The application of this diagnosis to the primary heterogeneous carbonates at Riversleigh allows alternative interpretations of lithofacies and depositional processes to the earlier interpretations of the system as a carbonate analogue of a siliclastic proximal alluvial as first proposed by Megirian (1992) and upon which subsequent models and interpretations rely (i.e. Ford and Pedley 1996, Creaser 1997, Archer *et al.* 1997).

5.2.3 Description and interpretation of primary heterogeneous carbonate host facies

This group can be divided into three lithological types:

1. Intraclast (heterogeneous intraformational) tufa facies.
2. Basal facies, including extraclast tufa and calcarenite.
3. Pedogenic facies, including altered silicate and calcrete.
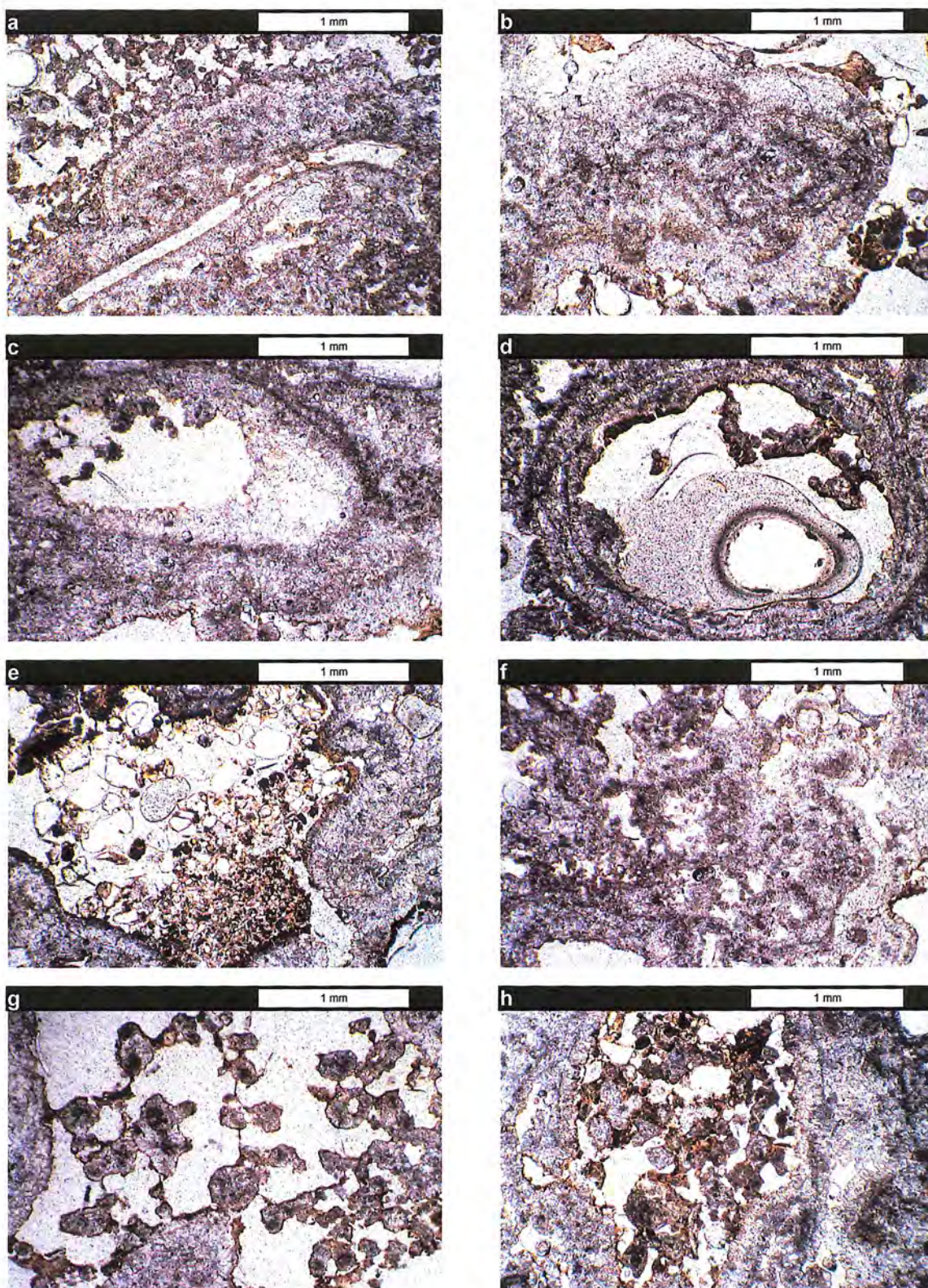
Figure 5.14: Petrography of recent tufa from Indarri Falls, Lawn Hill, Queensland. a) Laminated micritic binding a shell fragment and open coated grains texture (PP; EP69). b) Laminated micrite with 'clotted' texture (PP; EP69). c) Laminar micrite (PP; EP69). d) Laminated micrite formed around a large ovate void, probably originally filled by organic matter such as a plant tissue (PP; EP69). e) Lump of siliceous sandy sediment (PP; EP69). f) Bio-precipitated micritic texture, at lower left is a small void with laminar binding resembling a small insect burrow (PP; EP69). g) Open fabric comprised of coated grains texture (PP; EP69). h) Combination of coated grains and laminar micritic textures (PP; EP69).

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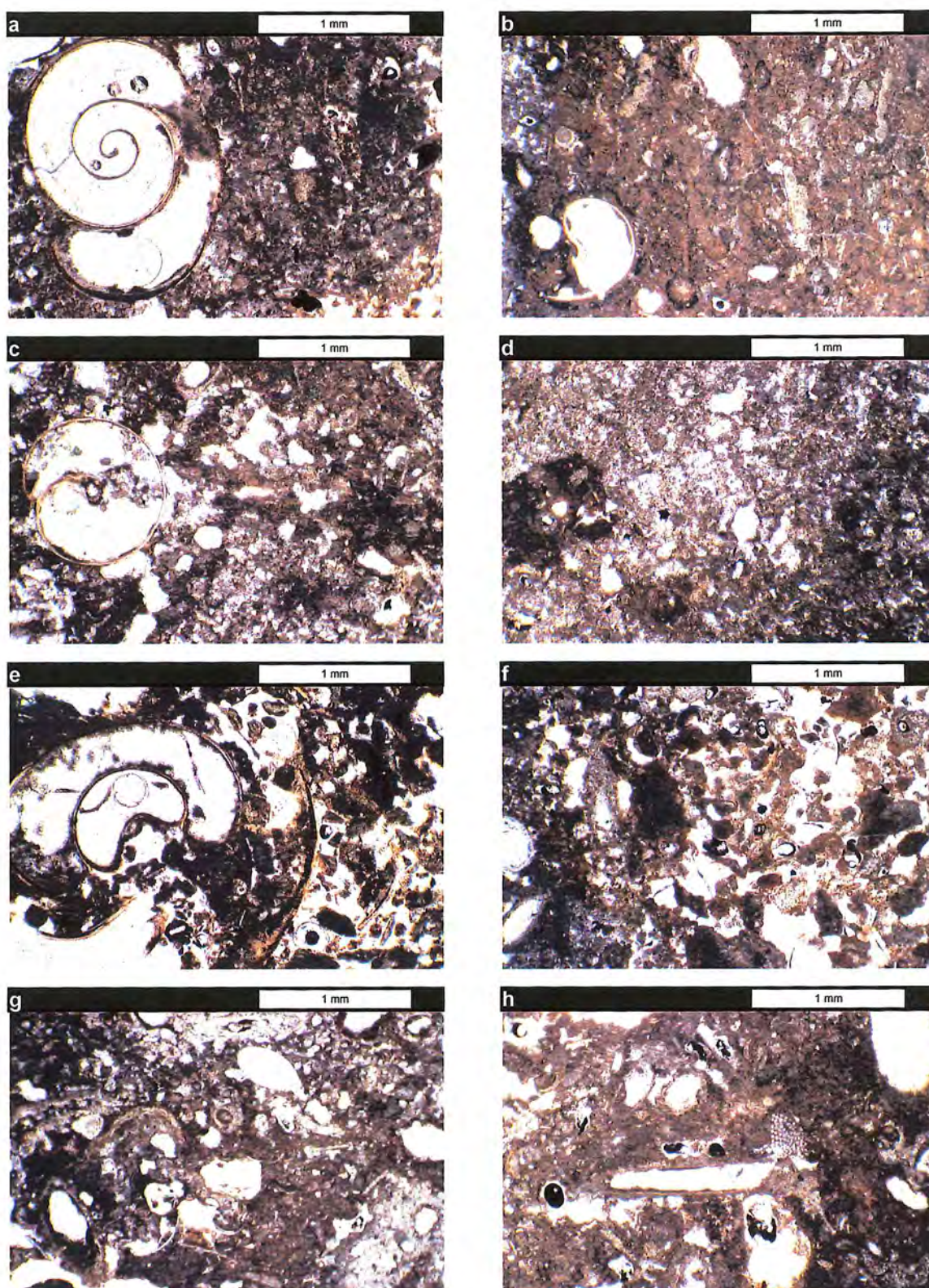
Figure 5.15: Petrography of recent micritic tufa from Bitter Springs, Mataranka, NT. a) Dense micritic texture containing a gastropod (PP; RA2003-5B). b) Dense micritic texture containing gastropods and irregular voids (PP; RA2003-5A). c) Micritic texture containing gastropods and irregular voids (PP; RA2003-5B). d) Micritic texture containing reworked tufaceous intraclasts and irregular voids (PP; RA2003-5B). e) Gastropod shell partially filled with bio-precipitated micrite and detritus (PP; RA2003-5B). f) Open fabric consisting of micrite-bound particles (PP; RA2003-5B). g) Heterogenous texture showing laminated precipitation around ovate voids, irregular voids and ostracods (PP; RA2003-5A). h) Dense micritic texture containing a variety of structures including ovate voids, shell fragments and a structure resembling the eye of an insect (PP; RA2003-5B).
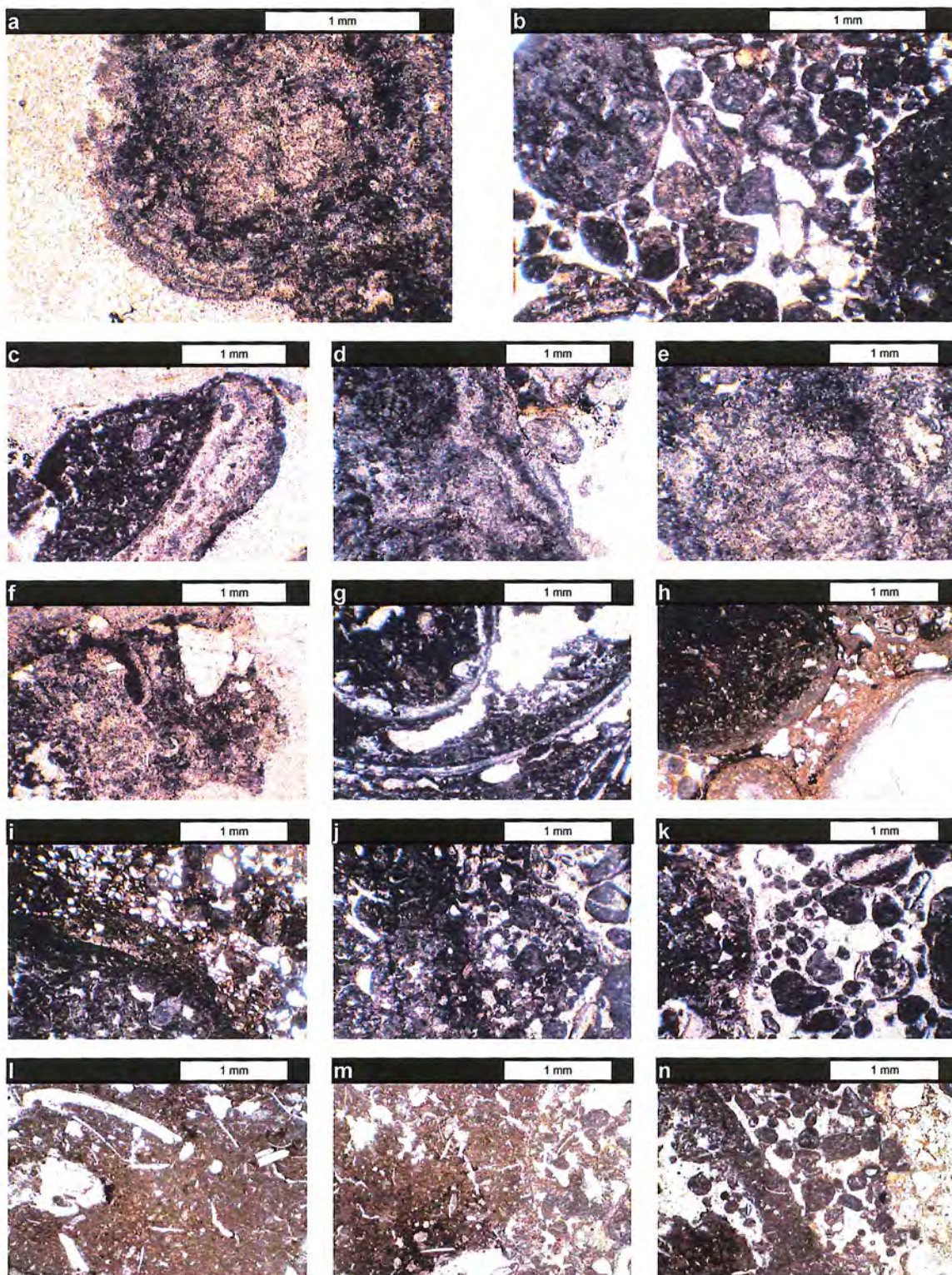
Figure 5.16: Petrography of tufaceous lithotextures from outcrops of typical Tertiary heterogeneous carbonate deposits at Riversleigh. Most voids are filled with calcite. a) Bio-precipitated laminated micrite with 'clotted' texture, fine crystalline matrix (PP; RA2003-1; Mesa 3). b) Open fabric of large tufaceous intraclasts and peloids with nuclei including tufaceous intraclasts, shell fragments and sand or rock fragments (PP; RA2003-3B; Hal's Hill). c) Micritic tufaceous intraclast with secondary bio-precipitated coating in sparry matrix. (PP; RA2003-1; Mesa 3). d) Laminated micritic texture (PP; RA1; Mesa 3). e) 'Clotted' texture of bio-precipitated micrite (PP; RA1; Mesa 3). f) Bio-precipitated micrite and a large rounded siliceous sand grain (PP; RA2003-1; Mesa 3). g) Gastropod shell partially filled with bio-precipitated micrite and detritus (PP; RA2003-3A; Hal's Hill). i) Tufaceous intraclast and gastropod

bound in laminar and peloidal micrite (PP; RA2003-4; Lane's Leap). g) Gastropod shell partially filled with bio-precipitated micrite and detritus (PP; RA2003-3A; Hal's Hill). i) Tufaceous intraclasts in matrix with abundant siliceous sand particles (PP; RA2003-4; Lane's Leap). j,k) Open fabrics comprised of globular textures (peloids). l,m) Dense micritic textures with irregular voids, shell fragments and coated particles (PP, 150A, above White hunter Site). n) Open fabric comprised of combination of micritic, coated grains and arenaceous textures (PP, 150A, above White hunter Site).
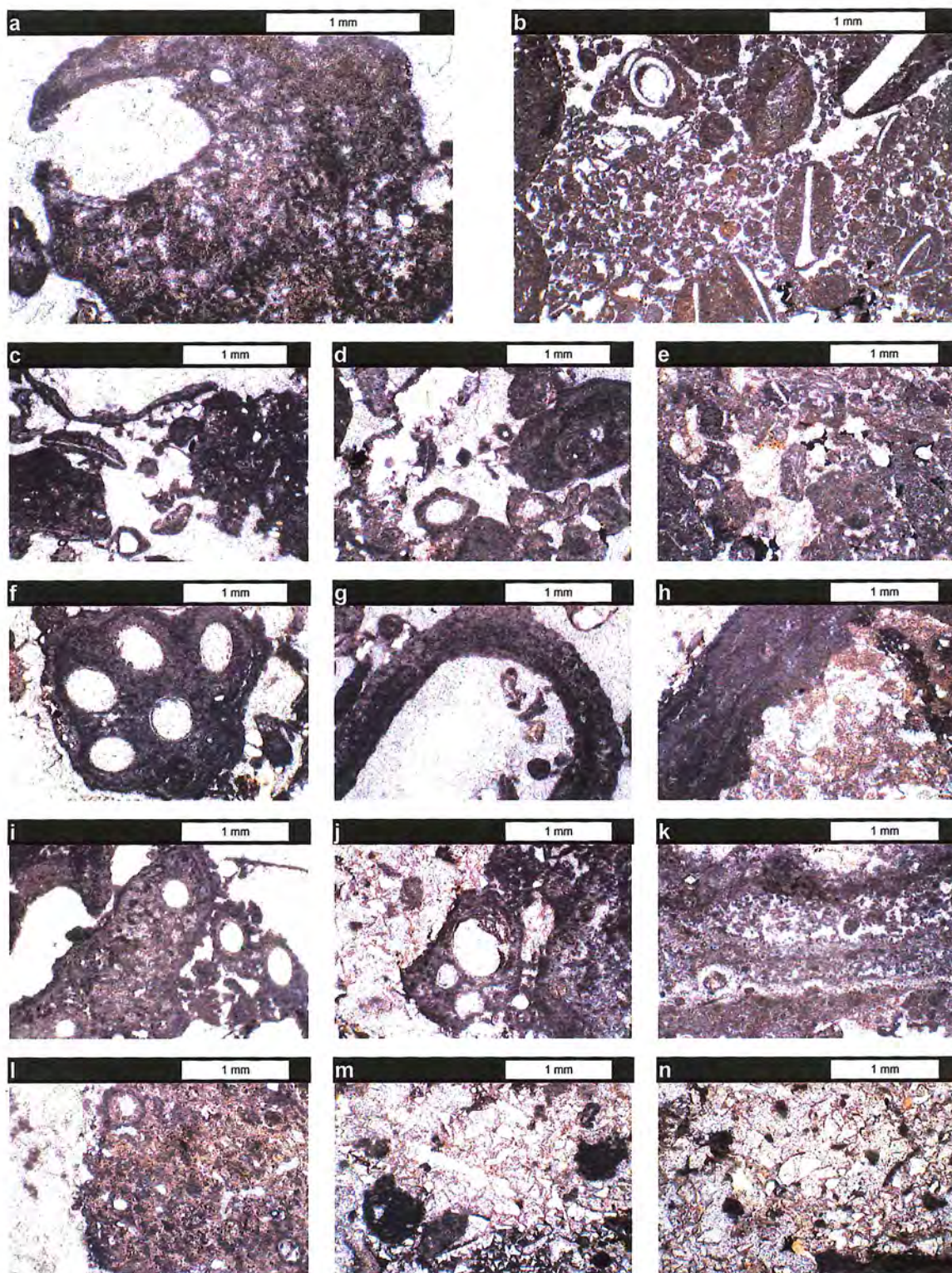
Figure 5.17: Petrography of tufaceous lithotextures from the outcrop at Ringtail Site, Riversleigh. a) Ovate void with surrounded by laminar micrite with 'clotted' texture (PP; R137A). b) Coated particles texture. Particles are different sizes and may be comprised of fragments of intraclasts, coated voids, shell, bone and sand and are often bound together by laminar micrite. (PP; EP23). c,d) Open fabric comprised of coated grains texture and intraclasts with irregular spar-filled voids (PP; R137A). e) Intraclasts and coated particles bound by laminar micrite with irregular voids (PP; R137). f,g) Laminar micrite coating ovate voids of probable organic origin, representing mould of either insect tube holes or plant material (PP; R137A). h) Dense laminar micrite (PP; R137). i) Micrite with 'clotted' texture surrounding ovate voids resembling insect tube holes (PP; R137A). j) Micrite with 'clotted' texture surrounding ovate voids

resembling insect tube holes, matrix composed of detrital crystals (PP; R137). k) Laminar micrite with 'clotted' texture (PP; R137). l) Small detrital intraclasts and sand grains in micrite, detrital crystals in matrix on left (PP; R137). m) Detrital crystals texture (PP; R137). n) Arenaceous texture comprised of sand grains, detrital crystals and bone fragments (PP; R137).
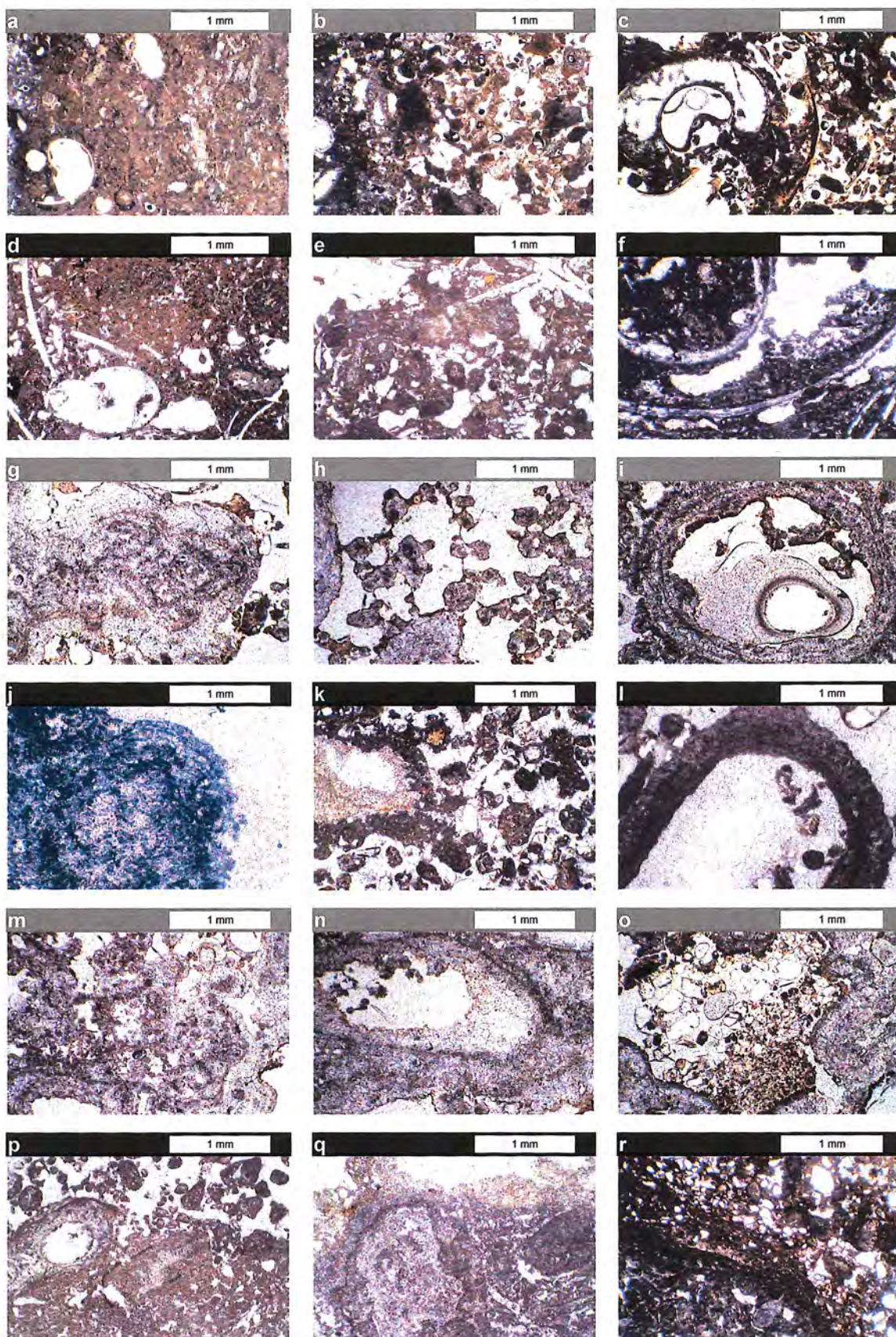
Figure 5.18: Comparison of petrography of tufaceous lithotextures in samples of recent tufa and middle Tertiary carbonates from Riversleigh. Images of recent specimens are labelled in grey, fossil specimens are labelled in black. a/d) Dense micritic tufa containing abundant gastropods, ostracods, shell fragments

derived from these organisms and irregular voids (PP; RA2003-5A; Bitter Springs, Mataranka/ PP; R107; Jaw Junction Site). b/e) Open fabric consisting of connected irregular voids and a variety of particles bound by biologically precipitated micrite (PP; RA5B; Bitter Springs, Mataranka/PP; R110; Main Site). c/f) Gastropod shells partially filled with biologically precipitated micrite and detritus (PP; RA2003-5B; Bitter Springs, Mataranka/PP; RA2003-3A; Hal's Hill). g/j) Laminar bio-precipitated micrite exhibiting 'clotted' texture (PP; EP69; Indarri Falls, Lawn Hill/PP; RA2003-1; Mesa 3). h/k) Open fabric consisting of coated particles textures (PP; EP69; Indarri Falls, Lawn Hill /PP; EP74; White Hunter Site). i/l) Laminated micrite surrounding large voids that are probably formed by coating of original organic material that has subsequently decomposed (PP; EP69; Indarri Falls, Lawn Hill /PP; R137A; Ringtail Site). m/p) Open bio-precipitated fabric consisting of laminar micrite and small ovate voids that resemble insect tubes. n/q) Laminated micritic textures (PP; EP69; Indarri Falls, Lawn Hill /PP; EP74; White Hunter Site). o/r) Clumps of siliceous sandy sediment (PP; EP69; Indarri Falls, Lawn Hill /PP; RA2003-4; Lane's Leap).

Selected stratigraphic logs of outcrops of primary heterogeneous carbonates are illustrated in Figure 5.19.

5.2.3.1 Intraclast tufa facies

This facies consists of micritic gastropod-rich carbonates and heterogeneous poorly-sorted carbonate containing reworked sand to cobble-sized clasts of micritic carbonate. This includes the clastic carbonates of Tedford (1967) and calclutites, conglomeratic limestone, calcarenite, calcwacke (also described as conglomerates and breccias) of Megirian (1992).

Distribution

This ubiquitous facies type comprises the majority of deposits at Riversleigh including D Plateau, Gag Plateau, Southern Gag Plateau and the mesas, including a large number of fossil localities (see Figure 5.3).

Structure and depositional geometry

Contact with the basement and/or basal facies is undulating and is often obscured by scree. Megirian (1992) estimated the maximum thickness of outcrops to be approximately 30m, Creaser (1997) calculated the maximum thickness of the D Plateau deposits to be approximately 40m.

There are two forms of bedding-like structure:

1. Large-scale bedding. This is more easily recognisable from the air and in airphotos, is usually not readily distinguished by lithology on the ground. These beds usually exceed 2m in thickness and are often distinguished by differences in overall outcrop weathering morphology that can be traced for tens or hundreds of metres (Figure 5.20 a, b).

2. Small-scale discontinuous bedding. On the ground, variations in lithology are often recognisable as random vertically and laterally discontinuous changes in the concentration of reworked Tertiary carbonate clasts (Figure 5.19). These 'beds' can be normally graded; can occasionally appear to exhibit lenticular profiles and to dip gently; and can be traced for several metres to tens of metres.
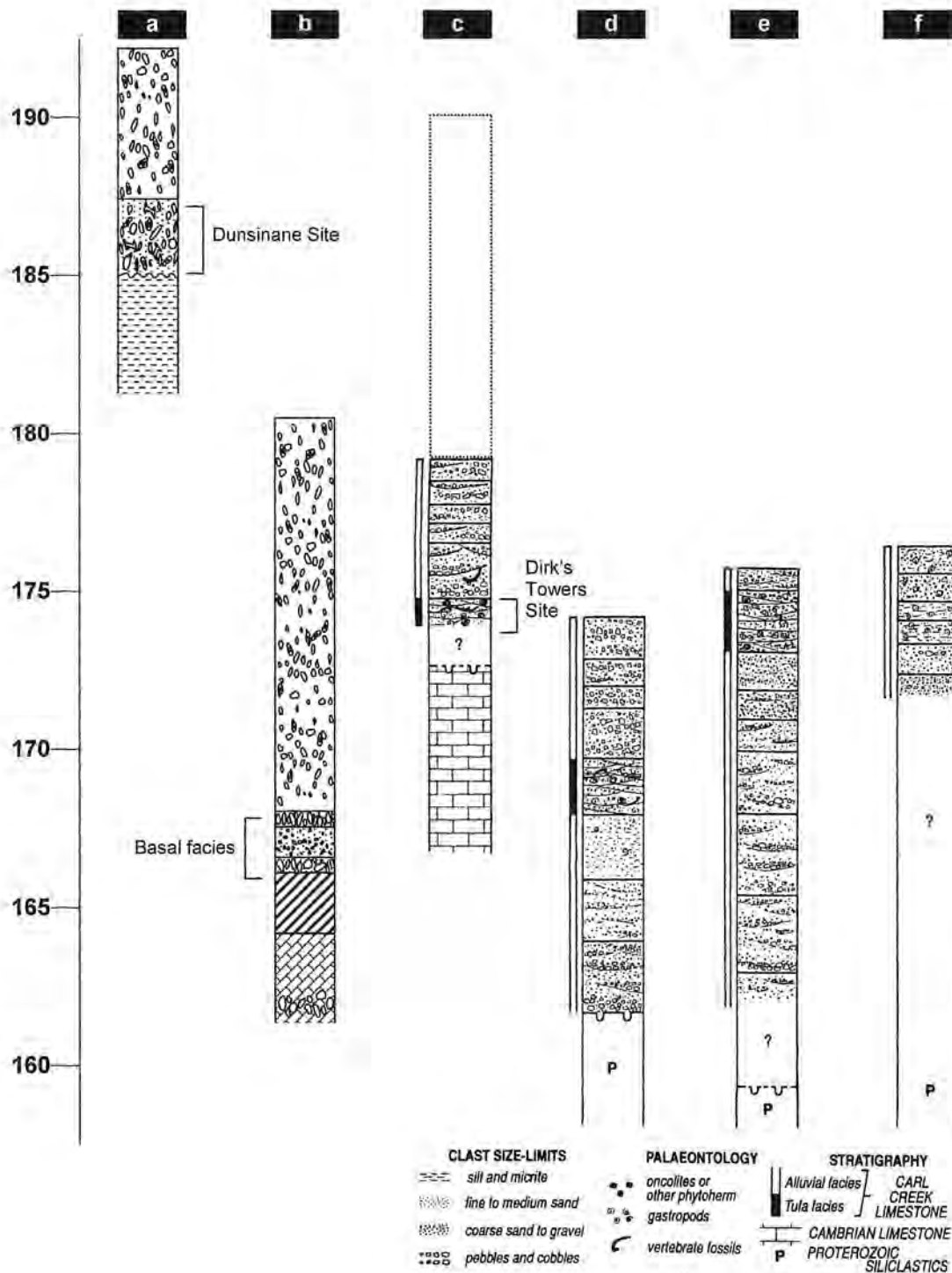
Figure 5.19: Stratigraphic logs from selected profiles of Tertiary heterogeneous carbonate deposits (=Carl Creek Limestone) at Riversleigh. Profile a is from Dunsinane Site, profile b is from Lane's Leap, profile c is from D Plateau, profile d is from Mesa 6 and profiles e and f are from Mesa 7 (see Figure 2.4). Profiles c, d, e and f are from Megirian (1992), these logs appear to be of vertical exposures only and do not include entire relief of outcrops (i.e. do not show total thickness). Section a is comprised of 4m Cambrian chert; 2.5m weathered intraclast and micritic tufa with abundant quartz sand, vertebrate fossils and phosphatic nodules; 5m intraclast tufa with heterogeneous texture. Section b is comprised of Cambrian limestone basement with chert nodules; 2m scree; 2m basal facies including 50cm extraclast tufa with arenaceous texture, 1m intraclast tufa with abundant chert pebbles and 50cm extraclast tufa; 12-13m intraclast tufa with heterogeneous texture. The fossil deposit at the base of Section c is a probable cave deposit, rather than a primary host deposit. A further 10m of overlying intraclast tufa that completes that profile is depicted with dotted lines. These logs illustrate successions of lithologically similar, poorly

sorted intraclast tufa and micritic tufa facies that do not correlate between separate profiles. Because of the complexity of the deposits, interpretations of distinctions between lithology and clast-sizes as depicted by Megirian are to a large degree subjective. As a result, structure of intraclast tufa is not represented in profiles a and b (provided by the author). There are no marker beds or distinctive lithological features that span the entire deposit. Note the undulating basement contact and varying thickness of Tertiary outcrops. In sections c to f, the 'oncolites or other phytoherm' are actually spelaean deposits of cave pearls and flowstone misinterpreted as alluvial tufa facies; there is no distinction made between chert lithoclasts and Tertiary carbonate intraclasts; the 'alluvial facies / tufa facies' distinction is an artificial division of these lithotypes that are actually the same. These problems with previous interpretation are discussed in more detail in the text. After Megirian (1992).

Occasionally, extensive horizons containing fossil bone may extend for hundreds of metres (i.e. near Hiatus Site and on Mesa 1).

Delineation of bedding by exposure or contact surfaces is often unclear or not apparent and there are no horizons that could be used as markers throughout the entire deposit. Additionally, the karst weathering pattern of outcrops can superimpose apparent horizontal 'stratification' that does not necessarily conform to the patterns of lithological variation (Figure 5.20 e, f). Because of the random distribution of variations in lithological texture and difficulty identifying and tracing individual beds, definitive vertical and/or lateral stratigraphic correlation of profiles or deposits separated by distances of even tens of metres is usually not possible.

Some apparent small-scale layering is apparent at Dunsinane Site, which has been mapped and studied in greater detail (Arena 1997; Figure 5.30d, e). This is discussed in more detail below (Section 5.2.5).

Stratigraphic logs (Figure 5.19) illustrate vertical successions of intraclast tufa facies, and the lateral discontinuity between beds from different sections.

Flow structures, particularly cross-beds are absent. Some apparent scour-and-fill structures were reported by Megirian (1992).

Features of these deposits exhibiting unrestricted depositional geometry and heterogeneous texture are illustrated in Figure 5.21.

Description and interpretation

In outcrop deposits of this facies type are usually very hard and dense, ranging in colour from white to yellow, orange and brown (Figure 5.21). Micritic intraclasts are often contrasting shades of yellow, orange and brown, producing a 'mottled' appearance. Karst weathering morphology is a characteristic feature of outcrops.

Examples of characteristic petrography of this facies type from a number of localities at Riversleigh are illustrated in Figures 5.22, 5.23.
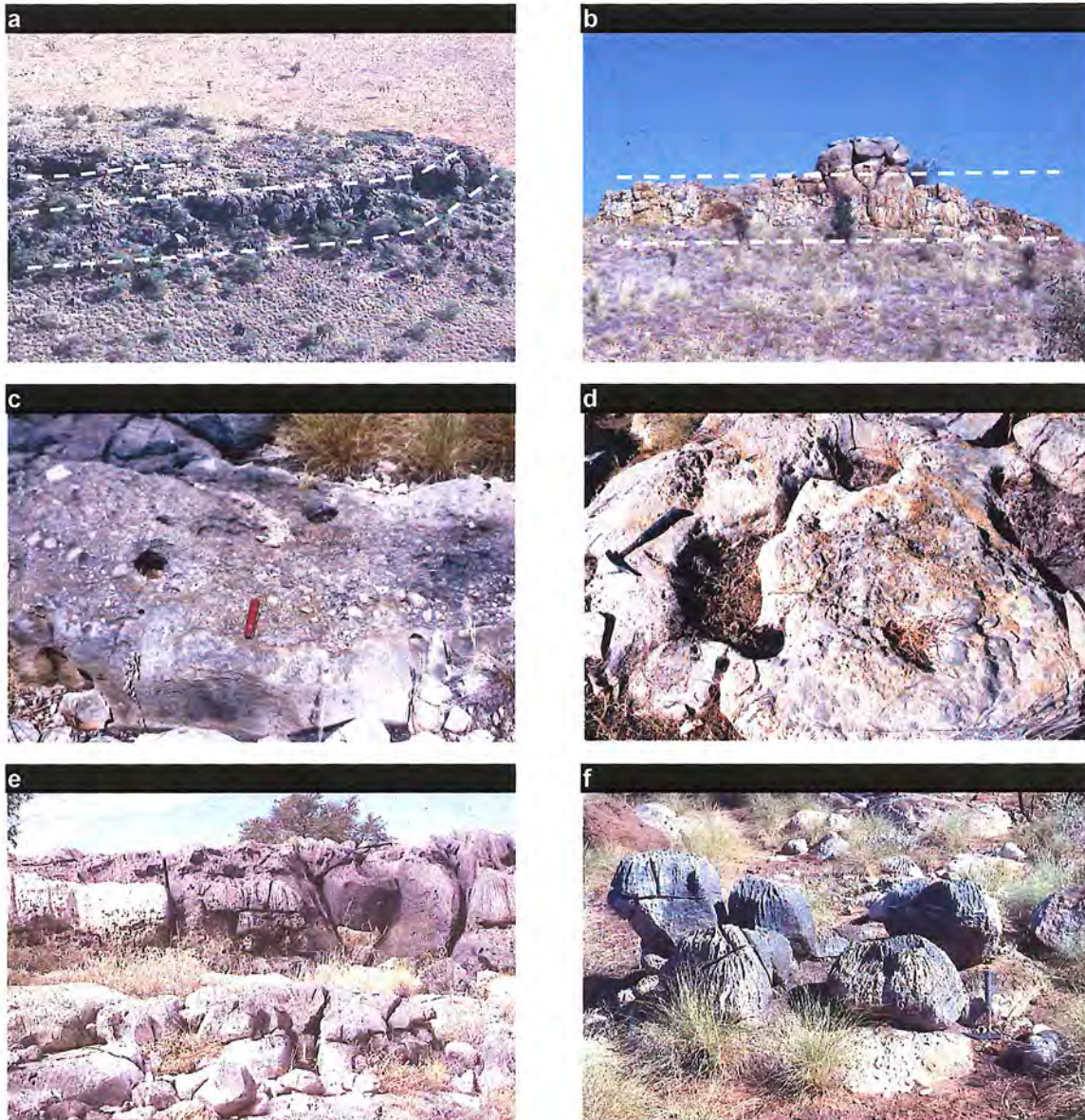
Figure 5.20: Bedding and apparent 'stratification' in Riversleigh Tertiary carbonates. a) Large-scale bedding indicated by differential weathering of beds, and aligned sub-horizontal lineaments that suggest bedding patterns, the high point at centre left appears to be a remnant of an overlying large-scale bed. The apparent dip of bedding in this image is due to perspective error. Mesa 3 from the air, looking east, the lower bed is several metres thick. b) Differential weathering of successive large-scale beds. The lower layer contains basal facies and is approximately 2-3 m thick. C Site, looking west. c) A rare clearly delineated contact between intraclast tufa overlying gastropod-rich micritic tufa. The contact is undulating and neither lithology can be traced laterally to any useful degree. Note the outcrop in the background appears different to the intraclast tufa in the foreground which is on the same horizon. Gag Plateau. d) Lateral variation in distribution of tufaceous intraclasts in micritic matrix. The concentrations of large intraclasts occur in a pattern that does not appear to form a horizontal layer. This irregularity is typical of Riversleigh heterogenous carbonates, and combined with karst sculpting that does not conform to changes in lithology or internal structures in the rock, makes discerning any stratigraphic patterns impossible. Southern Gag Plateau. e) Apparent 'stratification' caused by karst weathering patterns. The step-like layering producing horizontal surfaces and the differential surface colouration of outcrops do not necessarily correspond to variations in lithology, but are at least in part attributed to karst processes, which are evident in the well-developed rills, grikes and karren that characterise the surface. The uppermost layer is approximately 2 m thick, Upper Burnt Offering Site. f) Apparent 'stratification' caused by weathering pattern in a small outcrop. The horizontal weathering surface and colouration pattern are as much the product of karst processes as the deeply etched solution structures on the surface of the outcrop. Unnamed locality near 7 Year Bitch Site.

Petrographically, this facies type is characterised by combinations of the following lithotextures described above:

1. Arenaceous texture
2. Intraclasts texture
3. Globular texture
4. Bio-precipitated texture
5. Micritic texture
6. Detrital crystals texture

Combinations of these lithotextures, as well as abundance of heterogeneous particles, moulds, gastropods, ostracods and irregular calcite-filled voids are typical of the lithotypes interpreted as tufaceous described above in Section 5.2.2. Micritic and globular textures are here considered to represent micritic and peloidal tufa. Thus, these facies which are comprised of tufaceous intraclasts in micritic and/or peloidal tufa matrix are considered to be intraclast tufa.

Detrital crystals texture is considered to be derived from calcite rafts. Drysdale (1995) observed calcite rafts forming at Louie Creek on the surface of quiet pools that were not part of the main flow system and were exposed to direct sunlight. Calcite rafts were observed in the active tufagenic system, and preserved in older deposits along the Gregory River by Carthew *et al.* (2003). This texture is considered indicative of the presence of standing water.

Networks of very large interconnected voids filled with fine, iron-oxide-rich calcareous sediment are common in some tufaceous outcrops (Figure 5.21h). These could represent macrophyte root structures preserved in situ by ongoing tufagenesis, although root patterns are not easily recognisable in these structures. It is also possible that these structures are in situ invertebrate burrows and cocoons. Larval tufa formed by a variety of insects was recognised and described from Louie Creek (Drysdale 1995). It is considered most likely here that this lithotype is a siliceous iron oxide-rich limy matrix containing reworked tufaceous intraclasts, producing a conspicuous characteristic weathering pattern.
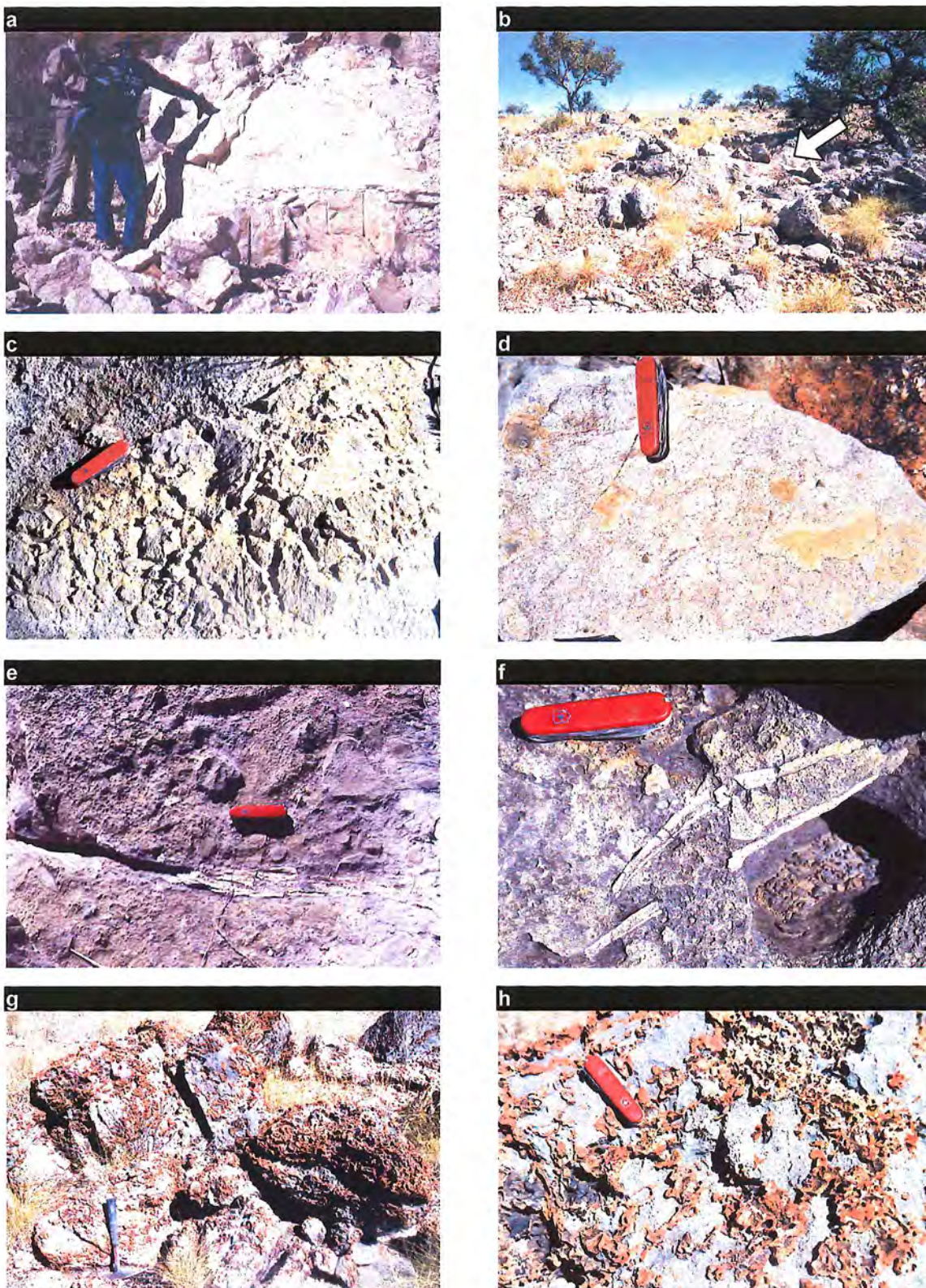
Figure 5.21: Features of outcrops of intraclast tufa deposits at Riversleigh. a) Section through thick beds of gently dipping micritic and intraclast tufa that contain occasional concentrations of vertebrate fossils, Hiatus Site. b) Outcrop morphology of fossiliferous tufagenic deposit at Courtenay's Cache Site. Vertebrate bone occurs in the outcrop marked with an arrow. The lithology is not delineated or different to surrounding outcrops in the section. c) Outcrop of unfossiliferous intraclast tufa showing characteristic texture enhanced by weathering, top of Gag Plateau. d) Fresh section through slab of intraclast tufa showing tufaceous intraclasts in micritic matrix, Jaw Junction Site. e) Large vertebrate bone in intraclast tufa, Main Site. f) Section through an *in situ* chelid turtle carapace and plastron, E Site. g, h) Infill/root mould/burrow structures, NW of Sticky Beak Site.

Age

Vertebrate faunas found in deposits of this facies-type are late Oligocene or middle Miocene in age (Archer *et al.* 1997). Late Oligocene faunas are dispersed widely throughout the system at D Plateau, Southern Gag Plateau, Mesa 1 and Mesa 3 (Figures 2.4, 5.3), whereas middle Miocene faunas from facies of this type are restricted to outcrops on the north western edge of Gag Plateau. While faunas have not been collected from outcrops on other mesas, their lithology is considered the same as outcrops that are conformable with deposits from which late Oligocene faunas have been collected (Megirian 1992). Thus all heterogeneous intraformational tufa deposits at Riversleigh are considered here to be late Oligocene in age, with the exception of the northwest parts of Gag Plateau, which are considered to be middle Miocene in age.

Vertebrate faunas and taphonomy

Faunal representation at the generic and species levels at Riversleigh is very complex and various patterns in Riversleigh faunas have been recognised (i.e. Cooke 1997a, Black 1997a, Myers 2002, Crosby 2002). By necessity, discussion here is in general terms only. Further detailed study of individual faunas and groups of faunas should contribute to the understanding of concepts outlined here.

Isolated bone fragments, usually chelid or crocodilian, are often encountered in outcrops of this facies type throughout the Riversleigh area. Vertebrate fossil deposits occur as higher concentrations of bone, usually without delineation marking the limits of bone occurrence.

Aspects of the taphonomy of vertebrate assemblages from selected localities, including Dunsinane Site, White Hunter Site and Ringtail Site, have indicated that preservation in these tufagenic deposits is likely to have occurred in low-energy environments without much transport (Arena 1997, Myers 2002, Bassarova 2004). In general broken specimens often exhibit sharp fracture surfaces, fragments are usually found in close association, and there is limited rounding by abrasion. Because small and fragile fossils, such as those of bats, birds and lizards that would normally be destroyed by transport are present in many assemblages along with the bones of much larger animals, transport
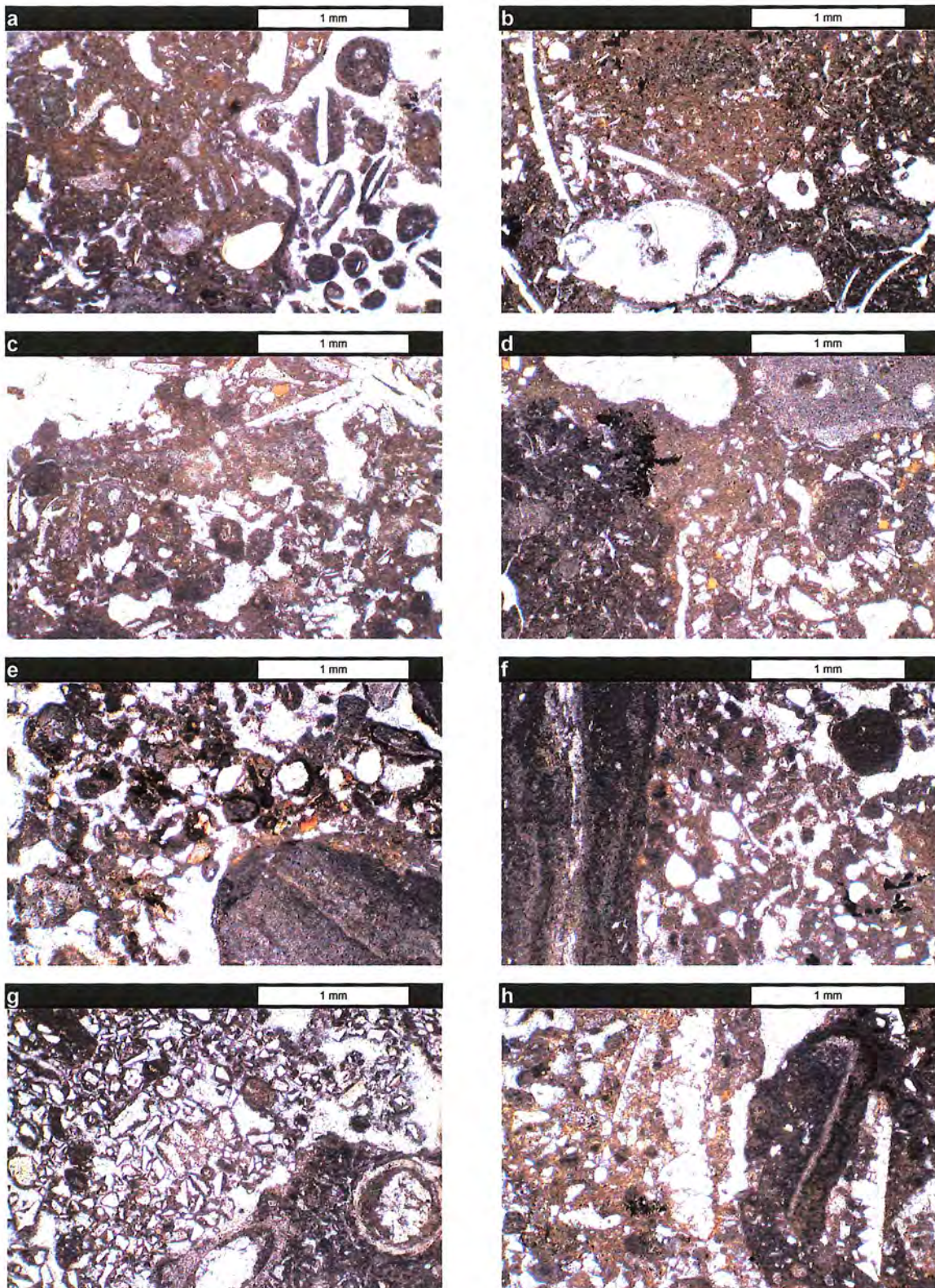
Figure 5.22: Petrography of intraclast tufa from various localities at Riversleigh. a,b) Micritic and coated particles textures with abundant gastropods and ostracods (PP; R107; Jaw Junction Site). c,d) Detrital crystals, intraclasts and micrite with irregular voids (PP; R110; Main Site). e,f) Intraclasts with coated particles and micritic textures (PP; R111; Skull Site). g) Organic moulds and abundant detrital crystals in micrite (PP; R121; Courtenay's Cache Site). h) Intraclasts in detrital crystal-rich micritic matrix (PP; R112; Bird Bone Site).
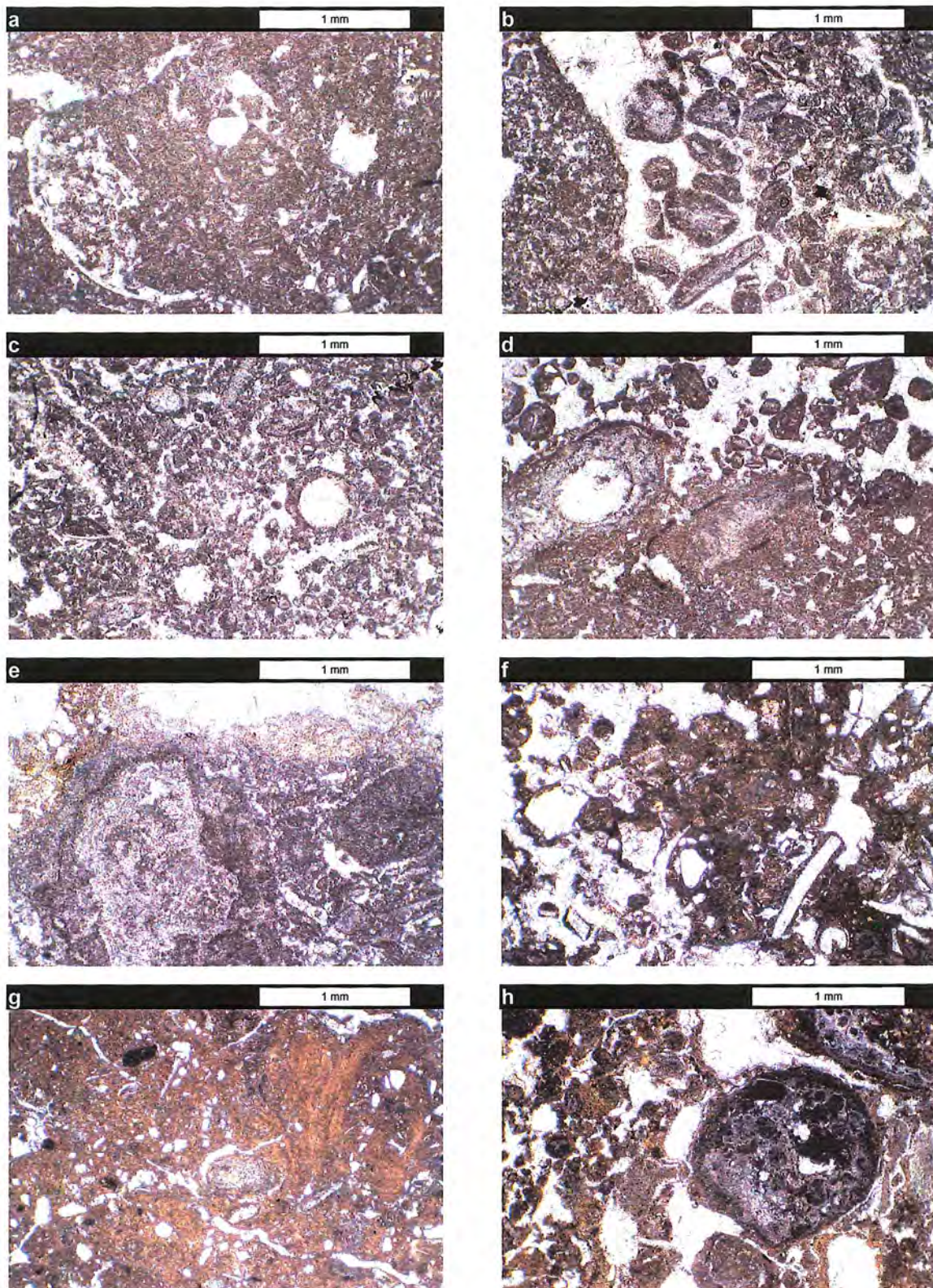
Figure 5.23: Petrography of intraclast tufa from various localities at Riversleigh. a) Micritic texture with gastropods and irregular voids (PP; R147B; Hiatus Site). b,c) Coated particles texture (PP; R147A; Hiatus Site). c) Hiatus Site (PP; R147A). d) Open fabric comprised of coated particles texture. Intraclast and an ovate void resembling an insect tube at centre (PP; R147B; Hiatus Site). e) Laminar micrite around intraclast with irregular voids (PP; EP74). f) Particles including intraclasts and shell fragments coated with micrite (PP; EP74). g) Dense micritic matrix (PP; R108A; Bob's Boulders Site). h) Micrite-coated intraclasts and coated particles with irregular and ovate voids (PP; R108A; Bob's Boulders Site).

is considered to have played a limited role in the accumulation of these assemblages which are thus generally considered to be largely autochthonous.

Faunas from deposits of this facies-type tend to exhibit greater abundance and diversity of aquatic taxa, including crocodilians, chelid turtles (Figure 5.21f), lungfish and bony fish (Archer *et al.* 1994, Creaser 1997).

The Riversleigh Local Fauna (Faunal List 1) and the White Hunter Site Local Fauna (Faunal List 2) are representative late Oligocene (Zone A) faunas from Riversleigh. Both faunas are characterised by abundant remains of large crocodilians of the genus *Baru* and chelid turtles. The White Hunter Site Local Fauna contains four species of crocodilian exhibiting a variety of different head shapes (Willis 1997) which, in combination with taphonomy indicative of autochthony of the assemblage (Myers 2002), indicates that these taxa were sympatric. True sympatry of 3 or more crocodilian species is unusual, and is comparable fossil faunas from Messel and Geisaltal in Germany that contain 6 species and modern faunas in large watercourses in the Amazon contain 3 species (Willis 1997). Additionally there are two indeterminate crocodilian forms from White Hunter Site. While the Riversleigh Local Fauna is actually a composite of faunas from several localities of late Oligocene age at Riversleigh, the representation of taxa, mainly collected from D Site, serves to illustrate the composition of key elements of faunas from this facies type. Chelid turtles from late Oligocene faunas, particularly the Riversleigh Local Fauna, tend to be large which has been interpreted as indicative of a prevalence of larger bodies of water at this time (White and Archer 1997).

The Ringtail Site Local Fauna (Faunal List 3) is a representative middle Miocene (Zone C) fauna from a tufagenic deposit at Riversleigh. Among aquatic vertebrates, this locality yields chelid turtles (of which there appear to be a number of indeterminate, apparently different kinds), the ornithorhynchid *Obdurodon dicksoni*, bony fish and lungfish, a large crocodilian of the genus *Baru*, the mekosuchine crocodilian *Mekosuchus sanderi* and the small armoured crocodilian *Trilophosuchus rackhami*. The latter taxon exhibits morphology that may indicate it was partly terrestrial and is considered similar to the modern small armoured crocodilians of the genera

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Faunal List 1: Riversleigh Local Fauna
Source locality: Sites A, B (=BMR Locality M103 and Sample Q11 locality of
McMichael (1965)), C, D, E, G, H; Locality Q12 of McMichael (1965).

CHORDATA
  NEOPTERYGII
    Orders indet.
      Families indet.
        Genera indet. spp.
  TESTUDOMORPHA
    TESTUDINES
      ?CHELIDAE
        Genus indet. sp. indet.
  ARCHOSAUROMORPHA
    AVES order indet.
      Family indet.
        Genus indet. sp.
    STRUTHIONIFORMES
      DROMORNITHIDAE
        Barawertornis tedfordi
    CROCODILIA
      CROCODYLIDAE
        Baru wickeni
  LEPIDOSAUROMORPHA
    SQUAMATA
      LACERTILIA family indet.
        Genus indet. sp.
      BOIDAE
        Morelia riversleighensis
      SERPENTES family indet.
        Genus indet. sp.
  MAMMALIA
    DASYUROMORPHIA
    DASYURIDAE
      Genus indet. sp.
    THYLACINIDAE
      Nimbacinus dicksoni
    DIPROTODONTIA
    BALBARIDAE
      Galanarla tesselata
      Balbaroo gregoriensis (G SITE)
    MACROPODIDAE
      Bulungamaya delicata
      Gumardee pascuali
      Wabularoo naughtoni
      Genus indet. sp. indet.
    MACROPODOIDEA family indet.
      Genus indet. sp.
    POTOROIDAE
      Genus indet. sp.
    ?PETAURIDAE
      New genus new sp.

DIPROTODONTIDAE
  Bematherium angulum
  Neohelos tirarensis
  Silvabestius sp.
  ZYGOMATURINAE genus indet. sp. indet.
PALORCHESTIDAE
  Ngapakaldia new sp.
  Propalorchestes ponticulus
THYLACOLEONIDAE
  Wakaleo sp. cf. *W. oldfieldi*
WYNYARDIIDAE
  ?*Namilamadeta* new sp.
CHIROPTERA
  Superfamily indet. family indet.
    Genus indet. sp.
DIPNOMORPHA
  DIPNOI
    NEOCERATODONTIDAE
      Neoceratodus sp. cf. *N. gregoryi*
MOLLUSCA
  GASTROPODA
    BASOMMATOPHORA
      PLANORBIDAE
        Physastra rodingae (Sample Q12 locality)
    STYLOMMATOPHORA
      CAMAENIDAE
        Meracomelon lloydi (Sample Q12 locality)

References for this list: Archer (1979, 1982), Archer *et al.* (1994), Black (1997a), Black and Archer (1997b), Boles (1997a), Flannery *et al.* (1982), McMichael (1965), Muirhead and Archer (1990), Scanlon (2001), Smith and Plane (1985), Stirton *et al.* (1968), Tedford (1967), Willis *et al.* (1990), Willis (1997).

Faunal List 2: White Hunter Site Local Fauna
Source locality: White Hunter Site

CHORDATA
 ARCHOSAUROMORPHA
  ACCIPITRIFORMES
   ACCIPITRIDAE
    ?Pengana sp
  ANSERIFORMES
   ANATIDAE
    Genus indet. sp indet
  CICONIIFORMES
   ?Ciconia sp.
  GRUIFORMES
   RALLIDAE
    RALLIDAE genus indet. *cf. Gallinula* sp.
  STRUTHIONIFORMES
   CASUARIIDAE
    Emuarius gidju
  CROCODILIA
   CROCODYLIDAE
    Baru huberi
    Baru wickeni
    Mekosuchus whitehunterensis
    Quinkana meboldi
    Genus indet. sp. indet. CRANIAL FORM 1
    Genus indet. sp. indet. CRANIAL FORM 2
 LEPIDOSAUROMORPHA
  SQUAMATA
   BOIDAE
    Morelia or *Python* sp. indet.
 MAMMALIA
  DASYUROMORPHIA
   THYLACINIDAE
    Badjicinus turnbulli
    Nimbacinus sp.
  DIPROTODONTIA
   ACROBATIDAE
    [Indet.]
   BURRAMYIDAE
    Burramys brutyi
   BALBARIDAE
    Balbaroo sp. 3
    Ganawamaya aediculis
    Nambaroo couperi
    [*Nambaroo* new sp. 1]
    [*Nambaroo* new sp. 2]
    Nambaroo sp. 8
    Wururoo dayamayi

   MACROPODIDAE
    Nowidgee matrix
    Nowidgee sp. 2
    Wabularoo naughtoni
    [*Gumardee* sp.]
   HYPSIPRYMNODONTIDAE
    Ekaltadeta ima
   PSEUDOCHEIRIDAE
    [New genus new sp. 1]
    [*Pseudocheirops* sp. 2]
   PETAURIDAE
    [Genus 2 sp. 1]
   THYLACOLEONIDAE
    ?Priscileo pitikantensis
    Priscileo roskellyae
   DIPROTODONTIDAE
    Bematherium angulum
   WYNYARDIIDAE
    Namilamadeta sp.
   ILARIIDAE
    Kuterintja ngama
   ACROBATIDAE
    Genus indet. sp indet
  PERAMELEMORPHIA
   YARALIDAE
    [*Yarala burchfieldi*]
    [New genus 2 new sp. 1]
    [New genus 3 new sp. 1]
    [New genus 5 new sp. 1]
  YALKAPARIDONTIA
   YALKAPARIDONTIDAE
    [*Yalkaparidon* sp.]
  CHIROPTERA
   HIPPOSIDERIDAE
    Rhinonicteris tedfordi
    Hipposideros (Brachipposideros) nooraleebus

References for this list: Archer *et al.* (1989, 1997), Black (1997), Boles, (1992, 1997a, 1997b), Brammall and Archer (1997), Cooke (1992, 1997a, 1997c), Hand (1997), Muirhead and Wroe (1998), Myers and Archer (1997), Myers (2002), Willis (1997).

Faunal List 3: Ringtail Site Local Fauna
Source locality: Ringtail Site

CHORDATA
  NEOPTERYGII
    Indet.
  TESTUDOMORPHA
    TESTUDINES
      MEIOLANIIDAE
        Meiolania sp. cf. *M. platyceps*
      CHELIDAE
        Genus indet. sp.
        ?*Emydura* sp
        ?*Pseudemydura* sp.
        Pseudemydura sp.
  ARCHOSAUROMORPHA
    PASSERIFORMES
      [Indet.]
    ACCIPITRIDAE
      [Indet.]
    CACATUIDAE
      [Indet.]
    CROCODILIA
      CROCODYLIDAE
        Trilophosuchus rackhami
        ?*Baru* sp.
        Mekosuchus sanderi
  LEPIDOSAUROMORPHA
    SQUAMATA
      AGAMIDAE
        Sulcatidens quadratus
        [Indet.]
      SCINCIDAE
        Eugongylus Group genus indet spp.
        Sphenomorphus spp. attenuate type
        Sphenomorphus Group genus indet. sp small insectivore
      BOIDAE
        Morelia riversleighensis
      MADTSOIIDAE
        [*Yurlunggur* sp.]
        [*Wonambi* sp.]
  MAMMALIA
    MONOTREMATA
      ORNITHORHYNCHIDAE
        Obdurodon dicksoni
    DASYUROMORPHIA
      THYLACINIDAE
        Maximucinus muirheadae
        [*Nimbacinus* new sp.]
      DASYURIDAE
        [Indet.]

    DIPROTODONTIA
      BURRAMYIDAE
        [*Burramys brutyi*]
      ACROBATIDAE
        [Indet.]
      PSEUDOCHEIRIDAE
        [*Marlu kutjumarpensis*]
        [*Marlu* sp. 1]
        [*Pseudocheirops* sp.]
        [New genus 2 new sp. 1]
        [*Pildra* sp. 4]
      PHALANGERIDAE
        [Indet.]
      PETAURIDAE
        [Indet.]
      DIPROTODONTIDAE
        Nimbadon lavarackorum
      WYNYARDIIDAE
        [*Namilamadeta* sp.]
    PERAMELEMORPHIA
      YARALIDAE
        [*Yarala burchfieldi*]
        [New genus 1 new sp. 3]
        [New genus 2 new sp. 1]
        [New genus 3 new sp. 1]
        [New genus 5 new sp. 1]
    NOTORYCTEMORPHIA
      NOTORYCTIDAE
        [*Notoryctes* sp.]
    CHIROPTERA
      HIPPOSIDERIDAE
        [Indet.]
      MEGADERMATIDAE
        [Indet.]
    DIPNOMORPHA
      DIPNOI
        [Indet.]
  MOLLUSCA
    GASTROPODA
      [Indet.]

References for this list: Archer *et al.* (1992, 1994), Black (1997a), Boles (1997a), Brammall and Archer (1997), Gaffney *et al.* (1989, 1992), Hutchinson (1992), Kemp (1991), Myers (2002), Willis (1993, 2000), Wroe (2001).

Paleosuchus and *Osteolaemus* that inhabit rainforest in South America and Central Africa respectively (Willis 1993).

Several specimens of a new genus and species of ostracod have been described from Ringtail Site and Gag Site, which both yield middle Miocene (Zone C) faunas and individual specimens of *Cyridosis* sp. and *Cypretta* sp. were also described from Gag Site (Archer *et al.* in prep.). The latter taxa are considered natatory whereas the former to be a sediment surface-dweller or endobenthic. The occurrence of all three types at Gag Site is considered comparable to modern southern Australian inland lacustrine assemblages that are characterised by clear, low-energy lacustrine conditions with swampy and/or grassy shallows in which ostracods live. The eggs of modern relatives of the new taxon are not resistant to desiccation indicating that water supply was permanent (*ibid.*). While this type of palaeoenvironment was thus interpreted as the likely conditions occurring at these fossil localities, it is possible that the occurrence of all of these ostracods at these localities is the result of their occurrence in reworked late Oligocene-aged tufaceous intraclasts. In either case, if the ostracods are either late Oligocene or middle Miocene, they could be considered as indicative of low-energy, relatively shallow lacustrine conditions.

Compared to faunas from cave deposits (below) the abundance and diversity of bat material in these late Oligocene and middle Miocene faunas is low.

Generally, the non-aquatic components of faunas from late Oligocene tufaceous deposits are less rich and diverse and are often restricted to large dromornithids and diprotodontids (Archer *et al.* 1994). Representatives of these groups occur in deposits of all ages and types at Riversleigh, and so do not appear to offer any diagnostic value by their presence. Some differences between faunas from tufagenic deposits and faunas from cave deposits are related to age differences between assemblages, some other possible reasons for such differences are discussed in Section 7.4.

5.2.3.2 Basal facies

The basal facies includes the 'basal conglomerate' of Tedford (1967) and Archer *et al.* (1989).
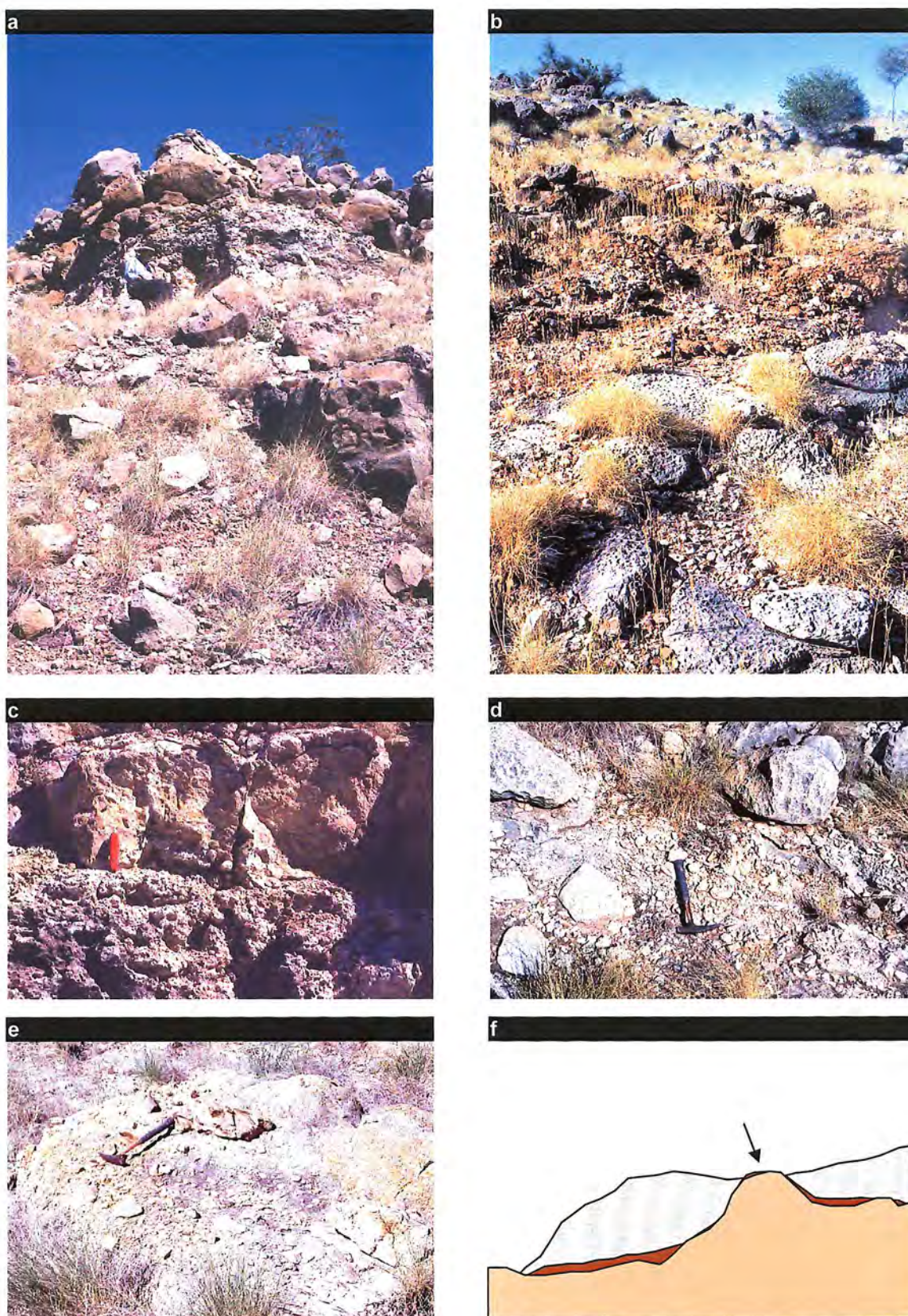
Figure 5.24: Outcrops of basal facies at Riversleigh. a) Section showing basal calcarenite (greyish) overlain by intraclast tufa (tan), below Don Camillo Site, looking south. b) Section showing Cambrian limestone in foreground overlain by basal facies comprised of brown extraclast tufa, which is overlain by grey intraclast tufa in the background. Note the characteristic texture of the intraclast tufa compared to overlying intraclast tufa. Western edge of Lane's Leap. c) Detail of part of section in 5.24a showing

contrasting textures at contact of basal calcarenite with overlying intraclast tufa. d) Outcrop of basal facies comprised of extraclast tufa, northern edge of Lane's Leap. f) *In situ* chert associated with extraclast and intraclast tufa on top of Godthelp Hill, at least 20m above basal level in the surrounding area, illustrating the extent of undulation of the basal surface. This outcrop is interpreted as a remnant of an *in situ* Cambrian deposit. g) Diagrammatic reconstruction of possible profile through Godthelp Hill looking east showing possible relationships of undulating basement (tan), basal facies (brown) and intraclast tufa facies (grey). The outcrop photographed in 5.24f is arrowed.

Distribution

Basal facies are distributed irregularly at the base of the Tertiary deposits, being absent in some areas. This facies type is present in places around the base of D Plateau, and around the northern and western base of Gag Plateau (i.e. Don Camillo Site, below Lockwood's Link Site). There is a small outcrop of this facies on the top of Godthelp Hill associated with some massive chert at approximately 185m altitude (Figure 5.24e). Rare, isolated deposits of this facies type can occur throughout the section.

Structure and depositional geometry

These deposits (Figure 5.24) vary in thickness and have been observed to be up to 2m thick. Contact with the basement is undulating. Flow structures, apart from fine layering of some calcarenites, are absent. The conformable contact with overlying intraformational heterogeneous carbonate facies is often undulating.

Description and interpretation

This facies-type is distinguished by the abundance of chert lithoclasts derived from Cambrian marine sediments in the area and the dominance of arenaceous lithotextures (Figure 5.25). If interpreted as clastic sediment, this lithology would be classified as matrix-supported chert conglomerate. Occasional thin beds of finely layered calcarenite are sometimes present. Because the sandy matrix also contains tufaceous textures, and tufaceous intraclasts are also present, the basal facies are interpreted here as extraclast tufa.

Age

These deposits are conformable with overlying intraformational heterogeneous carbonate deposits that are conformable with deposits that contain late Oligocene faunas and are thus considered to be late Oligocene in age. It is not clear whether basal facies underlying deposits containing middle Miocene faunas have a conformable contact, or are older late Oligocene deposits overlain by younger tufagenic deposits. The fossiliferous outcrop of this facies type at Sticky Beak Site has yielded a fauna considered to be Late Oligocene in age (Archer *et al.* 1997).
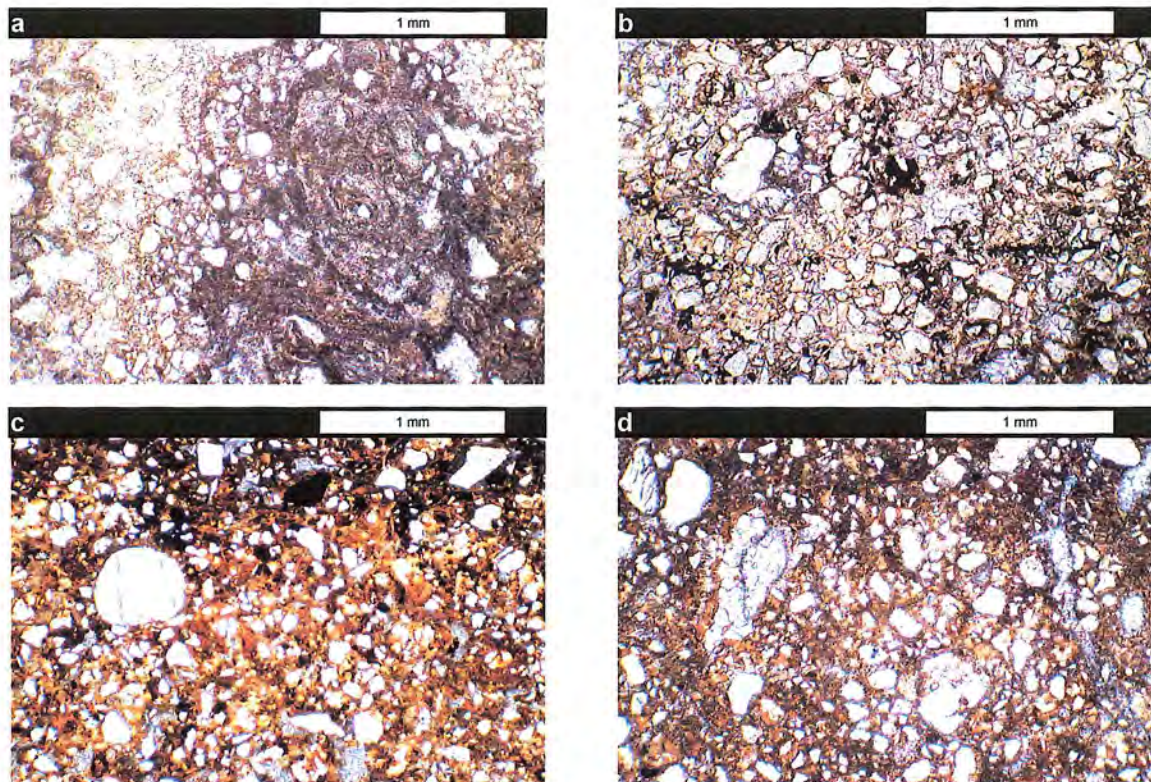
Figure 5.25: Petrography of lithotextures of basal facies. a) Extraclast tufa matrix composed of arenaceous carbonate with bio-precipitated texture (PP; R145; near Lockwood's Link Site). b) Extraclast tufa matrix composed of arenaceous carbonate (XP; R145A; near Lockwood's Link Site). c) Fine calcarenite (PP; R114; slope below Don Camillo Site). d) Fine calcarenite (PP; R115; cliff below Don Camillo Site).

Vertebrate faunas and taphonomy

Vertebrate fossils are uncommon in this facies, isolated chelid bone fragments have been observed. A fossiliferous outcrop of this facies type occurs at Sticky Beak Site.

5.2.3.3 Pedogenic facies

Altered silicate facies

Distribution

This facies occurs on the southwestern edge of D Plateau at the Coco Rox Site locality. A smaller deposit of this facies type outcrops just below Fig Tree Site.

Structure and depositional geometry

At Coco Rox Site, this facies type occurs as an undulating bed of variable thickness of up to 4m, extending laterally for tens of metres, with an apparent dip to the north. Tufaceous carbonates directly overlie and underlie the deposit. The depositional morphology is complex, and it is difficult to ascertain whether the deposit is horizontally incised or undercut and buried with tufaceous carbonate, or the deposit is itself a complex infill within the tufaceous carbonate (see Figure 5.26e). Tertiary carbonate, which extends for 2-3m below the level of the outcrop, is weathered and in relatively poor condition. Flow structures, roots or burrows are absent. This deposit requires further investigation. The outcrop near Fig Tree Site is apparently tabular and approximately 1 metre thick.

Description and interpretation

This lithotype is composed of lumps of fine-grained chalcedonic quartz forming pseudo-pisoidal structures in a matrix of quartz crystals with later sparry calcite infill (Figure 5.27). This facies is interpreted as an altered quartz-rich deposit, which may be a surficial deposit (i.e. form of silcrete), an altered siliceous infill within the Tertiary tufaceous host or altered sediment formed from siliclastic material recrystallised in the phreatic zone.

Age

No faunas have been collected from this facies type, and the uncertain relationships with the late Oligocene carbonate do not a permit confident assessment of age. Because these deposits do not resemble any other cave deposits from Riversleigh, it is more likely they are contemporaneous with late Oligocene carbonates, rather than a younger infill.

Vertebrate faunas and taphonomy

No fossils are present in this facies.

Calcrete

Outcrops of calcrete at Riversleigh are distinctive because of the contrast of their lithology and weathering morphology with tufaceous deposits, with which they may be interbedded. Calcrete deposits conspicuously lack the karst features and sculpting that characterises the tufaceous deposits (i.e. rillenkarren, grikes, etc).

Distribution

Calcrete has been observed at the western edge of Gag Plateau and at the western tip of the northwestern arm of Southern Gag Plateau.

Structure and depositional geometry

These deposits can exceed 2 m in thickness. Deposits appear massive, with primary structures such as bedding are not readily apparent (Figure 5.26).

Description and interpretation

These deposits are relatively poorly consolidated and do not exhibit karst weathering morphology (i.e. karren). Polygonal dessication cracks occur on horizontal exposure surfaces, which may be related to ongoing weathering. The deposits at the Red Cliffs locality are reddish brown in colour, and at Southern Gag Plateau brown to black. The lithology is comprised of a dense matrix rich in iron oxide, abundant quartz sand and cracks filled with spar are common (Figure 5.27). No recognisable sedimentary or tufaceous textures are present. Price (2002) interpreted this lithotype as calcrete.

Figure 5.26: Selected deposits at Riversleigh formed by pedogenic processes. a) Section of calcrete with alternating with intraclast tufa, near Dunsinane Site. This outcrop of calcrete is poorly consolidated lacks depositional structure and is rich in sand and iron oxides. b) Dark coloured *in situ* intraclast tufa, inter-bedded with calcrete in section of a. c) Habit of calcrete outcrops with distinctive weathering pattern that contrasts with classic karst weathering patterns of other Riversleigh carbonates. This outcrop is red-brown in colour and is otherwise similar to calcrete in a and b, Red Cliffs locality. e) *In situ* altered silicate at Coco Rox Site showing convoluted undulating morphology with inter-bedded intraclast tufa, approximate boundaries marked by dotted line. f) Freshly broken parts of excavated slab showing hardpan rind and nodular hardpan filling a solution pipe, Hiatus Site.
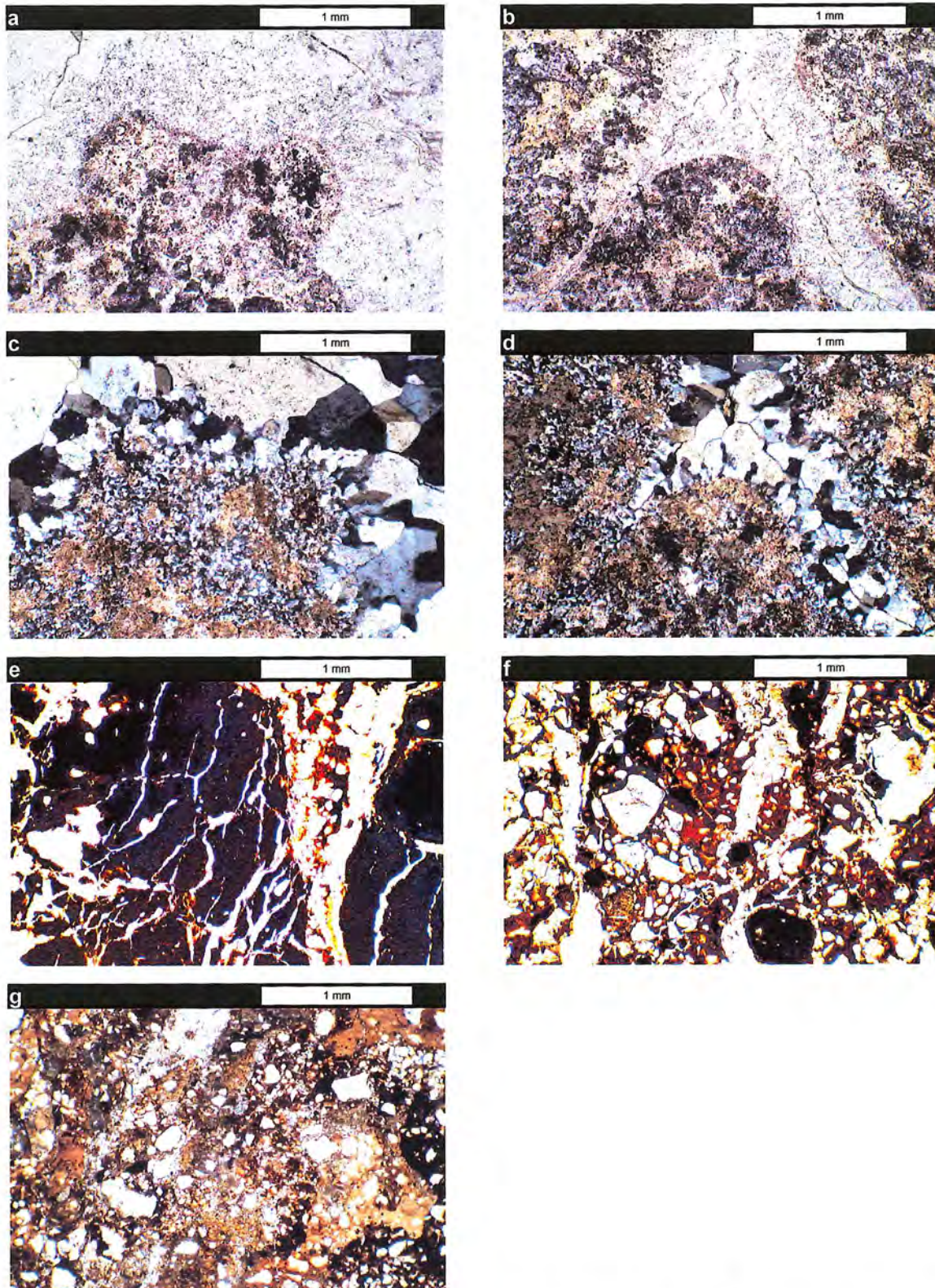
Figure 5.27: Petrography of Riversleigh lithotypes formed by pedogenic processes. a/c) Siliceous pisoid with prismatic quartz infill (PP; CR; Coco Rox Site). b/d) Siliceous pisoids with prismatic quartz infill (PP; CR; Coco Rox Site). e) Calcrete exhibiting dense amorphous matrix and spar-filled cracks (PP; R102; Red Cliffs Site). f) Calcrete containing abundant silicate fragments and spar-filled cracks (PP; R102; Red Cliffs Site). g) Calcrete exhibiting sandy texture (PP; R102; Red Cliffs Site).

Age

While no faunas have been collected from this facies type, it appears to conform with, and is interbedded with, tufagenic deposits that are conformable with deposits containing late Oligocene faunas (and possibly some deposits containing middle Miocene faunas), and thus are considered to be of comparable age.

Vertebrate faunas and taphonomy

No fossils have been observed in outcrops of this facies type, although bone has been observed in interbedded tufagenic deposits.

5.2.4 Discussion and general depositional model of primary heterogeneous carbonate facies

Vertically and laterally discontinuous deposits of intraclast and micritic tufa exhibiting normal grading and lenticular profiles could be considered representative of the tufaceous barrage pond infill component of the fluvial barrage system of Pedley (1990) and Ford and Pedley (1996). The cyclic infill, incision and localised reworking of tufaceous deposits recognised by Golubić (1969; see Figure 4.25) that characterises these systems would provide abundant reworked material to intraclast tufa deposits, rather than by transport from a distal source by high energy flow. The prevailing low energy conditions in barrage ponds would provide the depositional environment suitable for deposition of micritic lithotextures and the autochthonous accumulation of well-preserved vertebrate material of various different sizes and degrees of fragility that would comprise assemblages characterised by abundant and diverse aquatic taxa.

Based on the following characteristics of deposits, the depositional process that formed the heterogeneous carbonate deposits at Riversleigh can be interpreted as a tufagenic fluvial barrage system:

1. Dominance of tufaceous lithotextures exhibiting many similarities to modern tufaceous lithologies. Heterogeneous fabrics are comprised of laminated fragments and grains, bio-precipitated textures, coating and binding of particles and reworked fragments, abundant gastropod and ostracod shell fragments, open fabric with sparry calcite infills and calcite rafts, calcite crystals and large voids reminiscent of macrophytic tufa texture. Micritic tufas are characterised by

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dense micritic texture and abundant gastropods and ostracods. Both lithotypes are indicative of barrage pond depositional environments, micritic tufa deposits being formed in lowest-energy regimes.

2. Rarity of fluvio-clastic sediments, particularly clastics from the source area, indicating limited transport potential of the flow regime.

3. Lack of structural flow indicators (i.e. cross-beds) indicating flow energy was low in depositional environments.

4. Abundance of reworked tufa intraclasts comprising intraclast tufa throughout the system, indicating ongoing tufagenesis, infill and incision cycles.

5. Coarser lithologies can be normally graded indicating initial relatively high-energy flow and/or the presence of localised detrital lag followed by low energy deposition of finer material, which is characteristic of fluvial barrage basins (Pedley 1990, Ford and Pedley 1996). Drysdale (1995) observed fining upwards sequences in modern barrage pools in Louie Creek.

6. Vertically and laterally discontinuous irregularly distributed deposits that are interpreted as corresponding to the successive barrage deposits in a fluvial barrage system (Figures 4.26, 4.27, 4.29, 5.28).

7. Vertebrate taphonomy and relative abundance of aquatic taxa indicate low-energy conditions in which the presence of water supply was permanent (rather than ephemerally wet conditions in a dry depositional environment *sensu* the alluvial fan model of Megirian (1992)).

Fluvial barrage systems consist of dams that span flowing water bodies, forming low-energy lacustrine basins that fill with micritic and detrital tufa (Pedley 1990, Ford and Pedley 1996). Because tufa forms by precipitation from solution, large amounts of lithified carbonate can form and be reworked locally, supplying the detrital components of intraclast tufa. Because of the dynamic nature of barrage systems that alter the strength and direction of flow by damming, tufa deposits throughout the system are gradually weathered, eroded redistributed and redeposited in successive barrage basins. Because tufagenic systems can form without basinal containment, pre-existing basin structures are not required for fluvial barrage lake and pool deposits to form.

Taxonomic composition and taphonomy of fossil vertebrates and ostracods from Riversleigh Tertiary tufagenic deposits, can be interpreted as indicative that depositional environments were characterised by shallow, low-energy lacustrine-type conditions of fluvial barrage lakes and ponds. Ponds or pools were modelled by Archer *et al.* (1989, 1994) as the likely depositional environments of some kinds of deposits at Riversleigh.

The Riversleigh fluvial barrage depositional model and the general model of the Riversleigh fluvial barrage depositional environment are illustrated in Figures 5.28 and 5.29.

The fluvial barrage system was considered to be the depositional process that formed the extensive tufa deposits at Caerwys in Wales (Figures 4.26, 4.29) and the Wye and Lathkill Valleys (Figure 4.27) in eastern England (Pedley 1987, 1993). The structure of the Caerwys depositional system is considered here be analogous to the basic depositional unit at Riversleigh (Figure 5.29). Barrage ponds and lakes can range in dimension from metres to kilometres (Pedley 1990, Ford and Pedley 1996, Carthew *et al.* 2003). Their formation is not restricted by climatic conditions. Other active and fossil tufa barrage systems include the extensive system in Plitvice in Croatia; Ruidera Pools Natural Park, Spain; Band-e-Amir, Afghanistan; d'Immouzerand Ida du Tanane, Morocco; Onilahy Valley and Sept Lakes, southwestern Madagascar; Turner Falls, USA and tufa springs at Mt Etna in Queensland (Ford and Pedley 1996). Active and fossil fluvial barrage systems also occur in the karst-fed drainage systems in the Riversleigh area, including Louie Creek (Drysdale and Head 1994, Drysdale and Gillieson 1997, Drysdale 1995), Lawn Hill Gorge (Drysdale and Gale 1997) and the Gregory/O'Shanassy River System including Carl Creek (Drysdale *et al.* 2002, Carthew *et al.* 2003).

The pattern of vertically and laterally discontinuous tufagenic deposits at Riversleigh can be interpreted in terms of the pattern of fluvial barrage development, deposition and incision. Figure 5.28 shows a hypothetical sequence of successive barrages that indicates how deposits can form throughout the profile at any time, producing a randomly distributed sequence of deposits in which vertical position is not related to relative age. Younger deposits can form within and adjacent to older deposits, and can
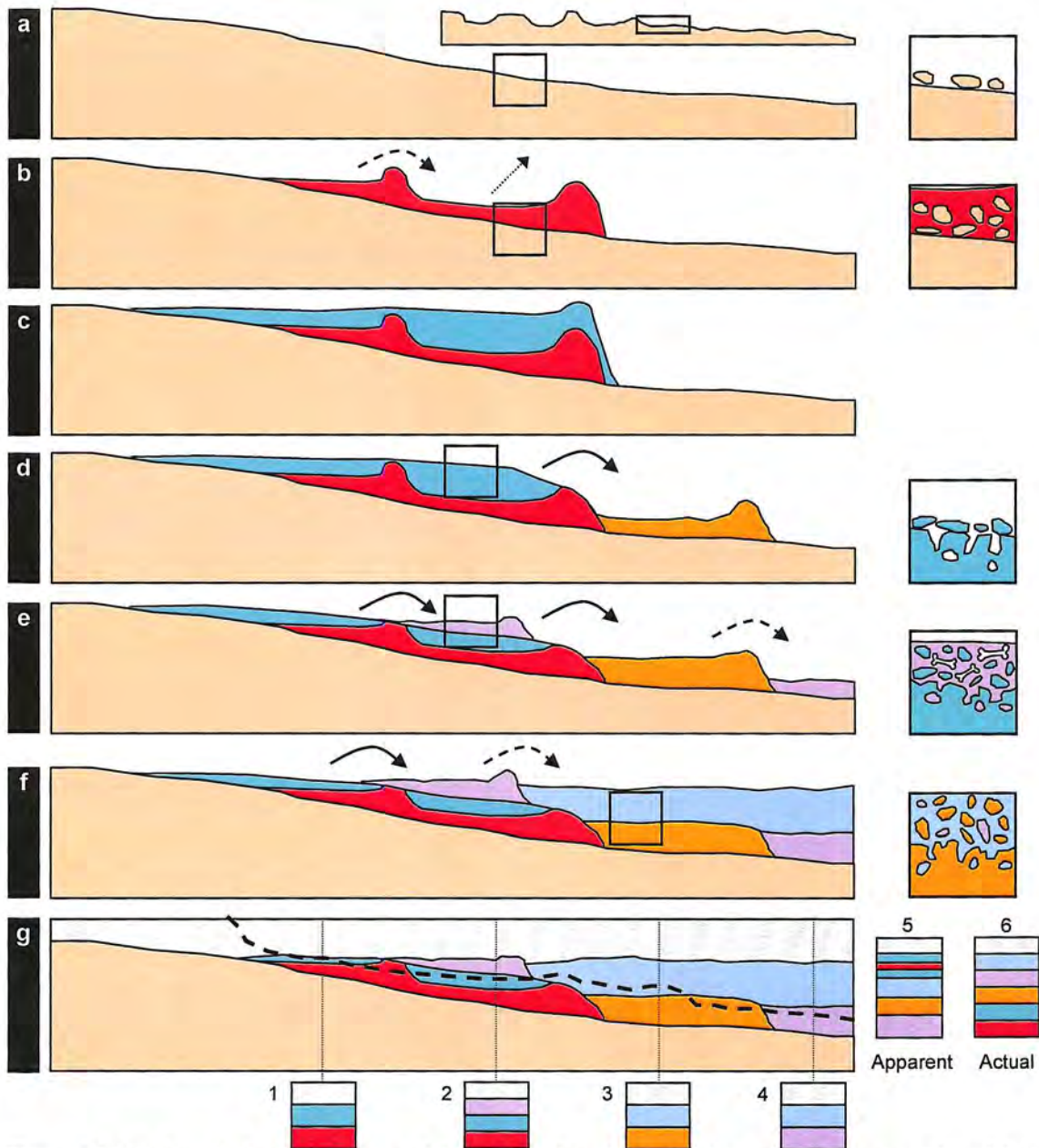
Figure 5.28: Tufagenic fluvial barrage model depicting deposition of tufaceous carbonates at Riversleigh. Stages a to f (portion of regional profile marked top right) depict successive damming, infill, incision and reworking cycles resulting in the random lateral and vertical distribution of different heterogeneous intraclast tufa deposits of different ages. Concentrations of vertebrate fossils accumulated within these barrage basins. Flow direction is from left to right. Solid arrows indicate major reworking of tufaceous components by incision and erosion of older barrage deposits, dashed arrows indicate latent transport of tufaceous components through the system while barrages are active. These processes provided the reworked components in intraclast tufa facies. Stage a shows weathered Cambrian/Proterozoic basement prior to deposition, inset shows Cambrian chert lag on the surface. Stage b shows initial fluvial barrage formation, with extraclast tufa basal facies comprised of chert lag inset in arenaceous tufaceous matrix. The dotted arrow in stage b indicates the expected direction of grading from coarse to fine. Laterally extensive deposits formed behind large barrages that had drowned older barrages upstream (stages c and f) and are representative of conditions that formed laterally extensive 'bone-bed' deposits. Insets in stages d and e show exposed infill in an incised fluvial barrage that has become weathered and this surficial lag contributes to the heterogeneous intraclast tufa infill of a subsequent barrage. Inset in f shows combination of reworked *in situ* infill and detritus from an upstream barrage comprising heterogeneous intraclast tufa barrage infill. Note how younger deposits can form lower in the profile than older deposits and how deposits of the same age can form contemporaneously at different points (both vertically and

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laterally) in the profile. Deposits formed at basal level (i.e. basal facies), are thus also not contemporaneous throughout the entire system. The grey layer in stage g is representative of a later succession(s) of fluvial barrage deposition rather than an individual deposit. The sequences labelled 1-4 indicate different apparent sequences observable at different points in the profile. Sequence 5 indicates an apparent profile observed at the weathered (i.e. modern) surface (dashed line) that could lead to a misleading interpretation of 'stratigraphic sequence'. The actual depositional sequence is illustrated in sequence 6. This principle of random vertical and lateral distribution of depositional environments within a fluvial barrage regime can also be applied to the relative positions of entire suites of deposits from successive regimes. This model is based on the cyclic model of Golubić (1969) and the reconstruction of the Caerwys fluvial barrage deposit in Wales of Pedley (1987), see Figures 4.25, 4.26, 4.27 and 4.29.

form lower in the profile than older deposits, including at basal level. Deposits of the same age can form at two different levels in the profile at the same time. The distribution of tufagenic deposits at Louie Creek (Figure 4.28) also indicates how over time, deposits of different ages can be irregularly distributed across the terrain by a dynamic fluvial system.

The fluvial barrage depositional process could therefore have produced the profile observed at Riversleigh which is characterised by discontinuous heterogeneous tufa deposits that are not traceable across the area (see Figure 5.19). Implications of this depositional process for stratigraphic interpretation and correlation are discussed in more detail in Section 7.5.

Large-scale bedding of deposits (Figure 5.20) can be interpreted as representative of different suites of tufagenic deposits formed by successive fluvial barrage regimes. These deposits are similar lithologically, but may differ slightly because of relative variations in flow energy, flow direction and elements of textural composition, producing bedding patterns. Because these suites of deposits would have been formed under the influence of the same kind of dynamic cyclic conditions that formed individual fluvial barrage deposits (Figure 5.28), these large-scale beds may also not necessarily be correlated across Riversleigh by their topographic position in the profile or position relative to the basement, as deposits at the same level may have formed at different times, and deposits at different levels may be contemporaneous.

Relatively extensive 'bone-beds' (i.e. at Mesa 1 and above Hiatus Site) can be interpreted as depositional horizons in larger barrage lakes that formed when rapid downstream barrage growth drowned upstream barrages, according to the cyclic model of Golubić (1969; Figure 4.25) and the Caerwys depositional model of Pedley (1987; Figure 4.26, 4.29). These larger basins may also have accumulated deposits forming large-scale beds.

The basal facies is interpreted as *in situ* surficial material incorporated into tufa in fluvial barrage deposits at basal level, where flow energy did not displace coarse siliclastic material. This is considered analogous to the late Devensian peat deposits
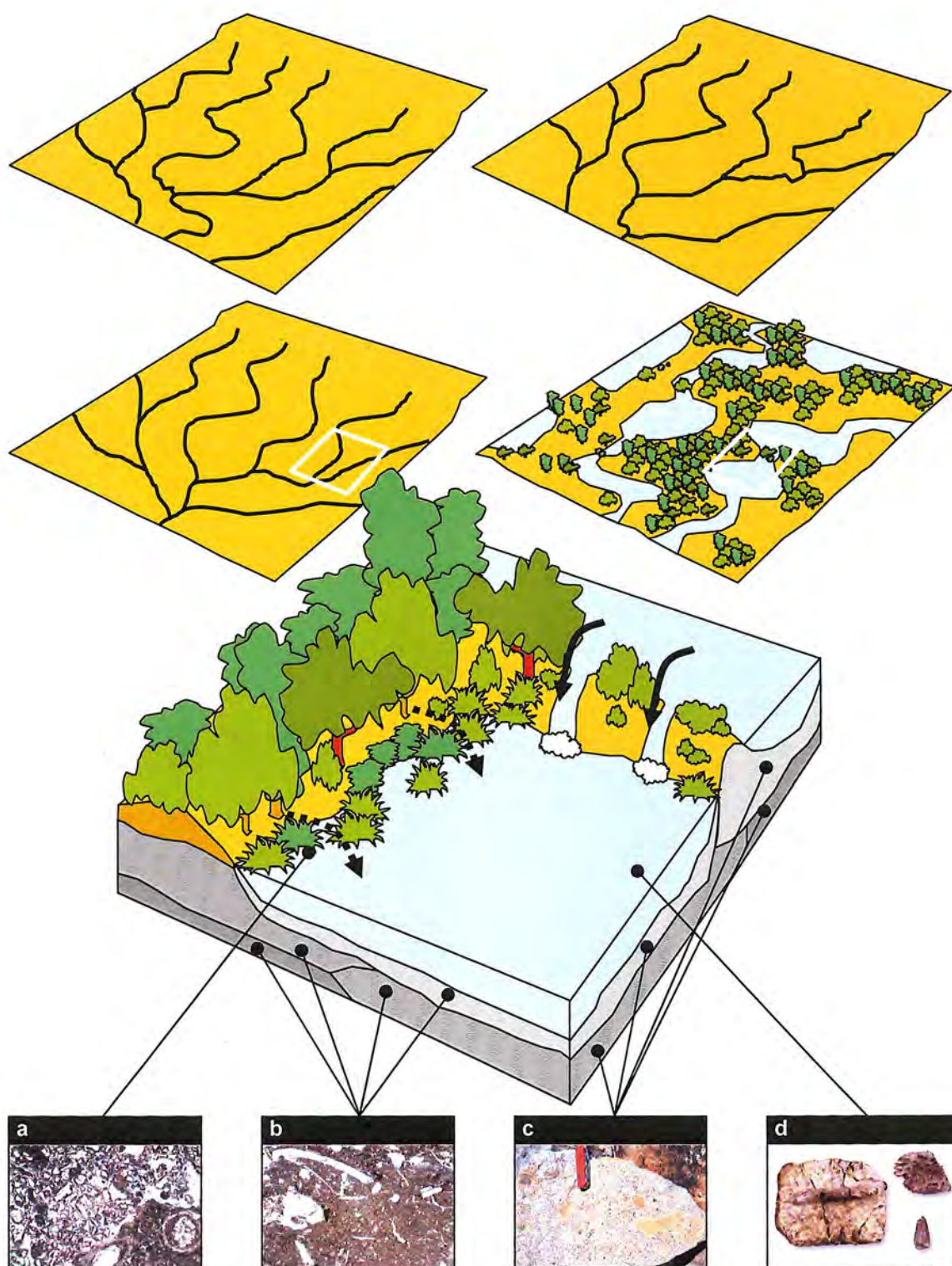
Figure 5.29: General model of tufagenic fluvial barrage depositional environment of late Oligocene tufaceous carbonates at Riversleigh. Main image is inset from local area (centre right), which is inset from regional area (centre left) which is part of a succession of phases of a hypothetical anastomosing fluvial system issuing from multiple exsurgences in the Cambrian karst terrain (looking roughly S-SE). Fluvial barrages were distributed randomly throughout the drainage system, with the net effect of deposition of vertically and laterally discontinuous tufaceous deposits of different ages throughout the system. Vegetation cover and type is hypothetical and depicted only to assist visualisation. This model applies to tufagenic deposits at localities including White Hunter Site, D Site (Riversleigh Local Fauna) and also to Ringtail Site, although the Ringtail Site deposit formed during the apparently more localised

tufagenic event of Phase 3. Larger fluvial barrage systems produced more extensive 'bone-bed' deposits that can be traced for hundreds of metres. Successive fluvial barrage regimes (i.e., formed during different stages of drainage pattern development) produced large-scale bedding patterns, like individual deposits, these suites of deposits would also be vertically and laterally discontinuous and of different ages. Solid arrows indicate localised transport of quartz sand and intraclasts (and possibly some vertebrate remains) from upstream sources and from erosion of the barrage at that point and/or incision and breakdown of the barrage once the barrage pond behind had filled. Dotted arrows indicate provenance of vertebrate fossil material which probably usually entered pond environments in the form of decomposed and/or isolated body parts of dead animals and occasionally in the form of living animals that became trapped in the water or fell victim to ambush predators such as crocodilians. Along with the remains of medium to large-sized animals, the low energy conditions in the pond allowed the preservation of smaller, fragile vertebrate remains including those of birds, bats and lizards and small marsupials. The barrage pond itself would have been inhabited by gastropods, ostracods, other crustaceans, aquatic insects, lungfish, fish, crocodilians and chelid turtles (and ornithorhynchids during the middle Miocene). Invertebrate and vertebrate material was preserved in the intraclast and micritic tufa (light grey) that was deposited in the barrage pond (b, c, d), which also occasionally preserved some macrophyte tissue moulds (a). The vegetated bank was comprised of unconsolidated siliclastic sediment and tufaceous clasts which would usually have been eroded by ongoing fluvial processes, but occasionally was lithified by pedogenic processes to form calcrete if left exposed or if overlain by tufagenesis then recrystallised by phreatic processes to form altered silicate facies.

preserved *in situ* beneath the Caerwys tufa barrage system in Wales (Pedley 1987; Figure 4.29) and the reworked basement material that occurs irregularly at the base of the fluvial barrage deposits in the Lathkill Valley, England (Pedley 1993; Figure 4.27). The occurrence of basal facies on top of Godthelp Hill, in association with massive chert, is interpreted as basal facies overlying a Cambrian outlier (Figure 5.24f).

The pedogenic facies are interpreted as representative of the non-tufaceous components of the fluvial system affected by different diagenetic processes. Calcrete is considered to be derived from poorly-lithified arenitic carbonate deposits. The altered silicate facies can be interpreted in three ways:

1. This facies-type could be considered analogous to the tufaceous palaeosol facies of Pedley (1990), which, being interbedded with tufa, may have been subject to inundation and recrystallisation in the phreatic zone

2. Because this facies-type is underlain by weathered tufaceous carbonate, it could represent siliceous surface material (i.e. soil) that was lithified by surficial processes producing a form of silcrete. Dynamic flow conditions during the late Oligocene could have resulted in the stranding and burial of some tufaceous deposits by unconsolidated siliceous material that was subsequently lithified to form a silcretised cap, over which subsequent tufaceous deposits were eventually formed.

3. This deposit could represent some kind of younger silicified infill of solution fissures formed at a later stage.

Throughout a fluvial barrage system at Riversleigh, vertebrate fossils would have been preserved in barrage ponds (Figure 5.29) as isolated fragments and occasionally higher concentrations formed where local conditions favoured accumulation and preservation. These favourable conditions (or combinations of favourable conditions) would probably have varied from locality to locality and may have resulted from circumstances including:

1. Interior and marginal pond morphology (i.e. floor and bank and slope and shape) may have influenced influx and entrapment of vertebrate remains and/or living animals, and created microbasins and/or directed material into favourable microenvironments within fluvial barrage ponds.

2. Pond depth may have influenced preservation because damage by (underwater) exposure and scavenging may have been limited in deeper water

3. Pond-size may have had an effect because in certain circumstances influx of material may have exceeded the rate of attrition (i.e. by scavenging). For example preservation may have been favoured in small ponds with a large influx, or in large ponds with few scavengers.

4. The active depositional lifetime of the pond, because larger and richer accumulations may have formed in longer-lived depositional environments.

5. Vegetation cover and in and around ponds may have influenced influx of vertebrate remains into the deposit, or alternatively may have influenced entrapment of live animals. Archer *et al.* (1994) postulated that floating mats of carbonate- and/or algally-bound plant debris may have served as an entrapment mechanism of live animals in small lacustrine basins at Riversleigh.

6. Deposition rate within the pond would have been significant because rapid burial would have favoured preservation

7. The presence or absence of scavengers (i.e. fish, turtles, crocodiles and possibly types of snails) would have been significant because of their potential to vertebrate remains.

The irregular distribution of these conditions favourable to preservation, and the irregular distribution of the development of depositional environments in which they formed may be responsible for the irregular occurrence of rich bone occurrences that are mapped as fossil localities at Riversleigh.

Tufa accumulation rates over long periods of time (calculated in Section 4.4.5.) indicate that tufagenic deposits could have accumulated across the Riversleigh area (if the area of deposition was considered to be 100-400 km^2 see Section 7.2) within a period in the order of 10^6 years (i.e. say 1-5 Ma) if conditions and depositional processes remained consistent, and particularly if there were multiple exsurgences and/or multiple channels in which deposition occurred.

5.2.5 Dunsinane Site: representative tufagenic deposit

Aspects of Dunsinane Site were a focus of study during the course of this project, and a summary of outcomes of that research is presented here. The preliminary investigation of the geology and palaeontology of Dunsinane Site was conducted by Arena (1995, 1997 see Appendix D). However, some interpretations of geology in the earlier work were incorrect or reflect limitations in the understanding of Riversleigh geology at that time and have been revised and superseded here.

The deposit is very weathered, and the majority of primary structures and lithotextures have been destroyed. The lithological contrast with overlying carbonate is considered to be mainly due to the leaching and weathering of the deposit. The deposit is adjacent to and appears to overlie Cambrian chert. While chert clasts are absent from the Dunsinane Site deposit, arenaceous lithotexture (abundant quartz sand grains and bone fragments) is dominant (5.31a, b). Although tufaceous intraclasts are not readily observed in hand specimen, gastropod-rich micritic tufa intraclasts have been retrieved by acid etching of the matrix (Figure 5.31d). Along with the distinctive weathering morphology, which contrasts sharply with overlying intraclast and micritic tufa that displays typical karst sculpting, the Dunsinane Site deposit is comparable to calcarenites present in basal facies (see Section 5.2.3.2).

Because the Dunsinane Site deposit appears to exhibit a lenticular pattern (Figure 5.30 a, b, c), it was originally interpreted as a discrete lacustrine deposit (Arena 1995, 1997). Some undulating primary bedding structures were observed (Figure 5.30d/e). These apparently tabular layers are 15-20cm in thickness and can be considered indicative of low-energy sedimentary processes occurring in the depositional environment. The undulations are probably due to post-diagenetic slumping of the deposit.

The vertebrate assemblage (Faunal List 4) includes abundant crocodilian remains (Figure 5.31c), a turtle, large dromornithids, wynyardiids, large diprotodontids, small kangaroos, a hipposiderid bat and a rail. The assemblage is considered to be a equivalent to late Oligocene Riversleigh faunas because the presence of the diprotodontine diprotodontid *Bematherium*, the plesiomorphic balbarine kangaroo

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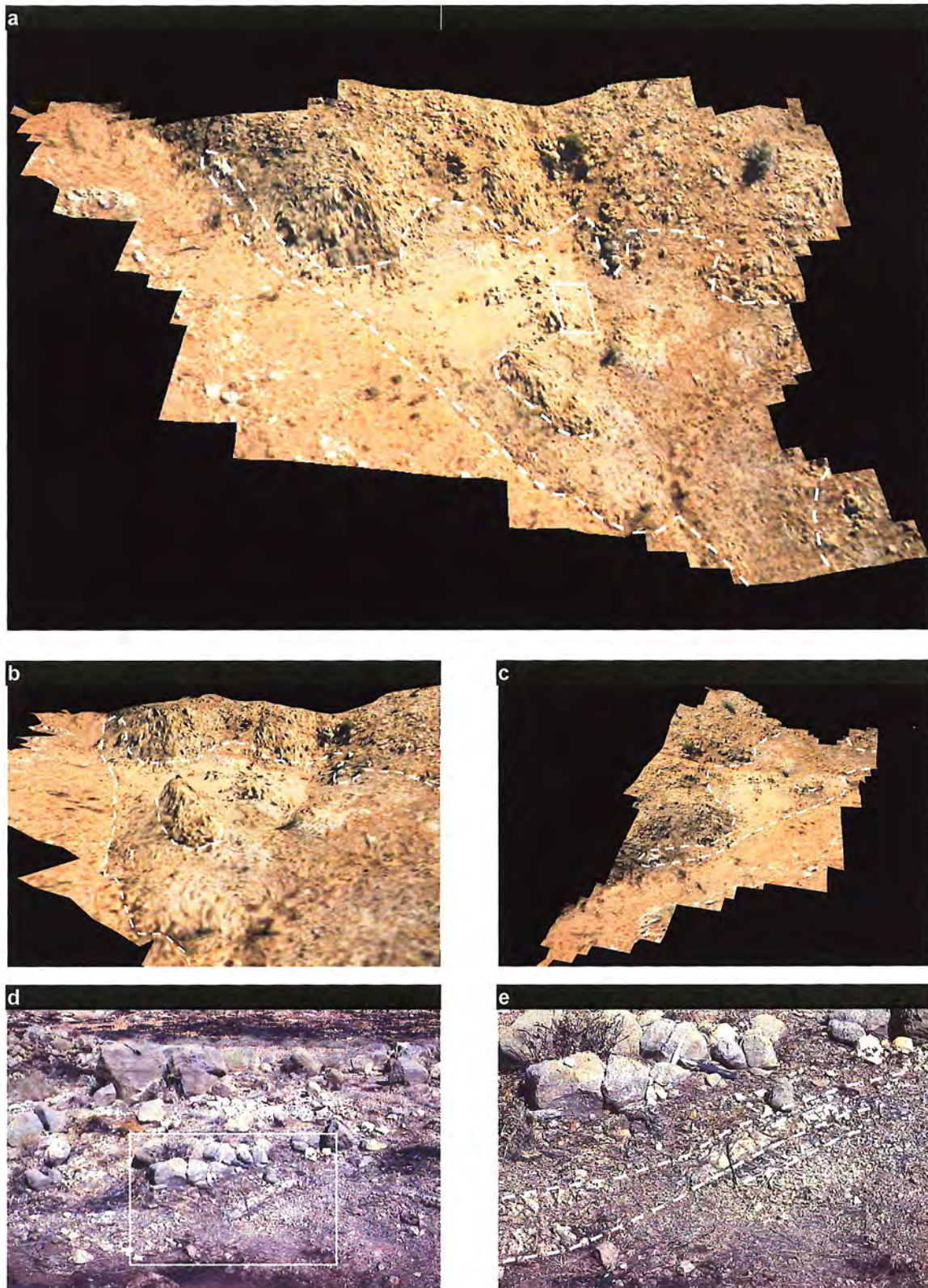
Figure 5.30: Structure of the deposit at Dunsinane Site. a-c) The fossiliferous deposit appears to occur in a lenticular pattern. Direct lithological contacts were not observed and are inferred from contrast with adjacent *in situ* outcrops. The Dunsinane Site deposit differs from overlying intraclast and micritic tufa because of the distinctive lack of karst weathering morphology, the dominance of arenaceous textures, including abundant bone fragments and the presence of phosphatised fossiliferous nodules. Model width is 270m, vertical exaggeration x2. d,e) Detail of area highlighted in 5.30a showing undulating bedding structures.

Nambaroo sp. 8 correlate with other faunas at Riversleigh that are considered to be late Oligocene in age.

The vertebrate taphonomy indicates a low-energy depositional environment. A skull of *Bematherium sp.* with articulated dentaries indicates that preservation occurred prior to much exposure or disturbance, since the jaws are among the first skeletal parts to disarticulate from a skeleton (Hill 1980, Hill and Behrensmeyer 1984). The presence of bat and small bird material, including the delicate carpometacarpus of a rail (Figure 5.31e) also indicates low-energy conditions conducive to the preservation of fragile material. While most skeletal remains are badly fractured, fragments are often in close association, isolated tooth-rows are usually fully intact, despite loss of surrounding bone. This damage to bone material, which varies throughout the deposit is probably related to post-diagenetic weathering.

Because the Dunsinane Site deposit contains a vertebrate assemblage with dominant crocodilian remains which is similar to other faunas with a dominant aquatic component at Riversleigh (i.e. containing crocodilians, turtles, large dromornithids and large diprotodontids), was apparently formed under a low-energy conditions, is laterally extensive with an apparently lenticular geometry and contains abundant arenaceous and micritic lithotextures and reworked micritic tufa intraclasts are present, it can be interpreted as a basal low-energy deposit, comparable to deposits interpreted as barrage infills above.

A key component of the Dunsinane Site deposit is the occurrence of fossiliferous nodules that are up to 15 centimetres in diameter and contain a diverse assemblage including wood fragments, twigs, leaves, stems, fruits, seeds, pollen, arthropods, gastropods and mammalian coprolites (Figures 5.31f, g, 5.32a, i, j, k, l). There are also unfossiliferous nodules of similar proportions, which appear to have been partially recrystallised by weathering. While the majority of nodules occur as a surficial lag on the surface of the deposit, fossiliferous and unfossiliferous nodules have been retrieved by excavation, and appear to occur irregularly throughout the deposit.
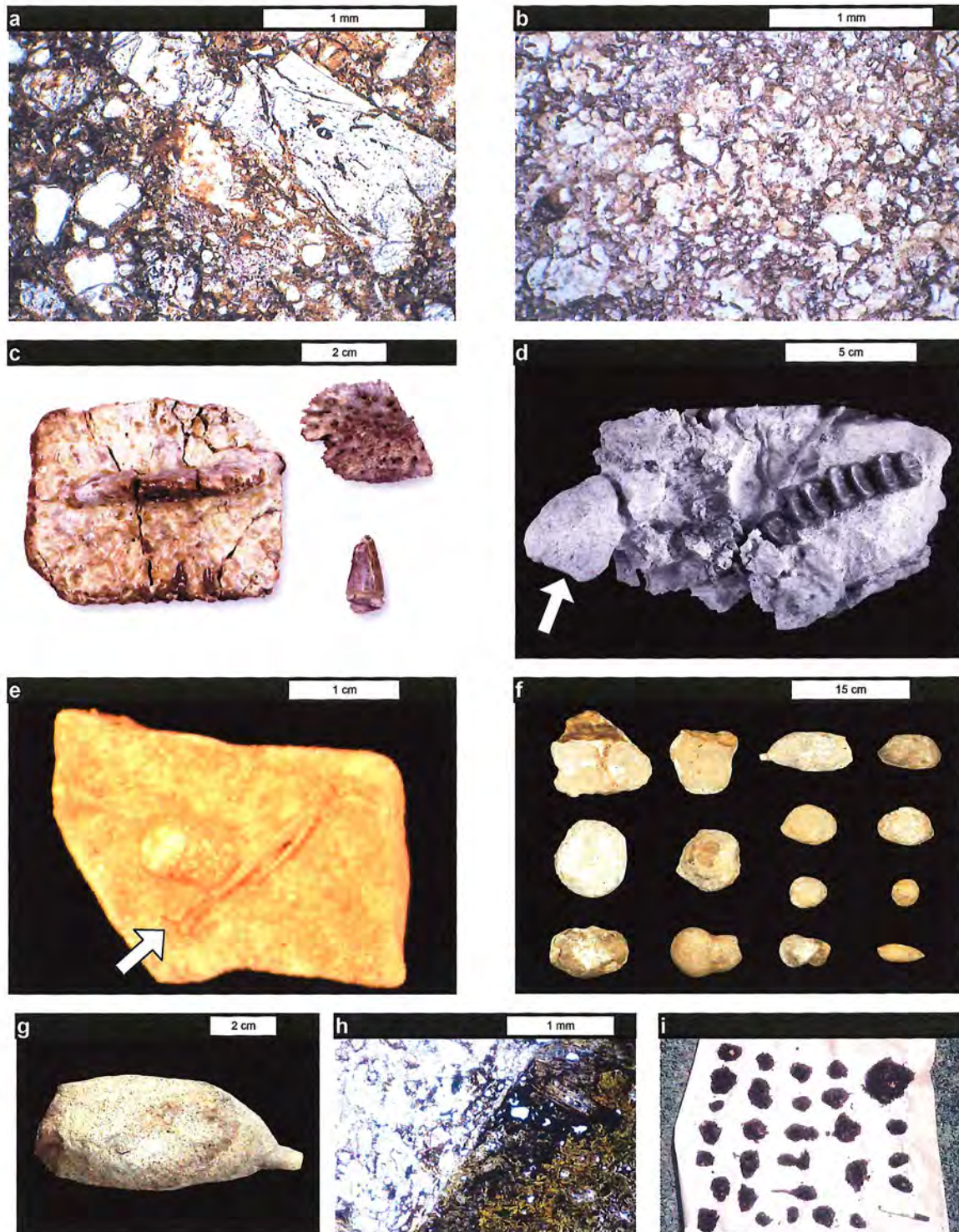
Figure 5.31: Features of the geology and palaeontology of the deposit at Dunsinane Site. The deposit is dominated by arenaceous lithotextures with abundant quartz sand and bone fragments. Primary structures typical of tufaceous lithologies are not apparent. Brown colouration is probably due to staining by mobile iron oxide and phosphate due to weathering. a) Arenaceous lithotexture with abundant bone fragments (PP; RA1995-9). b) Arenaceous lithotexture with abundant quartz sand (PP; RA1995-7). c) Osteoderms and teeth of large crocodilians are abundant in the deposit (Large osteoderm QMF30770, small osteoderm AR19144, tooth QMF 30774). d) Partially etched fossiliferous matrix containing overlapping fragmented palates with intact tooth rows of the diprotodontid *Neohelos tirarensis* and the wynyardiid *Namilamadeta*. Arrowed is a typical tufaceous intraclast containing gastropod shell fragments. (QMF51377). e) Carpometacarpus of a rail (proximal end arrowed). This tiny and fragile specimen is considered an

indicator of low-energy conditions in the depositional environment. (QMF40203). f) Phosphatised nodules from Dunsinane Site. While generally rounded, nodules are not smooth and are characterised by morphological irregularities, including protuberances of fossil wood. Shapes include circular, ovate, dumb-bell and irregular. g) Detail of a phosphatised nodule showing morphology and surface texture. h) Thin section of boundary of nodule in carbonate matrix showing clear delineation of lithology and apparent truncation of internal structures, indicating that the nodule is probably not derived from the matrix by concretion or mineralisation (PP; RA1995-1). i) Lumps of partially decomposed plant matter tumbled in a barrel exhibit similar range of morphology and sizes to phosphatised nodules from Dunsinane Site, including circular, ovate, irregular and dumb-bell forms. Note there is even a lump with a twig protruding. The shapes of phosphatised nodules may have been the result of reworking of lumps of organic matter prior to mineralisation.

The mineralogical composition was determined using X-Ray diffraction (Appendix C) and electron microprobe analysis to be primarily fluorapatite (= francolite, calcium fluoride phosphate, $Ca_5(PO_4)_3F$) enriched with goethite (FeO(OH)). Francolite can be formed by precipitation mediated by microbial activity under certain conditions of temperature, pH and phosphate ability in a medium or substrate, often in association with films of cyanobacteria. Layered structures considered to be microbial films were observed in thin sections some phosphate nodules from Dunsinane Site (Figure 5.32c, d). Distinctive textures that are characteristic of microbially-mediated phosphatisation were observed using scanning electron microscopy. These include mamillated and spherical masses of phosphate and sausage-shapes structures approximately 1-2μm in dimension that are interpreted as fossilised bacteria (Figure 5.32 b, c, d). Microbially-mediated phosphatisation has been identified as the mode of fossilisation in a number of exceptionally preserved assemblages (Balson 1980, Müller 1985, Pinna 1985, Seilacher *et al.* 1985, Soudry and Lewy 1988, Allison 1988a, 1988b, 1988c, Martill 1988, 1989, 1990, Lucas and Prévôt 1991, Wilby and Martill 1992, Briggs and Kear 1993, Briggs *et al.* 1993, Duncan and Briggs 1996, 1998).

Among the abundant phosphatised arthropod body parts are internal organs, heads, compound eyes, body segments, beetle elytra and prothoraces in various degrees of articulation. Samples etched with dilute hydrochloric acid have yielded three-dimensional organic material in the form of plant fibres, pollen, and arthropod body fragments, including cuticle fragments, elytra, heads, limbs, compound eyes, antennae, scales and setae (Figure 5.32f, g, h). Arthropod carapace fragments have retained fine texture and sheen, although they lack indications of original pigmentation. The small size and degree of fragmentation of the majority of the invertebrate material may indicate an origin in the droppings of insectivorous animals such as birds.

Based on study of fruits, thorns and leaves from Dunsinane Site, Guerin (2001) concluded that the vegetation contributing to the assemblage was open dry forest possibly analogous to modern seasonally dry monsoonal forest in northern Australia. Taxa present were dominated by a xeromorphic species of Casuarinaceae with close affinities to *Casuarina* and *Allocasuarina* and a number of other species including a species of *Alectryon* and possibly a species of *Rubus*. The latter taxa are known from

Faunal List 4: Dunsinane Site Local Fauna
Source locality: Dunsinane Site, Sue's Rocky Road Site, Custard Tart Site

CHORDATA
  ARCHOSAUROMORPHA
    STRUTHIONIFORMES
      DROMORNITHIDAE
      Indet.
    GRUIFORMES
      RALLIDAE
      Genus indet cf. *Gallinula* sp.
    CROCODILIA
      CROCODYLIDAE
      Baru sp.
  MAMMALIA
    DIPROTODONTIA
      BALBARIDAE
        BALBARINAE Genus indet. sp. indet.
        Nambaroo sp 8
      MACROPODIDAE
        cf. *Wabularoo* sp.
      DIPROTODONTIDAE
        Bematherium sp.
        Neohelos tirarensis
      WYNYARDIIDAE
        Namilamadeta cf. *N. snideri*
    CHIROPTERA
      HIPPOSIDERIDAE
        cf. *Brachipposideros* sp.
MOLLUSCA
  GASTROPODA
    STYLOMMATOPHORA
      CAMAENIDAE
      Indet.
UNIRAMIA
  HEXAPODA
    COLEOPTERA
      CURCULIONIDAE
      ~ 4 genera indet. spp.
      CARABIDAE
      Indet.
      SCIRTIDAE
      Indet.
    DIPTERA
      CYCLORAPHIDAE
      ~ 2 spp. indet.
    HETEROPTERA
      HETEROPTERA Family indet.
      ~ 2 spp. indet.
    HYMENOPTERA
      FORMICIDAE
        cf. *Camponotus* ?*nigriceps*
        cf. *Campomyra* sp.
        Indet.
      HYMENOPTERA Family indet.
      ~ 3 spp. indet.

References for this list: Arena (1997), Cooke (1997a).

dry country in New Guinea. The presence of tissues resembling pneumatophores (Figure 3.32i) may indicate that some permanently wet conditions occurred.

The insects in the Dunsinane Site nodules are considered to be Cainozoic in age (C. Reid personal communication 2003). Taxa identified so far include approximately 4 types of curculionid, a carabid and a scirtid beetle, two kinds of cyclorhaphid fly larvae, two kinds of pentatomoid heteropterans, approximately three kinds of non-ant hymenopterans and three kinds of ant including a member of the *Camponotus* ?*nigriceps* species group and *Polyrhachis* subgenus *Campomyra*. While this last taxon has no previous fossil record, at this stage none of these insect taxa offer much resolution of associated palaeoenvironmental conditions or time period within the Tertiary because their close relatives appear to have broad habitat distributions and fossil records spanning the Cainozoic.

The taphonomy of the phosphatised assemblage indicates that the mineralisation process must have been rapid, occurring soon after accumulation and before much decay or compression of the organic material. The nodules consist entirely of mineralised organic tissues (Figure 5.32a) and contain no sediment particles or structures attributable to sedimentary or concretionary processes. There is a clear distinction between nodule material and the limestone matrix, with some apparent truncation of structures at nodule boundaries (figure 5.31h). The composition of organs in the plant macrofossil assemblage is characteristic of a proximal assemblage accumulated by limited lateral wind transport (Collinson 1983, Spicer 1989). Cuticular and cellular detail of plant material is well preserved and three-dimensional leaves contain spongy mesophyll tissue (Figure 5.32j) that is otherwise normally broken down in the earlier stages of leaf degradation that begin immediately after immersion or contact with the ground (Ferguson 1985, Spicer 1989). Undistorted mammalian coprolites, which are prone to early degradation under phosphate-producing conditions (Lucas and Prévôt 1991), have their distinctive external features and internal detail well preserved (Figure 5.32l, m, n). The presence of organic tissue fragments is comparable to organic preservation in fossil amber and may have resulted from a similar mode of preservation involving rapid envelopment of tissues by an inert matrix.
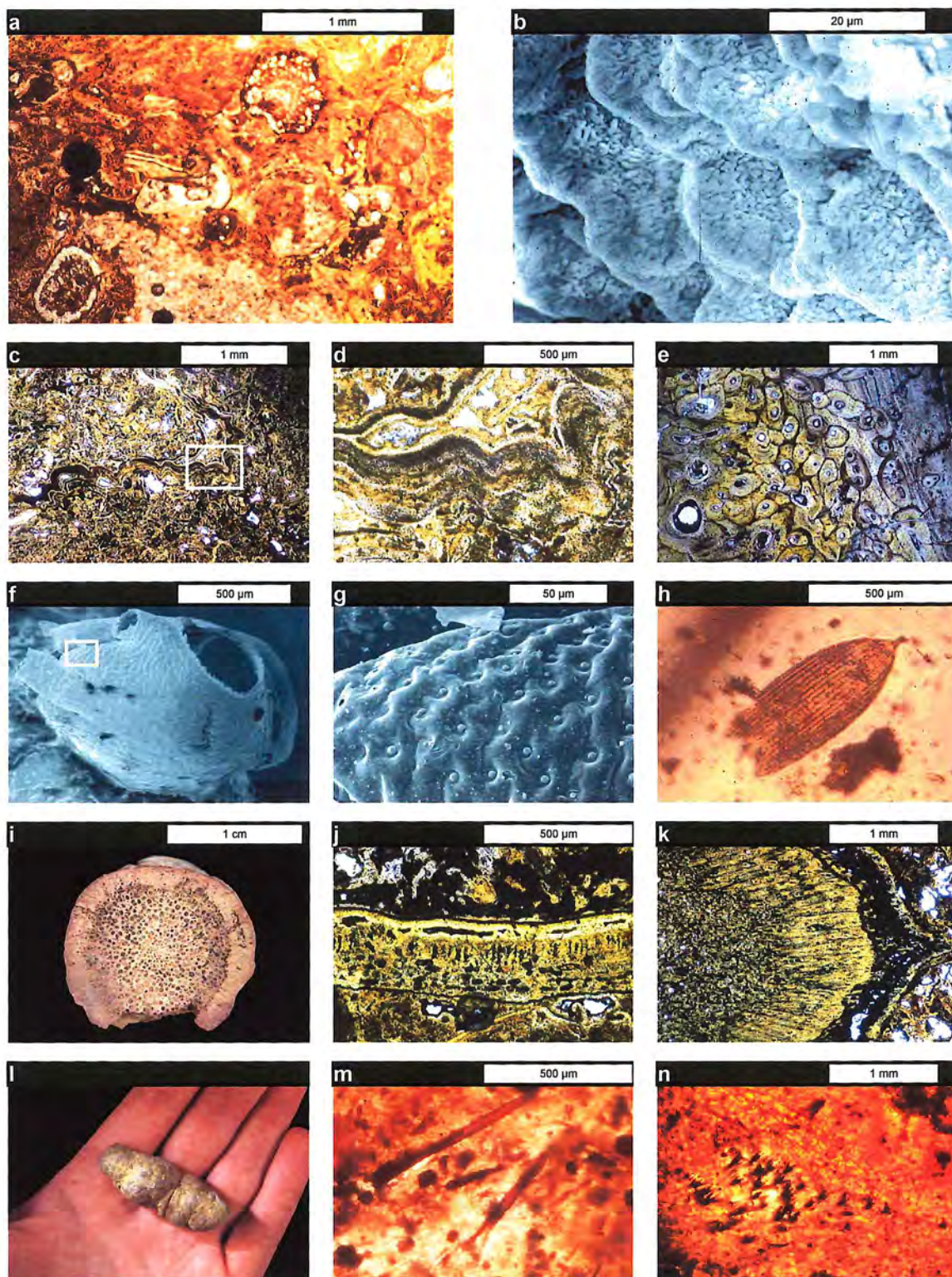
Figure 5.32: Features of the phosphatised assemblage from Dunsinane Site. a) Matrix of fossiliferous nodule comprised of exceptionally preserved plant and insect material (PP; RA101). b) SEM of phosphatised invertebrate eye structure showing characteristic surface coating of sausage-shaped particles approximately 1-2μm in dimension, interpreted as fossilised bacteria. c/d) Nodule matrix showing preserved layered microbial film (PP; RA1995-1). e) Fossil vertebrate bone showing staining by enrichment with iron-oxide-rich phosphate (PP; RA1995-11). f) SEM of organically preserved insect head retrieved by etching of phosphate matrix with dilute hydrochloric acid. g) Detail of 5.32f showing intact surface structures at very small scale. h) Insect scale comparable to lepidopteran or dipteran scales

retrieved by etching with hydrochloric acid. i) Plant macrofossil interpreted as a possible pneumatophore. j) Section through leaf showing cellular preservation. Epidermal and palisade cells are recognisable at the upper surface and spongy mesophyll cells are at the lower side. (PP; RA1995-1). k) Cellular detail of a plant organ (PP; RA1995-2b). l) Coprolite with well-preserved external morphology. This form is comparable to scat from a fox-sized mammalian carnivore or omnivore (QMF30780). m) Section from the coprolite in 5.321 showing elongate structures that may be mammalian hairs, worms or fungal hyphae (PP). n) Section through a coprolite of a presumed herbivore showing masses of plant fibres. (PP; RA111).

The volume of phosphate exceptionally preserving organic tissue in this assemblage is significantly greater than that observed previously in the fossil record and in laboratory experiments. The conditions for replacement by fluorapatite appear precise and require a delicate balance (Briggs and Kear 1993). Some tissues, usually those relatively high in organic phosphorous (Allison 1988a, 1988b, 1988c, Briggs and Kear 1993, Briggs *et al.* 1993) are susceptible to phosphatisation under conditions of high microbial activity (Allison 1988a, 1988c, Lucas and Prévôt 1991, Briggs and Kear 1993, Briggs *et al.* 1993). These conditions may be enhanced by containment by some form of 'closure', often in the form of microbial films or mats (Seilacher *et al.* 1985, Wilby and Martill 1992, Briggs and Kear 1993, Briggs *et al.* 1993). However even in ideal conditions phosphatisation is often selective, patchy or very limited (Müller 1985, Martill 1988, 1989, 1990, Wilby and Martill 1992, Briggs and Kear 1993, Briggs *et al.* 1993). Some examples of phosphatisation from the fossil record indicate rapid replacement of fresh tissues before appreciable decay or compression (Seilacher *et al.* 1985, Allison 1988a, 1988b, Duncan and Briggs 1996), possibly over a period of time as short as a few hours (Martill 1988, 1989, 1990). Selective phosphatisation of organic tissues has been achieved in laboratory experiments, although over a period of several weeks and yielding much less mineralised tissue (Balson 1980, Pinna 1985, Allison 1988a, 1988b, 1988c, Martill 1988, 1989, 1990, Briggs and Kear 1993, Briggs *et al.* 1993, Duncan and Briggs 1996, 1998).

While permineralisation of plant tissues with silica or calcium carbonate is well known from the fossil record, because they are relatively phosphorous-deficient (Lucas and Prévôt 1991), plant tissues are rare in phosphatised assemblages (Allison 1988b). Some of the Riversleigh nodules contain laminated structures interpreted as layered microbial films. Microbial mats or films are regarded as significant in confining and maintaining optimal conditions and supplying phosphorous to mineralisation sites (Seilacher *et al.* 1985, Martill 1988, 1989, 1990, Briggs and Kear 1993, Briggs *et al.* 1993) and have been reported in association with exceptionally preserved phosphatised assemblages (Martill 1988, Seilacher et al. 1985), although such structures are actually preserved within Riversleigh nodules.

The exceptional preservation of this assemblage by an extraordinary, high-yield, non-specific and rapid phosphatisation (early diagenetic microbially-mediated phosphatisation) of tissues relatively low in phosphorous appears to have been less selective and more prolific than previously described fossil and experimental evidence has shown (Balson 1980, Müller 1985, Pinna 1985, Seilacher *et al.* 1985, Soudry and Lewy 1988, Allison 1988a, 1988b, 1988c, Martill 1988, 1989, 1990, Lucas and Prévôt 1991, Wilby and Martill 1992, Briggs and Kear 1993, Briggs *et al.* 1993, Duncan and Briggs 1996, Duncan *et al.* 1998) resulting in this case in entrapment and preservation of fragments of organic tissue. This may have been the result of a rare convergence of micro-environmental conditions at the extreme of their range of suitability for phosphatisation to occur (i.e. pH, anoxia, phosphate availability and temperature). Temperatures exceeding those in laboratory experiments and in models of natural situations (i.e. sea-floor conditions (Soudry and Lewy 1988, Pinna 1985, Allison 1988a, 1988b, Martill 1988, 1989, 1990) may have been significant since phosphate output by micro-organisms under anoxic conditions increases geometrically with temperature (Shapiro 1967). The occurrence of microbial laminations within some nodules highlights the role of microbial colonies supplying phosphorous and maintaining the conditions causing this mineralisation process.

Given that the invertebrates are considered to be Cainozoic, there are no other Cainozoic deposits known in the area, the Dunsinane Site deposit lacks reworked Proterozoic or Cambrian basement material, and reworked tufaceous intraclasts are present in the deposit, the nodules are probably intraformational.

They were probably formed from an accumulation of organic material submerged in a shallow water body. This accumulation may have been either partially mineralised or completely mineralised and reworked, producing rounded nodules. Because nodules exhibit a wide variety of shapes, usually have rough and pitted exterior surfaces and many nodules often have protrusions of fossilised structures (Figure 5.31a, b), fragmentation and rounding due to mechanical abrasion after mineralisation is considered unlikely. If the nodules had formed by partial mineralisation of a layer, a greater degree of morphological variation and surface irregularities would be expected.

Alternatively, the nodules may have been fragments of a non-mineralised mat that were reworked and shaped while still soft. Lumps of non-mineralised plant material tumbled in a rotating barrel can produce masses of both size and shape that are very similar to the morphologies exhibited by nodules from Dunsinane Site (see Figure 5.31i). These lumps may then have been subsequently mineralised. While they vary in shape, nodules tend to be flattened on one axis, suggesting an origin from either a layer, or slight compression after fragmentation and before mineralisation. This is considered a more likely scenario.

Fossil bone material from Dunsinane Site is distinctive because fragments are often enriched with varying amounts of brown iron-oxide-rich fluorapatite (Figure 5.32e). If phosphatisation had occurred *in situ*, bone embedded in the substrate may have been partially phosphatised and partially demineralised in the prevailing acidic conditions, allowing compression and fracture in a process similar to that which affects bone in highly acidic substrates like peat (Connolly *et al.* 1986). This process may have released additional phosphorous into the system which, as well as iron hydroxides which accumulate under such reducing conditions (Allison 1988a, 1988c), contributed to the prolific precipitation of iron-oxide-rich fluorapatite.

However, because of the high acidity that prevails in environments where phosphatisation occurs, it is unlikely that phosphatisation occurred at Dunsinane Site because of the abundance of carbonate in the deposit. Phosphatisation is usually inhibited in conditions where carbonate is abundant (Lucas and Prévôt 1991). While some vertebrate material may have been subject to phosphatisation, the fragmentation and phosphate-enrichment of the majority of bone at Dunsinane Site more likely due to leaching and the redistribution of phosphate throughout the deposit by post-diagenetic weathering processes. Small amounts of phosphate were detected by XRD throughout the carbonate matrix, indicating that this is probably the case.

Therefore, phosphatisation probably took place elsewhere in the depositional system, probably in a relatively carbonate-poor environment. The apparent distribution of nodules throughout the Dunsinane Site deposit, rather than in a discrete layer, suggests they were transported from the site of phosphatisation and deposited at Dunsinane Site
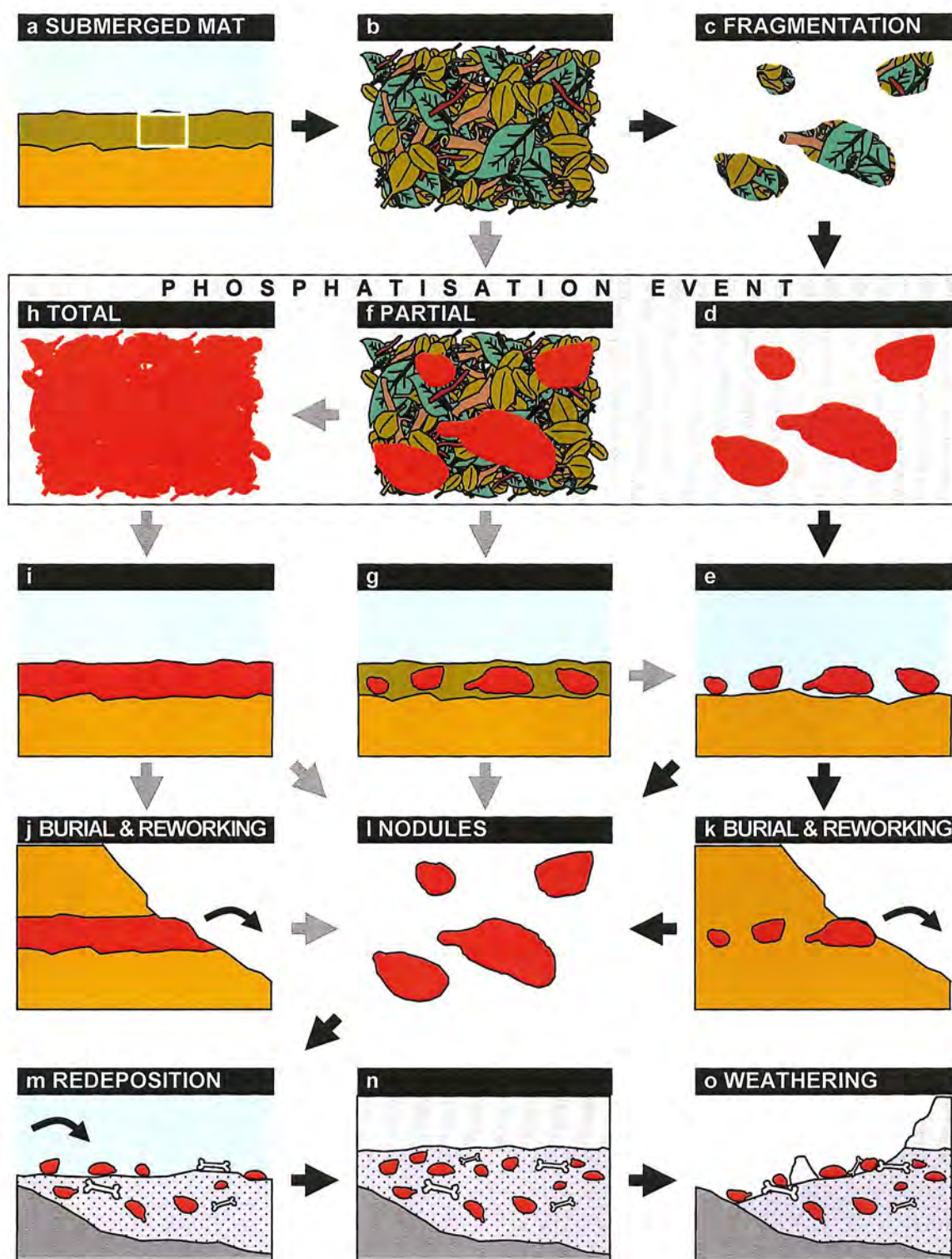
Figure 5.33: Flowchart of provenance and depositional history of fossiliferous phosphatised nodules from Dunsinane Site. The sequence of events a, b, c, d, e/k, l, n, m, o marked with black arrows is favoured as most likely. All sequences begin with the same setting involving a mat of organic debris (a, b) including leaves, twigs, fruits, invertebrates and vertebrate coprolites accumulates in a subaqueous environment where components are bound and partially decomposed by flourishing microbacteria. In the preferred sequence, the mat is fragmented (c) and lumps of organic material (see Figure 5.31i) are deposited in a subaqueous environment that lacks abundant carbonate, where phosphatisation occurs (d). Alternatively, the mat is either partially phosphatised, producing sub-rounded lumps (f, g) or entirely phosphatised (i) in an *in situ* carbonate-poor environment. In the latter case, possible burial and reworking of the

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phosphatised layer provides sub-rounded nodules that are supplied to Dunsinane Site (j, l). Alternatively, partially phosphatised mat fragments (g), or phosphatised reworked lumps of organic material (e) are either buried and reworked (k) or are supplied to the Dunsinane Site deposit directly by transport (l). These nodules are deposited in arenaceous carbonate at Dunsinane Site along with reworked tufaceous intraclasts and late Oligocene vertebrate material (m). After burial by successive intraclast tufa deposits (n), the deposit is exposed by erosion and denudation and subject to leaching and dissolution of minerals. Primary lithotextures are mainly destroyed, bedding and overlying deposits slump, some phosphate nodules are partially dissolved and vertebrate bones are fragmented by partial solution and subsidence of the matrix and are enriched with varying amounts of mobile phosphate and iron oxide. As the surface lowers, more resilient fossil components form a surficial lag (o).

over a period of time. The mode of phosphatisation of organic material in the Dunsinane Site nodules is so unusual that it is difficult to invoke a parsimonious scenario in which the process occurred more than once (i.e. repetitively at Dunsinane Site as new material accumulated). It is more likely that phosphatisation was a unique event that provided the material which was subsequently reworked and gradually deposited at Dunsinane Site. As the deposit was weathered, fossil bone was fragmented and dissolved and enriched by mobile phosphate derived from dissolved nodule material. Over time, the relatively resilient nodules formed a surficial lag as the carbonate matrix was corroded.

The revised depositional model for the Dunsinane Site deposit is illustrated in Figure 5.33. The Dunsinane Site deposit and its depositional model do not challenge the general tufagenic model at Riversleigh, and may in fact provide examples of the kinds of cyclic reworking and depositional processes occurring in such a system.

5.3 Riversleigh middle Tertiary cave facies

Cave facies at Riversleigh can be divided into two major lithotypes:

1. Speleothem (mainly flowstone)
2. Detrital cave sediment

These two lithotypes are usually associated with each other in deposits that can be very complex. They can be distinguished from tufagenic host facies by their contrasting lithology, restricted depositional geometry and aspects of their faunas.

5.3.1 Interpretations by previous workers

The presence of Tertiary cave deposits at Riversleigh was recognised by Archer *et al.* (1989, 1994, 1997), Megirian (1992), Creaser (1997) and Hand (1997a, 1997b, 1998a, 1998b).

Bitesantenary Site was previously recognised as a cave deposit because of the abundance and diversity of bat fossils, the presence of speleothem, including a structure interpreted as a broken stalagmite, a contact deposit coating the cave margin and the prevalence of a pink-coloured sediment with a phosphatic texture considered to be a phosphorite derived from guano (Megirian 1992, Archer *et al.* 1994, Hand 1997b, 1998a, 1998b). Microsite was recognised as a cave deposit because of the abundance of

bat material in that deposit (Hand 1993, Archer *et al.* 1994). The deposit at Gotham City
Site was interpreted as being associated with a bat roost (Hand 1990, 1996) because of
the prevalence of fossil bat material including and other small vertebrates in the size-
range of the ghost bat, *Macroderma malugara*, also found at that site. The prevalence of
phosphatic lithotexture in that deposit, and the presence of flowstone indicate that
Gotham City Site is most likely a cave deposit. Arena and Black (1996) interpreted the
deposit at AL90 Site as a cave deposit; this is described in more detail below.

However, some interpretations of lithology and depositional models in previous
literature are challenged by a number of factors, including petrography and the
application of karst concepts, particularly denudation.

The deposit at Neville's Garden Site was also recognised to contain speleothem and a
diverse and abundant fossil bat fauna, however, because of the presence of sediments
apparently formed under subaqueous conditions, and the occurrence of some aquatic
taxa including the ornithorhynchid *Obdurodon dicksoni*, the deposit was considered to
have formed in a pool adjacent to a cave opening at the early Miocene surface (Archer
et al. 1994, Hand 1997a). This depositional model is challenged here because deposits
forming on the surface during the Miocene are unlikely to have persisted to the present
because of denudation occurring since that time, and the presence of subaqueous
conditions and aquatic taxa need not be explained by a surface pool as the depositional
environment, because these facies also form in cave environments. Some
lithologies regarded to indicate 'pool' conditions and aquatic environments by Archer *et
al.* (1989, 1994) and Megirian (1992) have since been reinterpreted as cave deposits
(see below).

Flowstone deposits at Riversleigh have previously been interpreted as described as
evaporites and algal mats that formed in pools at the surface (Archer *et al.* 1989, 1994,
Duncan and Briggs 1996, Duncan *et al.* 1998).

A number of laterally extensive deposits of crystalline carbonate outcropping between
192 and 194m on Gag Plateau were interpreted as travertine formed during a regional
event and factored into stratigraphic correlation by Archer *et al.* (1989, 1994, 1997).

The petrology of samples from one outcrop attributed to this deposit collected from in Ray's Amphitheatre (Figure A7, Appendix A) lacks patterns of syntaxial calcite crystals typical of speleothem, but does exhibit laminations. These deposits appear to be contained within a tufaceous host with clearly delimited boundaries. They are thus considered to be variations of altered flowstone comparable to that from Upper Site (Figure 5.39a, c). Detrital crystals and calcite rafts in these deposits also indicate the presence of calcite precipitation in subaqueous conditions. Other outcrops on Gag Plateau previously attributed to a widespread deposit are actually discrete flowstone deposits.

The complex speleothem and cave deposits which occur within late Oligocene tufagenic host on Godthelp Hill were described as tufa lying unconformably on unfossiliferous alluvial sediments by Megirian (1992) and subsequently referred to as tufa by Creaser (1997). The "oncolitic gravel" from Upper Burnt Offering Site (Megirian 1992:231-233) was interpreted as evidence of dry exposed conditions analogous to those in which oncolite-like pisolitic concretions formed in a Bolivian playa lake subject to frequent evaporative conditions (Risacher and Eugster 1979). According to the fluvio-clastic model presented by Megirian (1992), a parsimonious interpretation would actually have been a diagnosis of oncoidal tufa that characterises channels in braided fluvial systems (Ordóñez and Garcia del Cura 1983, Nickel 1985, Pedley 1990, Drysdale 1995, Ford and Pedley 1996). The deposit is also associated with flowstone, which was interpreted as stromatolite by Megirian (1992). Given this association, and that the outcrop is in the vicinity of other cave deposits including the deposit at Bitesantenary Site, and the nucleus of one of the "oncolites" figured is a fragile bat jaw, the most parsimonious interpretation would be that this is actually a spelaean deposit of cave pearls and flowstone, rather than an alluvial deposit. Similar cave pearl deposits at Riversleigh include Bullseye Site, Nicole's Boulders Site and Inabeyance Site (see below).

Speleothem containing bacterial structures on Godthelp Hill was interpreted as bacterial travertine formed by hydrothermal activity (Megirian 1992) and considered indicative of harsh palaeoenvironmental conditions. Fossilised fungi, algae and bacteria are known from dripstones (Northup *et al.* 1997). Evidence of hydrothermal activity has not been

observed at Riversleigh. Similar structures have been described as sinter (Megirian 1992) and spring heads (Archer *et al* .1994).

Thus, key issues to be addressed here are:

1. Application of diagnostic criteria to identify flowstone and other forms of crystalline speleothem, which has been subject to problematic interpretations in the past.

2. Application of diagnostic criteria to thus identify cave deposits and distinguish them from non-cave deposits.

3. Identification of the general conditions under which these cave deposits could have formed.

5.3.2 Petrographic diagnosis of flowstone and other forms of crystalline speleothem at Riversleigh

A key aspect of the interpretation of cave deposits at Riversleigh is the recognition of flowstone and speleothem. Previous authors have interpreted these distinctive lithotypes in a variety of ways including travertine of hydrothermal origin and stromatolite (Megirian 1992), laminated pool deposits and evaporites (Archer *et al.* 1994) and algal mats (Duncan *et al.* 1998), which have then been applied as the basis of depositional models (see above). These deposits were not distinguished from those already recognised as having originated in caves (i.e. Bitesantenary Site). Because diagnosis of speleothem is an important component of the interpretation of both cave and non-cave facies, attention has been given here to the diagnosis of flowstone at Riversleigh, so that deposits previously interpreted otherwise can be properly assessed and appropriate models of depositional processes applied.

Although speleothems including dripstones such as stalagmites and stalactites differ morphologically from flowstone, they are formed by very similar processes at the molecular level, which results in very similar petrographic characteristics. The model of formation of the syntaxial crystalline structure of calcite speleothem, including flowstone, of Onac (1997) which produces a characteristic appearance under cross-polarised light (Figure 4.15), is described in Section 4.3.1.2.

Figure 5.34a/b, c/f shows sections from a sample of flowstone collected from an active cave environment, in Cutta Cutta Cave, Northern Territory. The rows of syntaxial 'palisades', with terminal triangular crystal surfaces marked by fine silt are clearly apparent, displaying the characteristic appearance of flowstone when viewed using cross-polarised light. This sample is compared with specimens recognised and interpreted as flowstone in the field at Riversleigh by their characteristic laminated crystalline appearance in hand-specimen and the morphology of deposits as coatings and infills. For comparison, there is also a section from a specimen collected from an outcrop in a karst terrain outside of Riversleigh (near Katherine in the Northern Territory; Figure 5.34d/g) which is identical to hand-specimens considered to be flowstone from Riversleigh (Figure 5.43e/h, i/l, j/m, k/n). All of these samples share very similar structure, including layers of aligned crystals marked by characteristic rows of triangular terminal surfaces which exhibit characteristic pattern when viewed using cross-polarised light. Fine silt may occasionally mark termination or exposure surfaces. Growth patterns are often affected by the morphology of the surface on which the flowstone has formed (Figure 5.34j/m, 5.35i/l, j/m), and probably also by dynamic conditions in the depositional environment that may have influenced the thickness of layers of calcite or disrupted the even formation of successive layers (Figure 5.35e/h). Variations of flowstone lithotexture in specimens from Riversleigh are illustrated in Figures 5.35. While alteration can affect some of the primary texture, some recognisable aspect of original crystal structure such as layering is usually maintained.

Thus deposits at Riversleigh that resemble those used in this comparison are considered to be speleothem and/or flowstone.

While it is possible for similar forms of lithotexture to form under circumstances other than a cave environment (i.e. subaqueous flow in a tufagenic environment proximal to source or otherwise limited in contaminants and other biological activity), other aspects of Riversleigh cave deposits including depositional structure and associated faunas strongly support the interpretation of these lithotypes as speleothem. Distinguishing characteristics of Riversleigh cave deposits are discussed in more detail below.
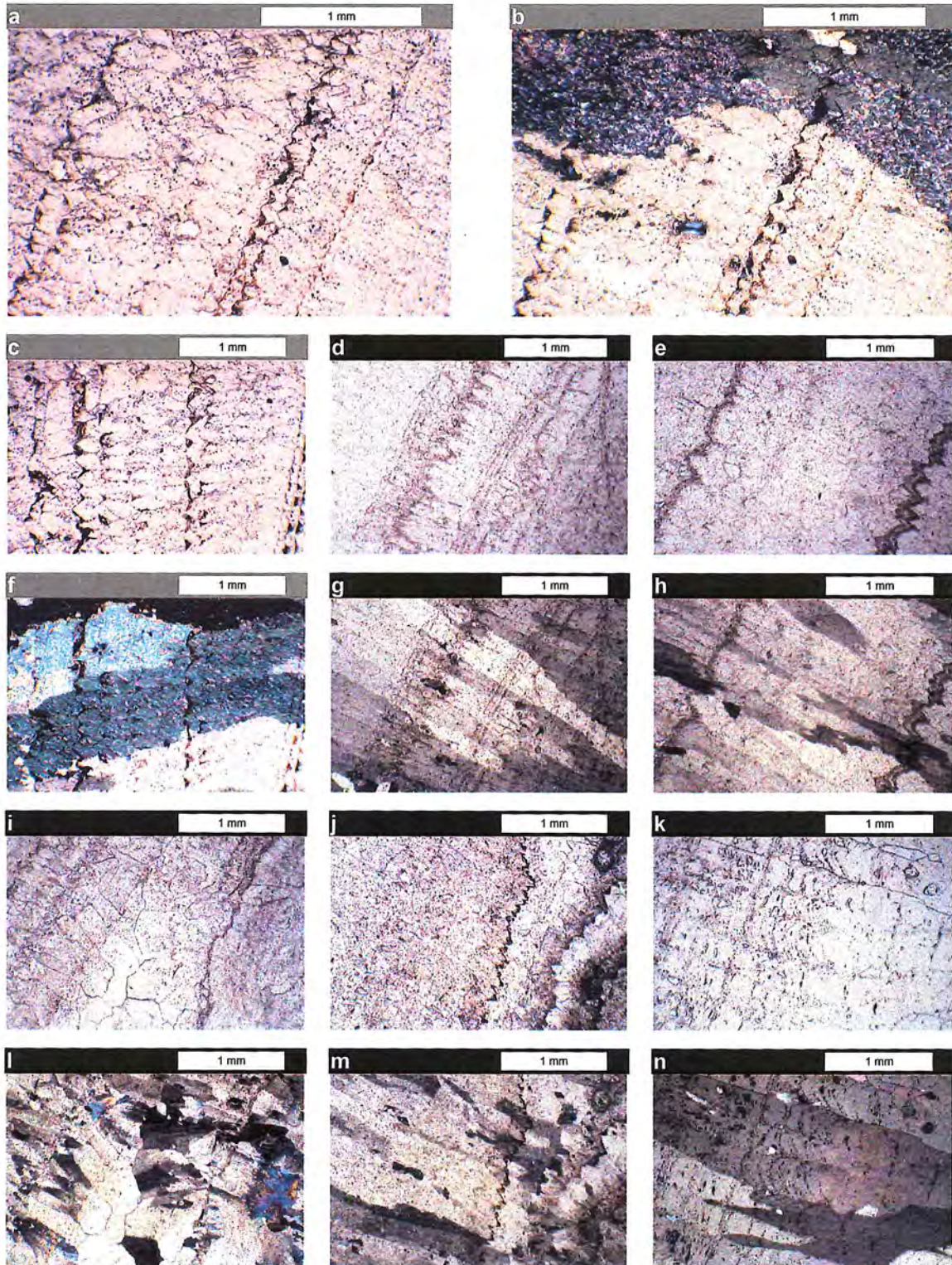
Figure 5.34: Comparative petrography of flowstone from recent and Tertiary samples. All specimens are oriented with the direction of growth to the left or upper left. a/b) Recent flowstone (PP/XP; RA2003-12; Cutta Cutta Cave, NT). c/f) Recent flowstone (PP/XP; RA2003-12; Cutta Cutta Cave, NT). d/g) Flowstone (PP/XP; RA2003-16; Cambrian karst north of Katherine, NT). e/h) Flowstone (PP/XP; RA2003-9B; AL90 Site). i/l) Flowstone (PP/XP; R120; Mikes Menagerie Site). j/m) Flowstone (PP/XP; RA2003-9A; AL90 Site). k/n) Flowstone (PP/XP; R153; RSO Site). Note the calcite crystals pointed in the growth direction and syntaxial orientation of adjacent crystals under crossed polars. Fine particles that fill 'valleys' between crystal peaks form oppositely oriented triangles.

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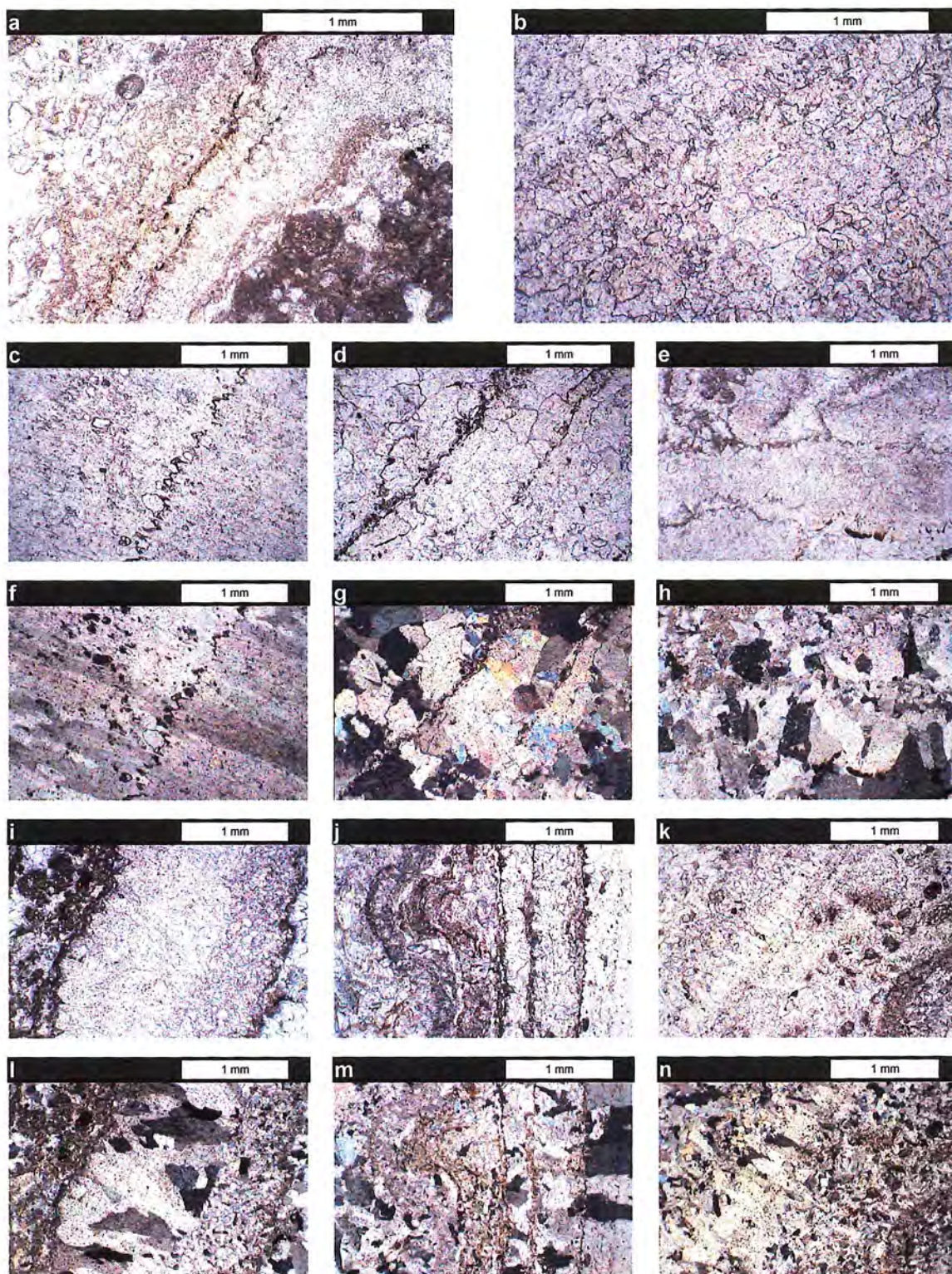
Figure 5.35: Petrography of variations of flowstone texture from Riversleigh samples. All specimens are oriented with the direction of growth to the left, upper left or top. a) Fine flowstone coating a tufaceous intraclast (PP; R151C; Wayne's Wok Site). b) Very fine flowstone (PP; RA2003-7; below Mike's Menagerie Site). c/f) Flowstone (PP/XP; R152B; RSO Site). d/g) Altered flowstone, compare to e/h (PP/XP; R156; Upper Site). e/h) Disrupted flowstone (PP/XP; RA22; AL90 Site). i/l) Fine flowstone with micrite coating and tufaceous lithotexture in the upper left (PP/XP; R158; Inabeyance Site). j/m) Succession of very fine flowstone showing coating of a tiny particle, terminated by coarse crystalline texture to the left (PP/XP; RA2003-9A; AL90 Site). k/n) Fine flowstone (PP/XP; R151B; Wayne's Wok Site).

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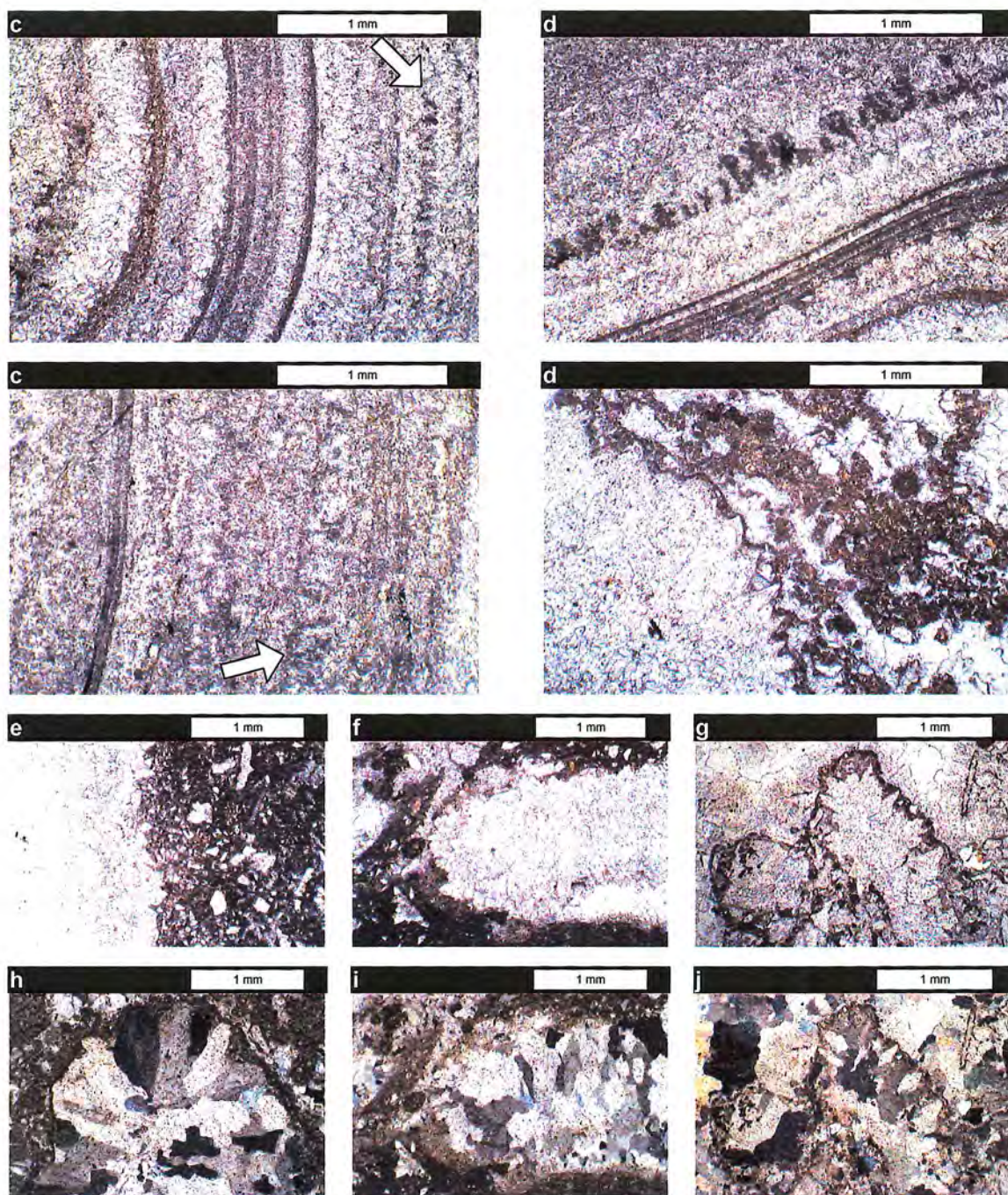
Figure 5.36: Petrography of various speleothem textures from Riversleigh samples. a) Cave pearl, nucleus is to the centre left (PP; R148; Bullseye Site). b) Detail of 'bacterial shrub' texture, left-hand end corresponds to point arrowed in 5.36a (PP; R148; Bullseye Site). c) Cave pearl with similar bacterial texture, arrow indicates a layer with 'bacterial shrub' texture similar to that detailed in 5.36a and 5.36a b (PP; EP2; Upper Burnt Offering Site). d) Layered sparite with bio-precipitated/crystalline matrix (PP; R158; Inabeyance Site). e) Shelfstone fragment in micritic matrix (PP; EP76; Camel Sputum Site). f/i) Shelfstone with micrite matrix (PP/XP; EP76; Camel Sputum Site). g/j) Double-tipped shelfstone (PP/XP; R152A; RSO Site). h) Shelfstone tip (XP; R158; Inabeyance Site).

Another distinctive form of speleothem recognised in cave deposits at Riversleigh are elongate structures that resemble flat double-sided flowstone sheets that can be several millimetres thick and several centimetres long (Figure 5.36e/h, f/i). These speleothems are present in samples from several cave deposits localities including Camel Sputum Site, RSO Site, Inabeyance Site and AL90 Site. These are interpreted as shelfstone, which is usually precipitated as flat deposits of calcite projecting from the edge of cave pools (Hill and Forti 1997a).

5.3.3 Description and interpretation of Riversleigh cave facies

Distribution

Cave deposits are widespread at Riversleigh, occurring on D Plateau, Gag Plateau and Southern Gag Plateau. There is a high concentration of cave deposits on Godthelp Hill (southern D Plateau).

Structure and depositional geometry

Cave deposits are typically restricted in horizontal and vertical geometry and are usually comprised of complex combinations of flowstone and cave sediment with contact surfaces that are often uneven and/or inclined. The outline of the voids in the host rock in which cave deposits occur may sometimes be marked by a coating of altered cave sediment or by flowstone. Flowstone often also coats bones, layers of sediment and lithoclasts of parent material.

Based on data available so far, these deposits do not appear to be aligned or areally restricted to the form or direction of any structural patterns in the parent rock. Detailed mapping of outcrops of Riversleigh cave deposits is required to help determine whether there are trends in their form or orientation. Regular joint patterns and other similar structural features are not apparent in the Tertiary deposits at Riversleigh (see below). In plan, shapes of cave deposits include from long and narrow fissures, ovate to sub-circular and complex irregular forms. Representative plans of two cave deposits at Riversleigh are illustrated in Figure 5.37. Deposit thickness may vary from a few centimetres to more than 2 m. Some deposits can extend laterally for tens of metres and may branch or form interconnected networks.

Legend

Observed margin

Probable margin

Inferred margin

N

1m
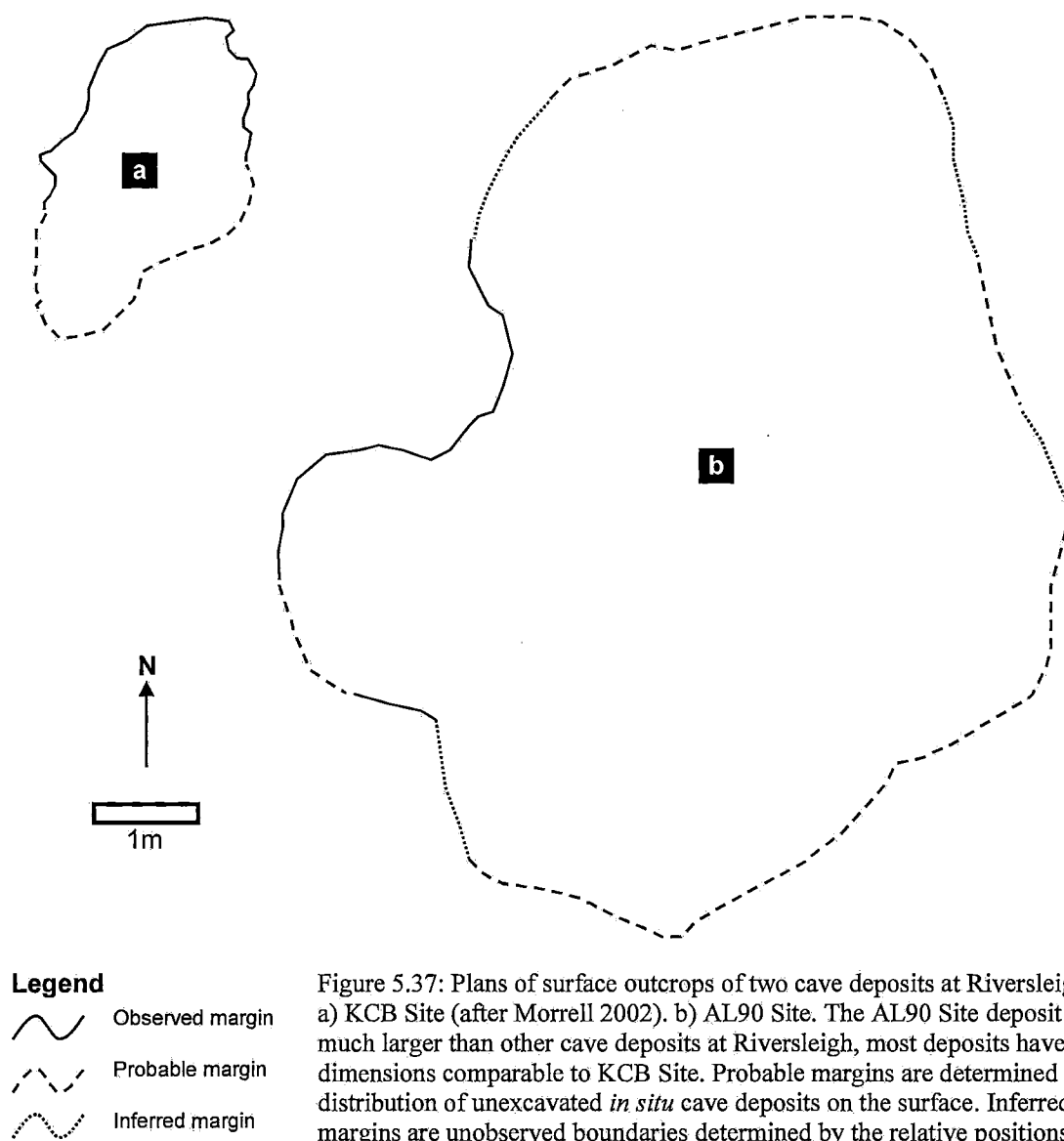
Figure 5.37: Plans of surface outcrops of two cave deposits at Riversleigh. a) KCB Site (after Morrell 2002). b) AL90 Site. The AL90 Site deposit is much larger than other cave deposits at Riversleigh, most deposits have dimensions comparable to KCB Site. Probable margins are determined by distribution of unexcavated *in situ* cave deposits on the surface. Inferred margins are unobserved boundaries determined by the relative positions of adjacent observed and probable margins.

The cave deposits at Godthelp Hill appear to represent parts of an well-developed cave system, with more than 20 fossiliferous cave deposits within an area measuring about 100m by 50m, which is characterised by abundant flowstone and cave sediments deposited within older tufaceous parent.

Description and interpretation

These deposits are considered to be cave deposits that are distinct from tufagenic deposits based on the following criteria:

1. The presence of flowstone and/or other speleothem.

2. The limited areal dimensions of deposits that are clearly delineated by their lithologies that are distinct from the heterogeneous tufaceous parent deposits.

3. The relatively low abundance of tufaceous textures and greater abundance of crystalline and phosphatic lithotextures in cave sediment.

4. A greater degree of association and articulation of skeletal parts in fossil deposits, indicating very limited transport and disturbance prior to and during preservation.

5. The relatively high abundance and diversity of fossil bats in contained faunas (and a relatively low abundance and diversity of aquatic taxa, including crocodiles, chelid turtles fish and lungfish).

Cave sediments are dominated by detrital crystals, phosphatic and crystalline textures. Micritic and intraclasts textures also occur, and are considered to represent deposits formed as talus or in cave pools by the accumulation of detrital material from an external source, or derived from the breakdown of material within the cave environment. Crystalline textures may be derived from more than one origin, for example forming as primary deposits of calcite formed in subaqueous environments, or by the alteration of speleothem or by the replacement of mud with spar by seepage. Globular texture (Figure 5.40b, 5.7c, d, i) is interpreted as 'porous cavity fill' texture formed by the gradual replacement of mud by calcite spar in debris deposits (Osborne 1986). This produces a globular texture that resembles tufagenic peloidal micrite (see above), although the mode of formation is different.
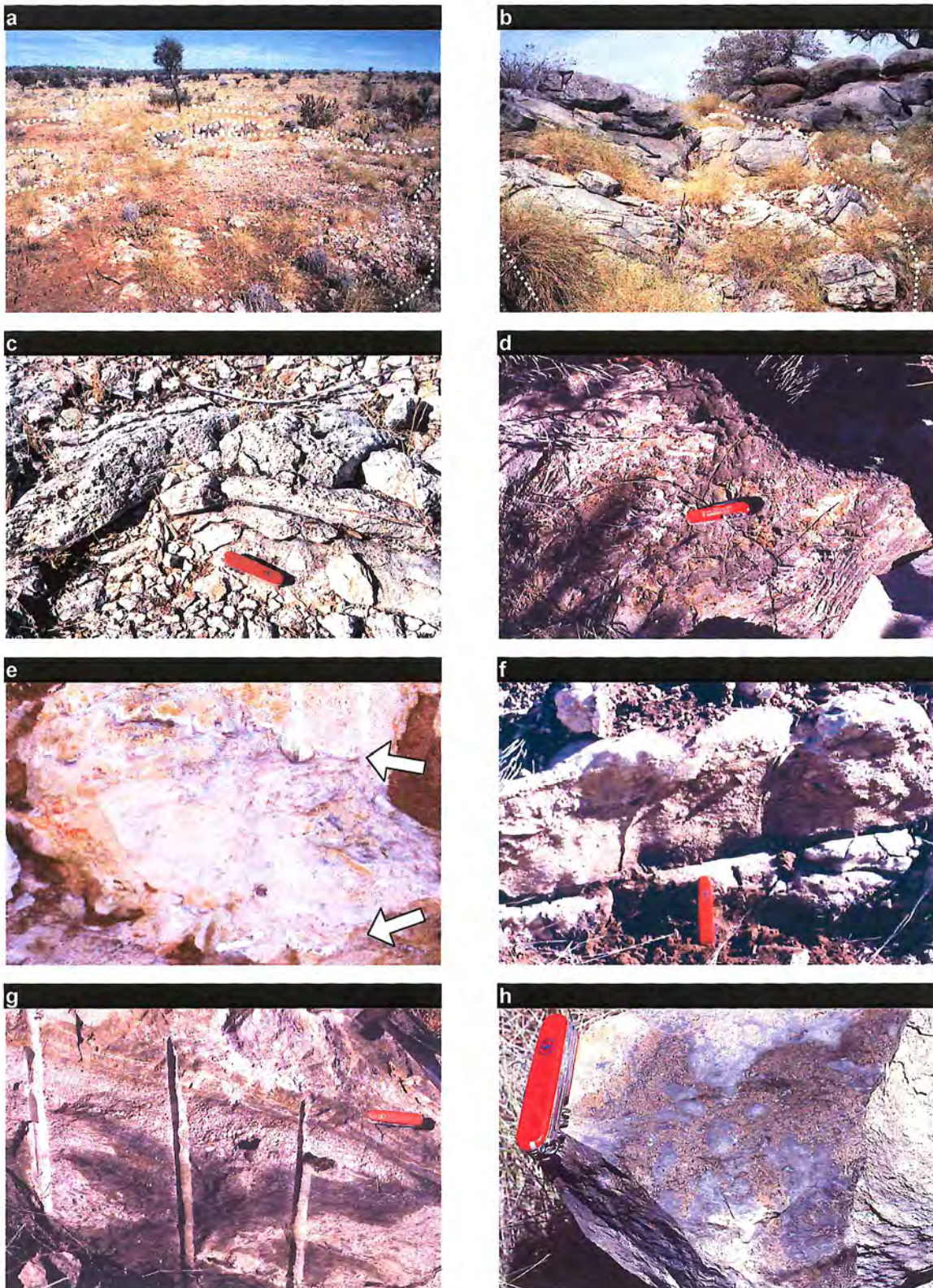
Figure 5.38: Various outcrops of cave deposits at Riversleigh. a) Extensive deposit of white flowstone. This deposit is approximately 20m long and varies in width to a maximum of about 3-4m. Boundaries of deposit marked with dotted lines, White Cave Site, Southern Gag Plateau. Pure crystalline flowstone and speleothem deposits such as this are common in several places at Riversleigh. These deposits may have been formed by vadose karst processes occurring deep below the surface in caves that were fed by solution conduits, into which introduction of contaminants was very limited. b) Morphology of a typical spelaean deposit showing layers of flowstone at various angles within tufaceous host. The entire outcrop,

which apparently narrows toward the base forming a 'V-shaped' profile is approximately 3m wide and 4-5m in apparent vertical thickness. Boundary marked by dotted line, Creaser's Ramparts Site. c) White unfossiliferous flowstone forming part of a narrow elongated deposit, 50m north of Encore Site. d) Black flowstone, Wang Site. e) Profile of a typical cave sediment deposit excavated by quarrying at Camel Sputum Site. A layer of white flowstone separates the upper host rock from fossiliferous cave sediment below (top arrow). A limb bone from a large animal and part of the articulated vertebral column of a large snake are visible in the lower deposit (bottom arrow). A detail of the articulated snake vertebrae is shown in Figure 57b. f) Fossiliferous cave fill with apparent dip, possibly caused by an inclined depositional surface or post-diagenetic movement, Encore Site. g) Oncolites with flowstone and cave sediment containing breccia, Nicole's Boulders Site. h) Dark black/brown cave fill rich in bat bones and reworked host rock fragments that is clearly delineated from the host rock by lithological variation and sharp contact boundary, Peter the Pilot Site.

Phosphatic texture (Figure 5.12) is probably formed from altered faecal material deposited in caves by bats (Megirian 1992). Guano and phosphatic minerals derived from guano are a typical component of cave deposits (Osborne 1984), usually forming as powdery nodules in guano or clastic sediment, or as a coating on host rock that is in contact with guano (Hill and Forti 1997b).

Flowstones and other speleothem are easily distinguished from other carbonates in the field and in hand specimen because of their layered crystalline form. They have been observed *in situ* on surfaces of all orientations and can coat bone, cave sediment and lithoclasts. While often white (Figure 5.38c), flowstones may also exhibit colour banding (usually yellow or brown) and at some localities, flowstone is black (Figure 5.38d). Yellow/brown/red colouration of speleothem is usually due to the inclusion of humic and fulvic acids, and ferric oxides and hydroxides; and black colouration can usually be attributed to inclusion of manganese oxides and carbon (White 1997).

Petrography of representative Tertiary cave deposits at Riversleigh is illustrated in Figures 5.39 and 5.40.

Finely laminated spherical structures have been recognised from Upper Burnt Offering Site, Bullseye Site, Inabeyance Site and Nicole's Boulders Site (see Figure 5.38g). These structures, which are usually closely associated with flows tone, are comprised of very finely laminated calcite with bacterial textures (Figure 5.36). They are interpreted as cave pearls formed in low-energy subaqueous condition, possibly under conditions where some light may have occurred (i.e. the 'twilight zone'). Cave pearls are concentrically banded concretions that form in cave pools (Hill and Forti 1997a).

Detrital crystals in cave deposits are considered to be reworked fragments of calcite rafts. While calcite rafts can form in surface environments, (see above), they also form on the surface of quiet pools of water in caves by degassing of CO_2 (Hill and Forti 1997a), and thus indicate the presence of standing water.

The presence of some bio-precipitated textures and structures that may be related to microbial activity could indicate that micro-organisms such as anaerobic bacteria
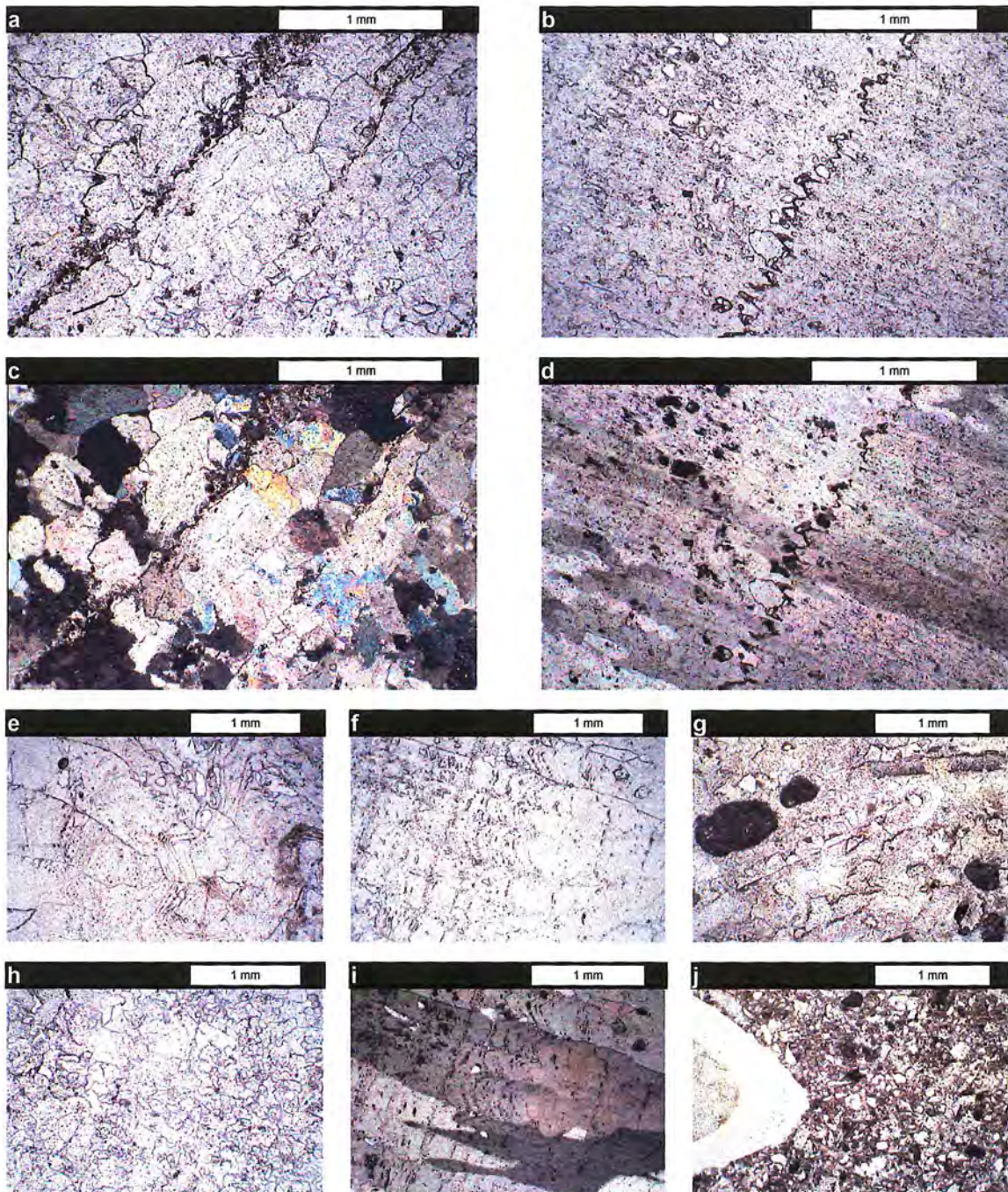
Figure 5.39: Petrography of lithologies from cave deposits at Upper Site and RSO Site on Godthelp's Hill. a/c) Layered calcite spar interpreted as altered flowstone. Characteristic layer surfaces and syntaxial crystal orientation appears to have been disrupted. Compare to b/d and travertine from Ray's Amphitheatre in Figure X.46 e/g (PP/XP; R156; Upper Site). b/d) Typical flowstone (PP/XP; R152B; RSO Site). e) Zoned or layered calcite similar to f/i (PP; R156; Upper Site). f/i) Flowstone. (PP/XP; R153; RSO Site). g) Detrital crystals and tufaceous intraclasts (PP; R152A; RSO Site). h) Crystalline lithotexture (PP; R151C; Upper Site). j) Section through a small bone in a matrix of fine particles with micritic cement (PP; R152A; RSO Site).
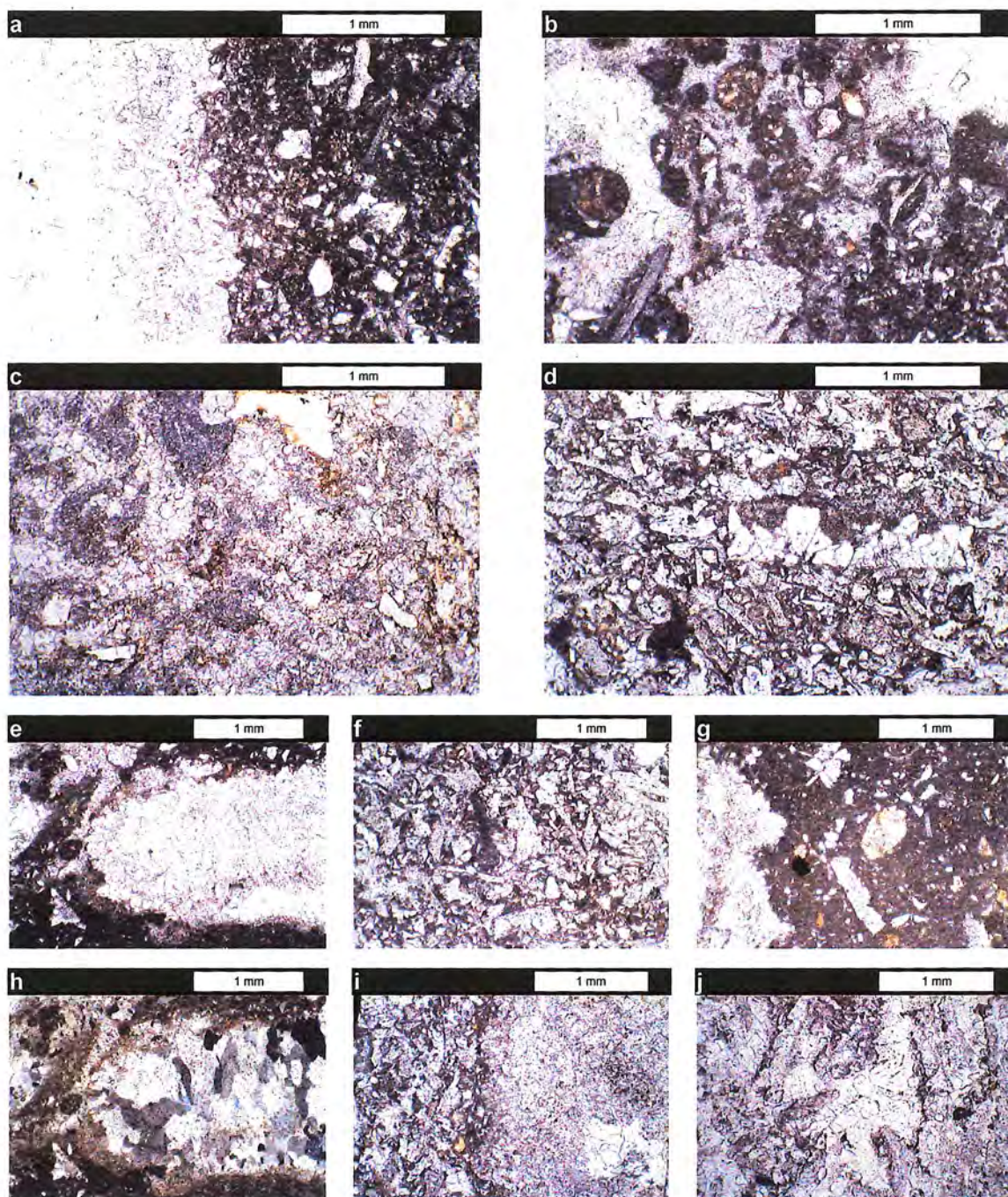
Figure 5.40: Petrography of lithologies from Camel Sputum Site. a) Speleothem with fine micritic matrix containing detrital crystal fragments (PP; EP76). b) Globular 'porous cavity fill' texture (PP; EP76). c) Matrix with crystalline texture and bone fragments (PP; EP77). d) Detrital crystals texture in fine micrite, calcite raft at centre (PP; R155). e/h) Tip of shelfstone in micritic matrix. (PP/XP; EP76). f) Detrital crystalline texture (PP; R155). g) Dense micritic matrix with detrital crystals, calcite raft at centre (PP; EP76). i) Coarse/ fine crystalline matrices (PP; R155). j) Zoned calcite filling irregular void in detrital crystalline matrix (PP; R155).

inhabited cave environments. This would be expected to occur in deposits containing
fossil animal remains that would have been subject to decomposition by bacteria.
Fossilised fungi, algae and bacteria are known from dripstones, although the role (if
any) of these microorganisms in the formation of carbonate speleothems is not fully
understood (Northup *et al.* 1997). Bacterial 'shrubs' occurring in speleothem on
Godthelp Hill (Megirian 1992) and cave pearls from Upper Burnt Offering Site and
Bullseye Site (Figure 5.36a/b, c) and could indicate that these speleothems formed in
cave environments where some light was available (i.e. 'twilight zone').

Structures resembling polygonal desiccation cracks have been observed in cave
sediments at AL90 Site and Cleft of Ages Site (Figure 5.41f, g), these may be indicative
of occasional lack of water in dynamic cave depositional environments.

Age

Faunas from cave deposits at Riversleigh are early Miocene, middle Miocene and early-
late Miocene in age (Archer *et al.* 1989, 1994, 1997).

Vertebrate faunas and taphonomy

Fossil bones can occur in both speleothem and cave sediments. Remains of
microchiropteran bats are usually more abundant and diverse in cave deposits, at least
40 species of bat have so far been identified at Riversleigh (Archer *et al.* 1997). This is
considered a result of the use of caves and fissures by bats for roosting, feeding and
habitation. Modern relatives of some hipposiderid bat taxa from Riversleigh roost in
deep caves in limestone vegetated with lowland rainforest and woodland in New Guinea
and northern Australia (Hand 1997a, 2003). The occurrence and diversity of different
bat taxa varies between localities. This may be related to different conditions within
cave environments, varying environmental conditions at the surface, competition
between different bat taxa for access to those environments and because of age
differences between assemblages.

Although articulated skeletal parts have occasionally been found in tufagenic deposits
(i.e. at Dunsinane Site, Arena (1997)), association and articulation of skeletal parts is
more common in cave deposits. Articulated skeletons and skeletal parts have been
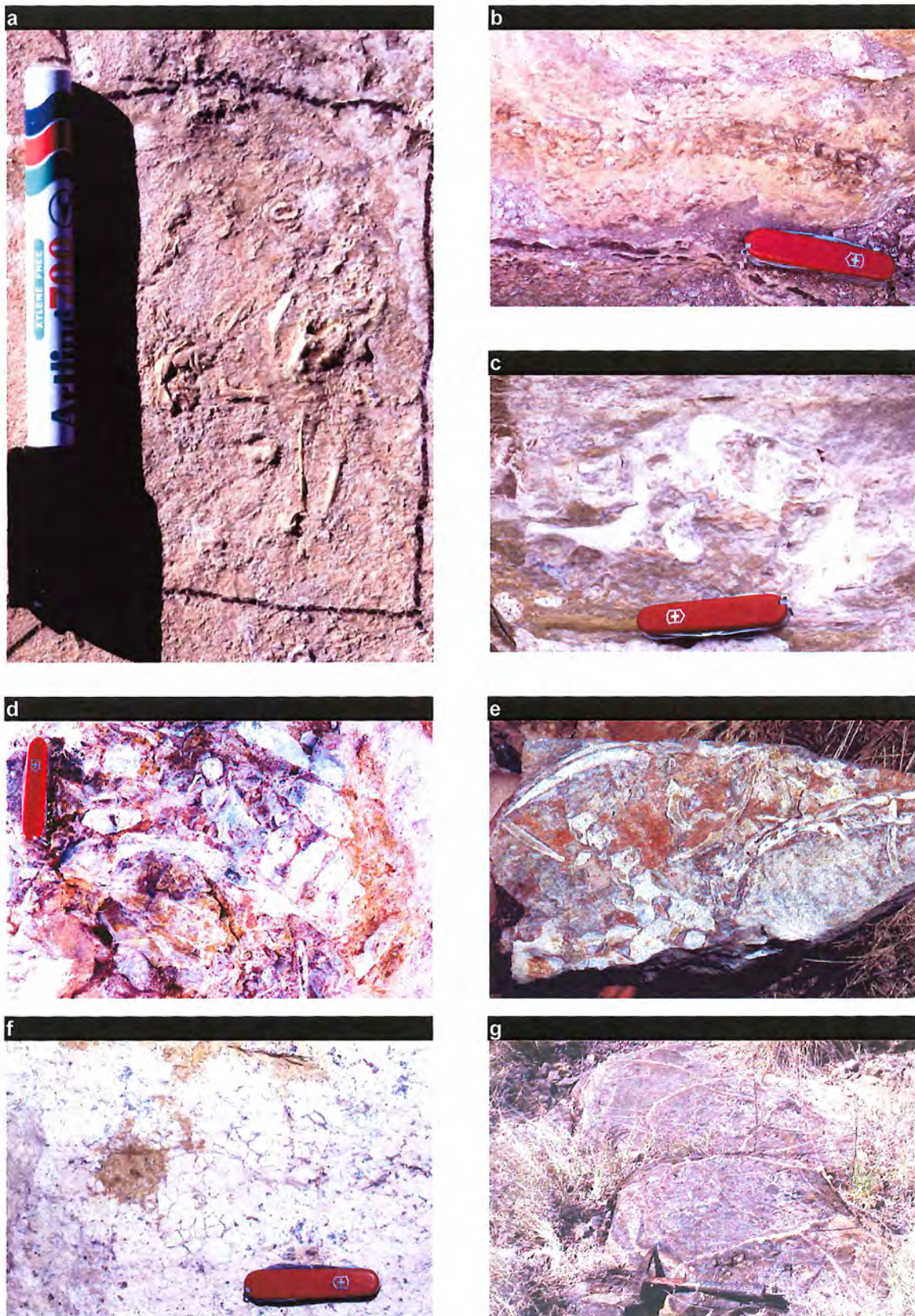
Figure 5.41: Articulated/associated skeletal parts and dessication cracks from Tertiary cave deposits at Riversleigh. a) Small polyprotodont marsupial skeleton *in situ* in flowstone that was successfully removed from the deposit by blasting with explosives, Dome Site. b) Excavated cave sediment face showing part of the articulated vertebral column of a large madstoiid snake *in situ*, Camel Sputum Site.

Photograph by A. Gillespie. c) Broken flowstone slab showing *in situ* associated cranial and post-cranial elements of the sheep-sized diprotodontid *Nimbadon lavarackorum*, AL90 Site. d) Broken slab showing *in situ* articulated skeletal vertebrae, sacrum and pelvic bones of *Nimbadon lavarackorum*, AL90 Site. e) Broken slab showing *in situ* articulated vertebrae and associated ribs of *Nimbadon lavarackorum*, AL90 Site. Photograph by A. Gillespie. f) Broken slab showing small dessication cracks, AL90 Site. g) Very large structures that resemble polygonal dessication cracks, Cleft of Ages Site.

recovered from Dome Site (a small marsupial), AL90 Site (including the sheep-sized diprotodontid *Nimbadon*, the fox-sized thylacinid *Nimbacinus* and a small marsupial), and Camel Sputum Site (snakes). Some *in situ* articulated specimens are illustrated in Figure 5.41.

While aquatic taxa including fish, lungfish, crocodilians, turtles and ornithorhynchids are present in faunas from cave deposits at Riversleigh, they are not as abundant or as diverse as those from deposits formed in non-cave deposits.

Remains of other small vertebrates with fragile skeletal components appear to be more common in cave deposits. Because this observation is based largely on the literature, it is not regarded as conclusive, as collection of material and reporting of faunal representation may not be consistent between localities selected for comparison here. Several smaller bird taxa (i.e. not large flightless forms such as dromornithids and casuariids) have been described from cave deposits including a log-runner, cockatoo, a possible stork, swiftlets, and a lyrebird (Boles 1993, 1995, 1997a, 1999, 2001). Several taxa of frogs have so far been recognised from assemblages that are almost all from cave deposits (Archer *et al.* 1989, 1994, 1997, Myers *et al.* 2001, Myers 2002, Tyler 1989, 1990, 1991a, 1991b, Tyler *et al.* 1990). Lizards and smaller snakes also appear to be better represented in more cave deposits than non-cave deposits.

The Bitesantenary Site Local Fauna (Faunal List 5), Neville's Garden Site Local Fauna (Faunal List 6) and Upper Site Local Fauna (Faunal List 7) are representative early Miocene (Zone B) faunas from cave deposits. Bitesantenary Site yields a very high abundance of bat material from a deposit characterised by phosphatic and flowstone/speleothem textures (Megirian 1992, Archer *et al.* 1994). At least nine species from five hipposiderid genera are represented. The occurrence of larger animals in this fauna is relatively limited.

The Neville's Garden Site Local Fauna (Faunal List 6) has a higher diversity of taxa with a higher representation of aquatic taxa including indeterminate lungfish and crocodilian remains and the ornithorhynchid *Obdurodon dicksoni*. At least 4 species of microchiropteran bats from 3 genera have been identified. Non-dromornithid birds,

Faunal List 5: Bitesantenary Site Local Fauna
Source locality: Bitesantenary Site, Bitesantenary East Site

CHORDATA
 NEOPTERYGII
  Orders indet.
   Families indet.
    Genera indet. spp.
 ARCHOSAUROMORPHA
  APODIFORMES
   APODIDAE
    ?Collocalia sp
  AVES order indet
   Family indet.
    Genus indet. sp. 1
    Genus indet. sp. 2
  CICONIIFORMES
   ?Ciconia sp
 LEPIDOSAUROMORPHA
  SQUAMATA
   AGAMIDAE
    Genus indet. sp.
   BOIDAE
    Genus indet. sp.
 MAMMALIA
  DASYUROMORPHIA
   DASYURIDAE
    Barinya wangala
  DIPROTODONTIA
   MACROPODIDAE
    Ganguroo bilamina
   PHALANGERIDAE
    [New genus 1 new sp. 2] (BITESANTENARY EAST SITE)
  CHIROPTERA
   HIPPOSIDERIDAE
    Hipposideros (Brachipposideros) nooraleebus
    ?Brachipposideros watsoni
    Brachipposideros sp. 1
    Brachipposideros sp. 2
    Brachipposideros sp. 3
    Brachipposideros sp. 4
    Hipposideros sp.
    Rhinonicteris tedfordi
    Riversleigha williamsi
    Xenorhinos halli
 TEMNOSPONDYLI
  ANURA
   ANURA families indet.
    Genera indet. spp.
   LEPTODACTYLIDAE
    Lechriodus intergerivus
MOLLUSCA
 GASTROPODA
  Orders indet.
   Families indet.
    Genera indet. spp.

References for this list: Archer *et al.* (1989), Archer *et al.* (1994), Boles (1997), Boles (2001), Cooke (1997a, 1997b), Hand (1997a, 1997b, 1998a, 1998b), Wroe (1999).

Faunal List 6: Neville's Garden Site Local Fauna
Source locality: Neville's Garden Site

CHORDATA
 TESTUDOMORPHA
  TESTUDINES
   MEIOLANIIDAE
    Meiolania sp.
 ARCHOSAUROMORPHA
  APODIFORMES
   APODIDAE
    ?*Collocalia* sp.
  PASSERIFORMES
   ORIOLIDAE
    Longmornis robustirostrata
    Genus indet. sp. indet.
  PSITTACIFORMES
   CACATUIDAE
    Cacatua sp.
  STRUTHIONIFORMES
   DROMORNITHIDAE
    [Indet.]
  CROCODILIA
   [Indet.]
 LEPIDOSAUROMORPHA
  SQUAMATA
   PYGOPODIDAE
    Pygopus hortulanus
   GEKKONIDAE
    [Indet.]
   AGAMIDAE
    Physignathus sp. *cf. P. leseurii*
   VARANIDAE
    [Indet.]
   SCINCIDAE
    Egernia sp. *cf. E. frerei*
    Eugongylus Group genus indet. spp.
    Sphenomorphus spp. attenuate type
    Sphenomorphus spp. robust type
    Genera indet. spp.
    Sphenomorphus Group genus indet. sp durophagous taxon
    Sphenomorphus Group genus indet. sp small insectivore
   BOIDAE
    Morelia riversleighensis
   PYTHONIDAE
    [Indet.]
 MAMMALIA
  MONOTREMATA
   ORNITHORHYNCHIDAE
    Obdurodon dicksoni
  DASYUROMORPHIA
   DASYURIDAE
    Barinya wangala
    [*Barinya* sp. 2]
    [*Barinya* sp. 3]
   THYLACINIDAE
    Thylacinus macknessi
  PERAMELEMORPHIA
   YARALIDAE

[*Yarala burchfieldi*]
[New genus 1 new sp. 2]
[New genus 1 new sp. 3]
[New genus 2 new sp. 1]
[New genus 3 new sp. 1]
[New genus 3 new sp. 2]
[New genus 5 new sp. 1]
  DIPROTODONTIA
   BURRAMYIDAE
    Burramys brutyi
   ACROBATIDAE
    [Genus 1 sp. 1]
    [Genus 2 sp. 1]
   BALBARIDAE
    Balbaroo gregoriensis
    Nambaroo sp. 5
    Nambaroo sp. 6
   HYPSIPRYMNODONTIDAE
    Hypsiprymnodon bartholomaii
    [*Ekaltadeta ima*]
   MACROPODIDAE
    Bulungamaya delicata
    Wabularoo naughtoni
   EKTOPODONTIDAE
    Ektopodon sp. *cf. E.serratus*
    [*Chunia* sp.]
   MIRALINIDAE
    Durudawiri anfractus
    [*Durudawiri inusitatus*]
   PILKIPILDRIDAE
    [Indet.]
   PHALANGERIDAE
    [New genus 3 new sp. 1]
    [New genus 3 new sp. 2]
   PETAURIDAE
    [Genus 2 sp. 1]
   PHASCOLARCTIDAE
    Nimiokoala greystanesi
   PSEUDOCHEIRIDAE
    [New genus 2 new sp. 1]
    [*Marlu kutjumarpensis*]
    [*Pseudocheirops* sp. 2]
   DIPROTODONTIDAE
    Neohelos tirarensis
   PALORCHESTIDAE
    Propalorchestes ponticulus
   WYNYARDIIDAE
    [*Namilamadeta* sp.]
   THYLACOLEONIDAE
    Wakaleo sp. *cf. W. oldfieldi*
  CHIROPTERA
   HIPPOSIDERIDAE
    Brachipposideros sp. 1
    Brachipposideros sp. 2
    Hipposideros bernardsigei
   MYSTACINIDAE

Icarops paradox
MEGADERMATIDAE
Macroderma sp.
[Indet.]
TEMNOSPONDYLI
ANURA
LEPTODACTYLIDAE
Crinia presignifera

Lechriodus intergerivus
Limnodynastes antecessor
HYLIDAE
[*Litoria rubelliformis*]
DIPNOMORPHA
DIPNOI
[Indet.]

References for this list: Archer *et al.* (1992, 1994), Archer *et al.* (1992), Black (1997), Black and Archer (1997a), Boles (1997a, 1999), Brammall and Archer (1997), Cooke (1997a), Crosby (2002a, 2002b), Hand (1997, 1998), Hutchinson (1992), Hutchinson (1997), Muirhead (1992), Murray *et al.* (2000), Myers (2002), Scanlon (2001), Tyler (1990, 1991), Tyler *et al.* (1990), Wroe (1999).

frogs, snakes and lizards are relatively well represented. Large terrestrial meiolaniid turtles such as *Meiolania* sp. are relatively common in faunas of this type and age (see also faunal lists in Appendix B).

The Upper Site Local Fauna (Faunal List 7) is considered the most diverse at Riversleigh (Archer *et al.* 1989, 1994, 1997). Microchiropterans are well represented with up to 9 rhinolophoid taxa and one or possibly two vespertilionoids. The crocodilian from Upper Site is considered comparable to the terrestrial crocodilian genus *Quinkana*. There is a high diversity of snakes, including small madstoiids, a large boid and also a possible elapid and a possible typhlopid. Lizards are well represented with agamids, scincids, gekkonids and a varanid present. There are at least 14 species of frog from two families and both non-dromornithid and dromornithid birds are represented by a number of taxa. A very high diversity of marsupials of all sizes is present.

The Gotham City Site Local Fauna (Faunal List 8) and the Encore Site Local Fauna (Faunal List 8) are representative middle to early-late Miocene (Zone C) faunas from Riversleigh. Hand (1990, 1996) noted the majority of remains of other taxa (aquatic and non-aquatic) at Gotham City Site were small and comparable in size-range to prey items of Ghost Bats, a species of which occurs in the fauna (*Macroderma malugara*). There are also a variety indeterminate hipposiderids and a molossid. The limited occurrence of other larger animals is comparable to the Bitesantenary Site Local Fauna. This may be related to the nature of the depositional environment to which access by other taxa might have been restricted, for example by the by size of entrance or features of the internal morphology of the cave.

With approximately 12 species of hipposiderids and a megadermatid, the Encore Site bat fauna (Faunal List 9) is comparable to that of Upper Site. Aquatic taxa include indeterminate lungfish and chelid turtle remains. Frogs, lizards and passerine birds are all represented, and a diversity of marsupials of all sizes is present. Differences in the composition of marsupials in this fauna are considered the result of changes in Australian environmental and climatic conditions that had occurred by the late Miocene (Archer *et al.* 1997, Myers *et al.* 2000).

Faunal List 7: Upper Site Local Fauna
Source locality: Upper Site

CHORDATA
ARCHOSAUROMORPHA
  PASSERIFORMES
    MENURIDAE
     Menura tyawanoides
    PASSERIFORMES families indet
     Genus indet. sp. 1
     Genus indet. sp. 2
     Genus indet. sp. 3
  STRUTHIONIFORMES
    CASUARIIDAE
     Emuarius gidju
    DROMORNITHIDAE
     Barawertornis tedfordi
     Bullockornis sp. cf. *B. planei*
  CROCODILIA
    CROCODYLIDAE
     Genus indet new sp *cf. Quinkana*
LEPIDOSAUROMORPHA
  SQUAMATA
    VARANIDAE
     Genera indet. spp
    GEKKONIDAE
     Genera indet. spp
    AGAMIDAE
     Genus indet. sp.
     New genus sp.
     Physignathus sp.
     Physignathus sp. cf. *P. leseurii*
    SCINCIDAE
     Egernia sp. cf. *E. frerei*
     Egernia sp. cf. *E. striolata*
     Eugongylus Group genus indet. spp
     Sphenomorphus spp. attenuate type
     Sphenomorphus Group genus indet. sp durophagous taxon
     Sphenomorphus Group genus indet. sp small insectivore
     Genera indet. spp.
    ELAPIDAE
     Genus indet. sp.
    BOIDAE
     Morelia riversleighensis
    MADTSOIIDAE
     Nanowana godthelpi
     Nanowana schrenki
     [*Yurlunggur* sp.]
     [*Wonambi* sp.]
    TYPHLOPIDAE
     ?*Rhamphotyphlops* sp.
MAMMALIA
  DASYUROMORPHIA
    DASYURIDAE
     Barinya wangala
     [*Barinya* sp. 2]
     [*Barinya* sp. 3]
     Genus indet. sp. 1
     Genus indet. sp. 2

     Genus indet. sp. 3
     Genus indet. sp. 4
    THYLACINIDAE
     Nimbacinus dicksoni
  DIPROTODONTIA
    ACROBATIDAE
     [Genus 2 sp. 1]
    BURRAMYIDAE
     Burramys brutyi
     Cercatetus new sp.
    BALBARIDAE
     Balbaroo gregoriensis
     Nambaroo sp. 5
     Nambaroo sp. 6
     Nambaroo sp. 7
    HYPSIPRYMNODONTIDAE
     Hypsiprymnodon new sp.
     Ekaltadeta ima
    MACROPODIDAE
     Bulungamaya delicata
     Ganguroo bilamina
     Nowidgee matrix
     Wabularoo naughtoni
     Wakiewakie lawsoni
    PETAURIDAE
     [Genus 1 sp. 1]
     [Genus 2 sp. 1]
    ?PETAURIDAE
     New genus new sp.
    PETAUROIDEA incertae sedis
     Djaludjangi yadjana
    PETAUROIDEA new family
     New genus new sp. 1
     New genus new sp. 2
    EKTOPODONTIDAE
     [*Chunia* sp.]
    MIRALINIDAE
     [*Durudawiri inusitatus*]
    PSEUDOCHEIRIDAE
     Paljara nancyhaywardae
     cf. *Pildra* sp.
     Pseudocheirops new sp. 1
     Pseudocheirops new sp. 2
     Pseudocheirops new sp. 3
     [New genus 1 new sp. 1]
     [New genus 2 new sp. 1]
     [*Pildra* sp. 3]
    PILKIPILDRIDAE
     ?*Djilgaringa* sp.
    PHALANGERIDAE
     [?*Caudipilosus dicksoni*]
     [New genus 3 new sp. 1]
     [New genus 3 new sp. 2]
    ACROBATIDAE
     Genus indet. sp 1
     Genus indet. sp 2

PHASCOLARCTIDAE
[*Nimiokoala greystanesi*]
Litokoala new sp.
Genus indet. sp. indet.
PHASCOLARCTOMORPHIA ?new family
New genus new sp.
DIPROTODONTIDAE
Genus indet. new sp.
New genus new sp.
Neohelos tirarensis
THYLACOLEONIDAE
Priscileo roskellyae
Wakaleo sp. cf. *W. oldfieldi*
VOMBATOMORPHIA new family
New genus new sp.
WYNYARDIIDAE
Namilamadeta new sp.
NOTORYCTEMORPHIA
NOTORYCTIDAE
New genus new sp.
PERAMELEMORPHIA
YARALIDAE
[*Yarala burchfieldi*]
[New genus 1 new sp. 2]
[New genus 1 new sp. 3]
[New genus 2 new sp. 1]
[New genus 3 new sp. 1]
[New genus 3 new sp. 2]
[New genus 5 new sp. 1]
[New genus 4 new sp. 1]
YALKAPARIDONTIA
YALKAPARIDONTIDAE
Yalkaparidon coheni
?MARSUPIALIA order incertae sedis
YINGABALANARIDAE
Yingabalanara richardsoni
CHIROPTERA
HIPPOSIDERIDAE
Brachipposideros sp. 1
Brachipposideros sp. 2
Brachipposideros sp. 3
Brachipposideros sp. 4
Brachipposideros sp. 5
Genus indet. sp. indet. 1
Genus indet. sp. indet. 2
Rhinonicteris tedfordi
MEGADERMATIDAE
Macroderma sp.
MOLOSSIDAE
Hydromops riversleighensis
VESPERTILIONOIDEA
Indet.
MYSTACINIDAE
[*Icarops* sp.]
TEMNOSPONDYLI

ANURA
HYLIDAE
Litoria sp. 1
Litoria sp. 2
Litoria sp. 3
Litoria sp. 4
Litoria sp. 5
Litoria sp. 6
Litoria sp. 7
Litoria sp. 8
LEPTODACTYLIDAE
Crinia sp.
Kyarranus sp. 1
Kyarranus sp. 2
Lechriodus intergerivus
Limnodynastes antecessor
Limnodynastes cf. *L. tasmaniensis*
CRUSTACEA
MALACOSTRACA
ISOPODA
Genus indet. sp. 1
MOLLUSCA
GASTROPODA
Genera indet. spp
UNIRAMIA
HEXAPODA
COLEOPTERA
OMMATIDAE
Genus indet. Coleopteran species D
CURCULIONIDAE
Genus indet.Coleopteran species A
HISTERIDAE
Genus indet. Coleopteran species C
POLYPHAGA family indet
Genus indet. Coleopteran species B
HEMIPTERA
CICADIDAE
Genus indet. sp. 1
HYMENOPTERA
FORMICIDAE
Genus indet. sp. 1
Genus indet. sp. 2
TRICHOPTERA
Genus indet. sp. indet.
MYRIAPODA
DIPLOPODA
DIPLOPODA family indet
Genus indet sp. 1
Genus indet sp. 2
Genus indet sp. 3
Genus indet sp. 4
JULIDA
JULIDA family indet
Genus indet. sp. indet.

References for this list: Archer *et al.* (1990, 1994), Archer (1989), Bassarova *et al.* (2000), Boles (1992), Boles (1995, 1997), Brammall and Archer (1997), Brammall (1998), Cooke (1997a, 1997b), Covacevich *et al.* (1990), Crosby (2002a), Duncan *et al.* (1998), Gillespie (1997), Hand (1997), Hand *et al.* (1997), Hutchinson (1992), Menu *et al.* (2002), Muirhead and Filan (1995), Myers (2002), Scanlon (1997, 2001), Tyler (1989, 1990a), Tyler *et al.* (1990), Wroe (1996, 1999).

Faunal List 8: Gotham City Site Local Fauna
Source locality: Gotham City Site

CHORDATA
NEOPTERYGII
  Indet.
TESTUDOMORPHA
TESTUDINES
  CHELIDAE
  Indet.
ARCHOSAUROMORPHA
 PASSERIFORMES
 Indet.
 CROCODILIA
  CROCODYLIDAE
  Indet.
LEPIDOSAUROMORPHA
 SQUAMATA
  LACERTILIA
  Indet.
  BOIDAE
  Genus indet. cf. *Morelia* sp.
MAMMALIA
 DASYUROMORPHIA
  DASYURIDAE
  Indet.
 DIPROTODONTIA
  BURRAMYIDAE
  Cercatetus new sp.
  POTOROIDAE
  Indet.
  PETAURIDAE
  Indet.
  PSEUDOCHEIRIDAE
  Indet.
  PHALANGERIDAE
  Indet.
  ACROBATIDAE
  Indet.
  PHASCOLARCTIDAE
  Litokoala kanunkaensis
 PERAMELEMORPHIA
  Indet.
 CHIROPTERA
  HIPPOSIDERIDAE
  Genera indet. spp
  MEGADERMATIDAE
  Macroderma malugara
  MOLOSSIDAE
  Petramops creaseri

TEMNOSPONDYLI
ANURA
  Indet.
 LEPTODACTYLIDAE
  Limnodynastes antecessor
DIPNOMORPHA
 DIPNOI
  Indet.

References for this list: Black and Archer (1997a), Boles (1997a, 2001), Hand (1990, 1996), Tyler (1990).

Faunal List 9: Encore Site Local Fauna
Source locality: Encore Site

CHORDATA
  TESTUDOMORPHA
    TESTUDINES
      CHELIDAE
        Genus indet. sp. indet.
  ARCHOSAUROMORPHA
    AVES order indet.
      Families indet.
      Genera indet. spp.
  LEPIDOSAUROMORPHA
    SQUAMATA
      SCINCIDAE
        Egernia sp.
        Sphenomorphus sp.
        Tiliqua sp. *cf. T. pusilla*
      ELAPIDAE
        HYDROPHEINAE new genus new sp.
      MADTSOIIDAE
        Nanowana sp. indet.
  MAMMALIA
    DASYUROMORPHIA
      DASYURIDAE
        Ganbulanyi djadjinguli
      THYLACINIDAE
        Thylacinus sp. *cf. T. macknessi*
      DASYUROMORPHIA incertae sedis
        Mayigriphus orbus
    DIPROTODONTIA
      BURRAMYIDAE
        Burramys brutyi
      HYPSIPRYMNODONTIDAE
        Ekaltadeta jamiemulvaneyi
      MACROPODIDAE
        Ganguroo new sp.
        Wanburoo hilarus
        Wanburoo sp.
        cf. Hadronomas sp.
      PETAUROIDEA family indet.
        New genus new sp.
      PSEUDOCHEIRIDAE
        cf. Pseudocheirops sp
        Genus indet. sp.
      PHALANGERIDAE
        [*Trichosurus* new sp. 1]
    PHASCOLARCTIDAE
      Litokoala kanunkaensis
      Phascolarctos sp.

    DIPROTODONTIDAE
      Neohelos sp.
    PALORCHESTIDAE
      Palorchestes anulus
      Palorchestes sp.
    THYLACOLEONIDAE
      Wakaleo vanderleuri
    VOMBATIDAE
      cf. Warendja sp.
    PERAMELEMORPHIA
      YARALOIDEA family indet.
        Genus indet. sp. indet.
    MARSUPIALIA *incertae sedis*
      Family indet.
        New genus new sp. (large 'Crackodonta')
    CHIROPTERA
      MICROCHIROPTERA families indet.
        Genera indet ~12 spp. indet.
      MEGADERMATIDAE
        Macroderma sp.
  TEMNOSPONDYLI
    ANURA
      Family indet.
        Genera indet. spp.
      LEPTODACTYLIDAE
        Lechriodus intergerivus
  DIPNOMORPHA
    DIPNOI
      Indet.
MOLLUSCA
  GASTROPODA
    Indet.

References for this list: Black (1997a, 1997b), Cooke (1997a, 1999), Kear *et al.* (2001), Myers *et al.* (2001), Wroe (1996, 1997, 1998).

White (1997) recognised that turtles from faunas from the early Miocene onward tend to be smaller and more diverse than late Oligocene turtles from Zone A faunas, and interpreted this as indicative of a prevalence of smaller low-energy bodies of water, compared to prevalence of larger water bodies during the late Oligocene.

While cave faunas are considered more diverse than faunas from late Oligocene tufagenic deposits, some aspects of the differences in the representation of groups are considered to be related to the different time periods during accumulation of faunas. Other possible reasons for differences between faunas from tufagenic deposits and faunas from vadose karst deposits are discussed in Section 7.4.

Other representative faunas from Riversleigh cave deposits are listed in Appendix B.

5.3.4 Discussion and general depositional model of cave facies

Combinations of speleothem (flowstone and dripstones), phosphatic, crystalline and clastic detrital facies are typical of deposits formed in the interior environment of the upper vadose zone (Osborne 1986). The heterogeneity of these cave deposits is indicative of the dynamic conditions that characterise depositional environments this part of the karst system.

Clastic deposits usually exhibit complex structure and heterogeneous lithology, often including reworked speleothem, host rock and flowstone coatings, which is typical of talus cones and debris accumulated primarily under the influence of gravity under changing conditions. While tabular and horizontal deposits do occur, flowstone deposits are often irregular, uneven or inclined, and often form coatings that follow various orientations on surfaces of host rock, cave sediments, bones and rock fragments. This type of speleothem formation, in addition to the presence of stalagmites and other forms of dripstones indicate vadose conditions, in which calcite would have been precipitated by thin films of running water, rather than by subaqueous flow.

Deposits that are indicative of subaqueous conditions such as calcite shelves, cave pearls, calcite rafts and euhedral spar are more likely to have formed locally in cave pools which are low-energy environments that commonly occur in caves in the vadose

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zone, rather than under widespread nothephreatic conditions related to the position of the water table. There is little evidence of dynamic phreatic deposition such as flow-deposited sediments with diagnostic structures (i.e. cross-beds, grading, etc.), or phreatic deposition of turbidites and laminated deposits. Many cave deposits are apparently volumetrically restricted and clearly delimited, and thus may not have formed part of a phreatic network in which sediment transport by energetic flow was possible.

Evidence of habitation by bats (phosphatic textures and skeletal parts) and possibly other non-aquatic animals (lizards, snakes and small mammals) indicates that cave depositional environments were not flooded. Vertebrate assemblages including with dominant bats are compare with those from deposits formed closer to the interior parts of cave environments by accumulation of clastic material through vertical openings accessing the surface (Horáček and Kordos 1989).

The presence of vadose cave deposits within tufagenic host deposits at Riversleigh indicates that speleogenesis must have been initiated by the early Miocene, because the oldest cave fill deposits date from this time. Because cave formation occurs prior to infill, the age of fossil faunas is only indicative of the age of cave infill deposits, and not the cavities in which they formed. Based on data available so far, the distribution and morphology of cave deposits at Riversleigh, and their distribution in the profile, does not appear to conform to a network or sinuous pattern that would be expected from a vadose/phreatically formed cave system fed by point recharge. The apparently irregular distribution and variable morphology and orientation of cave deposits could indicate sponge work patterns formed syngenetically during the early stages of diagenesis when host carbonate was still porous prior to induration and infill of voids by calcite spar. The morphology of the modern epikarst, which is characterised by well-developed surface fissures indicates that epikarstic speleogenesis may also have been responsible for the formation of cave environments. The epikarst would certainly have played a key role in the generation of access points from the surface to cave environments below, through which clastic debris, including fossil material, would have entered. It is probable that cave formation involved a combination of all of these processes in various degrees, further analysis of cave deposits is required to clarify this aspect of karst development at Riversleigh.
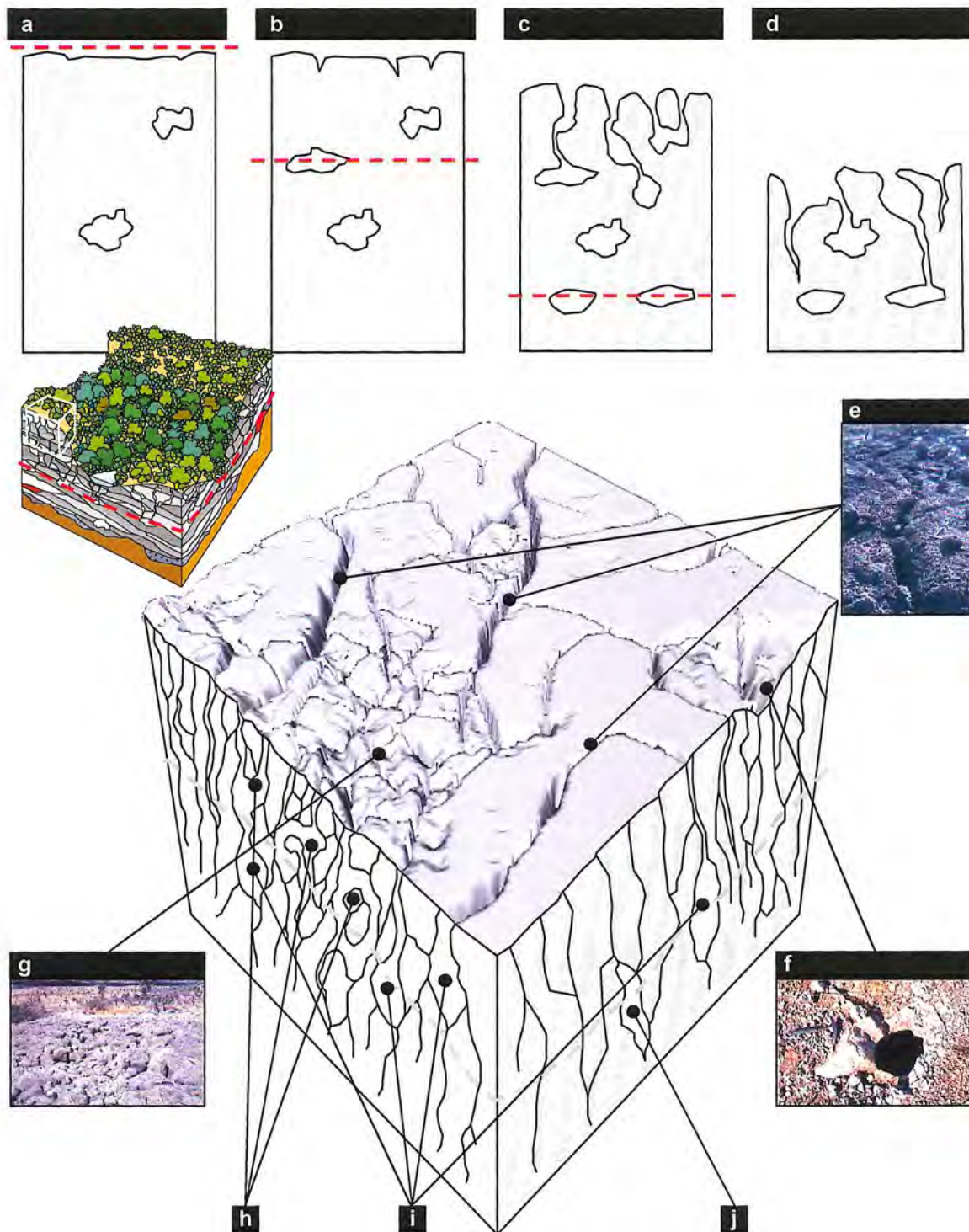
Figure 5.42: Modes of speleogenesis and the relationships of cave environments to the surface via the epikarst at Riversleigh during the middle Tertiary. Surface model depicts surface at a high-point with features based on the modern Tertiary carbonate surface at Riversleigh; vegetation and soil cover are not shown. The position of the modern post-denudation surface level is marked by grey dashed line, the r Red dashed line marks the position of water table. a) Syngenetic speleogenesis occurs during primary deposition by diffuse recharge through immature host. b) Vadose/phreatic speleogenesis by drainage flow at water table level as water table descends. c) Denudation and epikarst development connects older caves to the surface and epikarstic speleogenesis forms fissures and new caves. Speleogenesis at water table level also continues. d) As denudation and epikarst development progress, deeper caves are connected to the surface and new cave environments form in the epikarst. e) Vertical fissure accesses cave environments below. f) Chimney and epikarstic fissure cave. g) Deep fissuring of surface by epikarstic

development. h) Epikarstic speleogenesis related to deep fissuring at the surface. i) Older cavities formed syngenetically during primary deposition or at previous water table level by phreatic/vadose speleogenesis access surface via the epikarst. j) Some older cavities remain isolated from the surface.

Caves in which Miocene deposits formed are most likely to have developed in three ways:

1. Syngenetic caves formed during formation of the primary host.
2. Caves formed by flow in the phreatic zone or at the vadose/phreatic interface (water table level).
3. Caves formed by aggressive solution and widening of fissures in the epikarst.

Cave deposits occur throughout the profile above 170m (see Figure 6.8), which could indicate a corrosion basement at that level, suggesting that cave deposits were formed by phreatic/vadose flow or syngenetic speleogenesis related to a water table level moving in that range. However, because caves are apparently isolated, irregular in shape and distribution (i.e. reminiscent of sponge work patterns) and do not appear to follow a branching or sinuous drainage pattern, syngenetic and epikarstic processes could have been primary in speleogenesis rather than phreatic/vadose flow. Access to caves from the surface would certainly have been through the developing epikarst. In some cases, deep corrosion of the epikarst could have produced cave environments in which deposits formed that persist to the present day. Further detailed mapping of individual cave deposits and their pattern of distribution in the landscape is required, because only fossiliferous cave deposits have so far been mapped at Riversleigh, which does not provide a complete picture of the distribution of cave facies. Possible modes of middle Tertiary cave formation at Riversleigh are illustrated in Figure 5.42.

Because of ongoing denudation, the original thickness of the host carbonate must have been greater than the present apparent thickness. Deposits of pure, crystalline, uncontaminated and unfossiliferous speleothem (i.e. Figure 5.38a, c) that occur throughout the area could indicate that deposition was occurring in cave environments that far enough from the surface not to be subject to the influence of surficial processes (i.e. access via epikarst and input of clastic material and contaminants). There is no way to calculate the original maximum thickness of the tufagenic deposits, so only speculation is possible. The maximum thickness of carbonate outcrops at Riversleigh today is 40m Creaser (1997). A hypothetical denudation rate of 1 mm/ka would result in net loss of 25m of relief over 25 Ma. So a fair (even conservative) estimate of original thickness of the host deposits allowing for 5-30 m of denudation since the late

Oligocene is 45-70 m. This implies that cave deposits outcropping at the surface now may have been 5-30m from the surface Miocene surface.

Cave depositional environments at Riversleigh would have been characterised by the following:

1. They would have occurred some 5-30 m from the surface, prior to denudation.

2. The prevalence of clastic (talus) deposits suggests that access to cave environments was probably through vertical openings in the epikarst allowing debris to accumulate primarily by the force of gravity *sensu* Osborne (1986). Cave environments may have been formed by epikarstic speleogenesis, or cavities may have formed at an earlier time lower in the profile, either syngenetically during the early stages of deposition or subsequently by phreatic processes related to the position of the water table. Denudation and epikarst development may then have gradually opened these voids to the surface allowing infill of clastic debris. The modern epikarst, which is characterised by narrow vertical fissures, may be analogous to the Miocene surface.

3. Clastic material including mud, host rock fragments and organic debris that would have entered cave environments via the epikarst primarily under the influence of gravity, and in conjunction with reworked cave interior deposits, formed cave sediment deposits with complex morphology and structure, i.e. talus cones and debris piles.

4. Flowstone and speleothem deposits formed on host rock surfaces and on the surfaces of cave sediment deposits. In cave environments that were not open to the surface, permeating fluids would have formed deposits of relatively pure speleothem containing fewer contaminants and devoid of clastics, including fossils.

5. Ephemeral pools of standing water were occasionally formed in some cave environments. These pools accumulated cave sediments, speleothem and fossil material, and in some cases may have been inhabited by aquatic animals.

6. Bats inhabited some of these environments and may have contributed to the formation of phosphate-rich deposits and introduced a relatively higher abundance of bat bones, and bones of their prey items (i.e. frogs, lizards), to assemblages that accumulated.

7. Fragile remains of small vertebrates and articulated and associated skeletal parts were preserved more often because of the limited effects of bioturbation, extensive transport and other surface processes.

The general cave depositional model at Riversleigh is illustrated in Figure 5.43.

While clastic deposits and speleothem indicate that vadose conditions probably prevailed, there is evidence of localised subaqueous conditions occurring in many cave environments, indicating that pooling of water occurred. Presence of aquatic taxa in fossil assemblages may also indicate that aqueous conditions occurred proximal to cave environments and in some cave environments (although the remains of aquatic taxa are not necessarily indicative of habitation, also see below). Occasionally cave pools may have dried up causing exposed desiccation and polygonal cracking of sediments the degradation of crystalline speleothems. This is probably more an indicator of the dynamic conditions occurring within cave environments dictated by dynamic internal cave processes and the intermittent influence of conditions at the surface through the epikarst rather than being indicative of overall climatic or palaeoenvironmental conditions.

Bones of terrestrial vertebrates preserved in these depositional environments would have been introduced in the following ways:

1. Remains of dead and decomposed animals entered cave environments through the epikarst by clastic processes, along with other detrital material including rock fragments. Skeletal components may have been isolated or in various degrees of articulation. After death and decomposition on the surface, the articulated remains of parts of even very large animals could have entered very restricted entrance fissures through which passage in life would not have been possible. Bones and other clastic debris may have entered cave environments as occasional isolated particles, or masses of material could have jammed entrances close to the surface before dislodgement by water or gravity, providing an intermittent influx of remains and debris.

2. Cave environments may have been inhabited by certain taxa that occasionally died there, particularly bats, as well as snakes, frogs, birds, and various
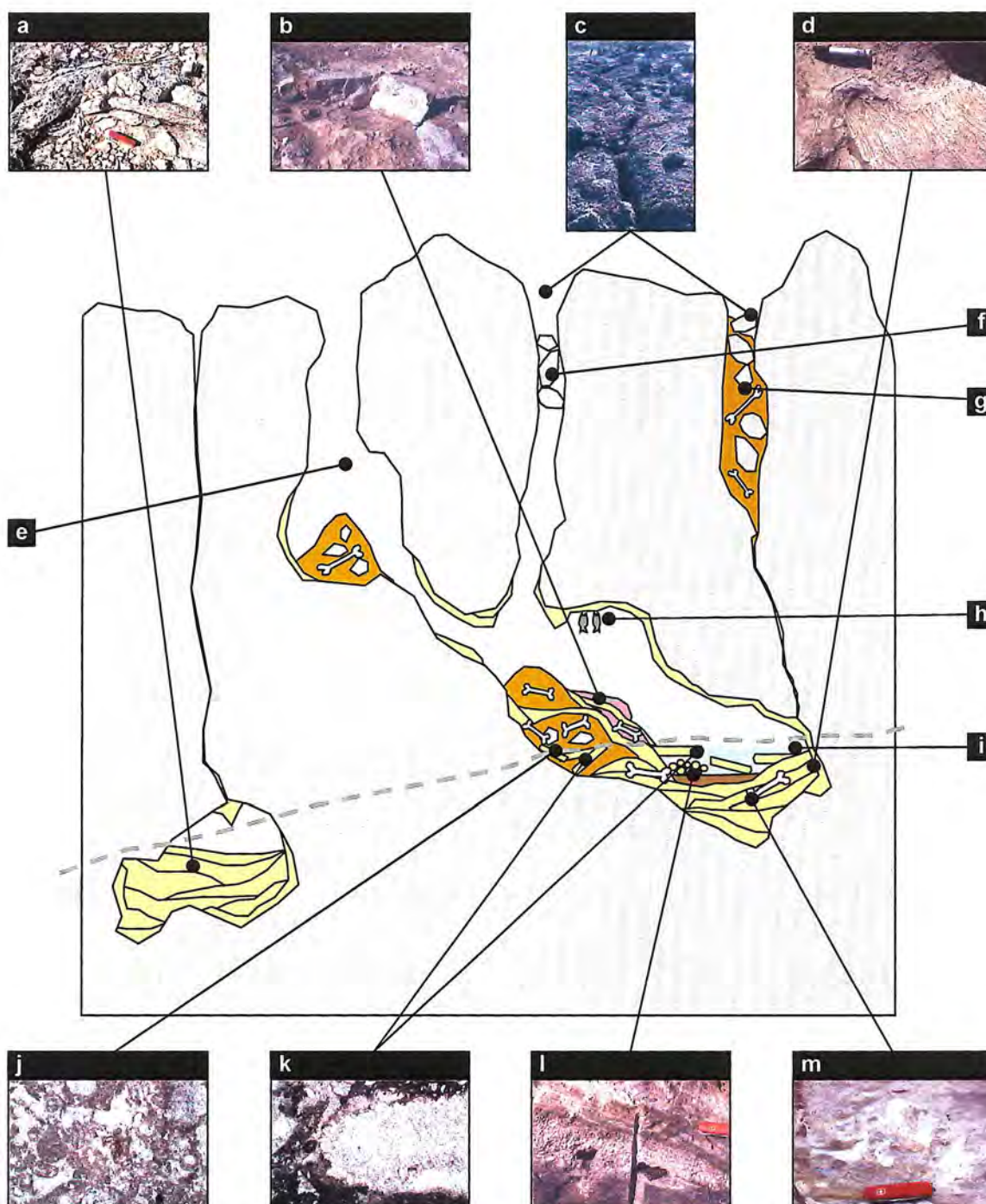
Figure 5.43: General model of cave deposition during the middle Tertiary at Riversleigh illustrating relationships between key components of the vadose depositional system and cave infill deposits. Grey dashed line indicates modern surface after denudation and ongoing karst development, scale is nominal. The system is above the water table. a) Relatively pure, uncontaminated flowstone formed in deep cave not open to the surface (extensive uncontaminated flowstone and speleothem, 'White Cave' locality). b) Successive deposits of cave sediment and flowstone accumulate under dynamic depositional conditions, these deposits do not necessarily exhibit true stratigraphic sequence in section, and may form and erode during weathering and infill events (unconformable contact younger phosphatic infill (red/brown) overlain by older incised flowstone (white), AL90 Site). c) Surface fissures, comparable to those on the modern Riversleigh surface access cave environments through the epikarst, providing the main pathway for input of clastic material including mud, rock fragments, animals and bones. Fissures may be inhabited by animals such as bats, snakes, lizards and small mammals. They may also be used by animals from the surface to enter cave environments and may also function as pitfall traps. (Fissure in modern surface, top

of Mesa 3). d) Generations of flowstone coatings on cave interior surfaces including the primary cave wall and subsequent infill deposits. (Cave wall coated with flowstone against which successive later generations of flowstone onlap, west wall, AL90 Site). e) Entrance environments closer and more open to the surface would have accumulated entrance facies and been subject to the influence of processes in the surface environment to a greater degree. Some may have contained ponded water and supported aquatic taxa (see Figure 5.44). Deposits formed in the majority of these have probably been lost to denudation. f) Access to cave environments may have been intermittent due to occasional blockage of fissures in the epikarst by debris. g) Fissures close to the surface may have filled with debris including bone, as they do in the modern environment, however the majority have probably been lost to denudation since the Miocene. h) Bats would have inhabited cave environments and contributed bat bones, bones of prey items and guano to cave deposits. i) Ephemeral perched pools of standing water accumulate sediments comprised of crystalline and detrital crystals textures. These pools may be inhabited by aquatic vertebrates such as fish and lungfish, and occasionally dry out. j) Clastic talus debris and breakdown piles comprised of mud, bones, reworked host rock and reworked cave interior deposits accumulated primarily by influence of gravity. Percolation of water through the unconsolidated sediments would have produced globular 'porous cavity fill texture'. As changes in clastic input and conditions in the cave environment occur, interbedded flowstone deposits form. ('Porous cavity fill' comprised of globular micrite in crystalline matrix (PP; R158; Inabeyance Site)). k) Shelfstone and calcite rafts formed in cave pools contribute to subaqueous deposits rich in detrital crystals and are reworked in debris piles as conditions change. (PP; EP76; Camel Sputum Site) l) Cave pearls form in subaqueous conditions in cave pools (oncolites, flowstone and cave sediment with tufaceous breccia fragments, Nicole's Boulders Site). m) Vertebrate material accumulates in cave infill deposits, usually by clastic input from parts of cave environments closer to the surface or directly from the surface via the epikarst. Skeletal elements may be in various degrees of articulation and/or close association because they are derived from carcasses that entered the cave environment from upper parts of the system intact, or may be derived from living animals enter the cave environment alive and die in there. Preservation is favoured by limited disturbance and exposure within the cave interior. (Associated cranial and post-cranial skeletal elements of *Nimbadon lavarackorum* in flowstone, AL90 Site).

mammals. Caves may also have been used as temporary shelters by animals that occasionally died.

3. Remains may have been introduced by predators or scavengers using the cave as a den or roost such as Ghost Bats, snakes and carnivorous marsupials. The remains of many small vertebrates in the Gotham City Site deposit were interpreted as remains of prey items of carnivorous bats including *Macroderma malugara* (Hand 1990, 1996).

4. Accidental entrapment of live animals may have occasionally occurred. Animals may have voluntarily entered cave environments and become trapped because of steep or treacherous surfaces within, or fallen into fissures by accident and been killed or injured, or otherwise unable to escape. In the former case carnivorous animals may have been lured into caves by the presence of carrion. In the latter case larger animals may have become trapped and decomposed in entrance fissures close to the surface before eventual dislodgement introduced the remains into depositional environments.

Taphonomic analysis of bones from Camel Sputum Site, Mike's Menagerie Site, Encore Site and Bitesantenary Site indicated that components of these assemblages show limited signs of transport or exposure and skeletal part representation indicates they are autochthonous (Bassarova 2004). Morrell (2002) reached similar conclusions about the taphonomy of the assemblage at KCB Site. These aspects of faunas from cave deposits indicate that conditions in the depositional environment were favourable to the preservation of fragile remains, and that some remains were preserved undisturbed by bioturbation, transport or other unfavourable conditions occurring on the surface.

Differences in the abundance of terrestrial animals in faunas from different cave deposits may be related to different conditions in and around cave environments, particularly the size and complexity of caves and the fissures through which animals and/or their remains entered. It is reasonable to suggest that some faunas may lack large animals because their remains were physically unable to enter spatially restricted depositional environments or their entrances. Other influences of the karst landscape on the accumulation and composition of faunal assemblages are discussed in more detail in Chapter 7.
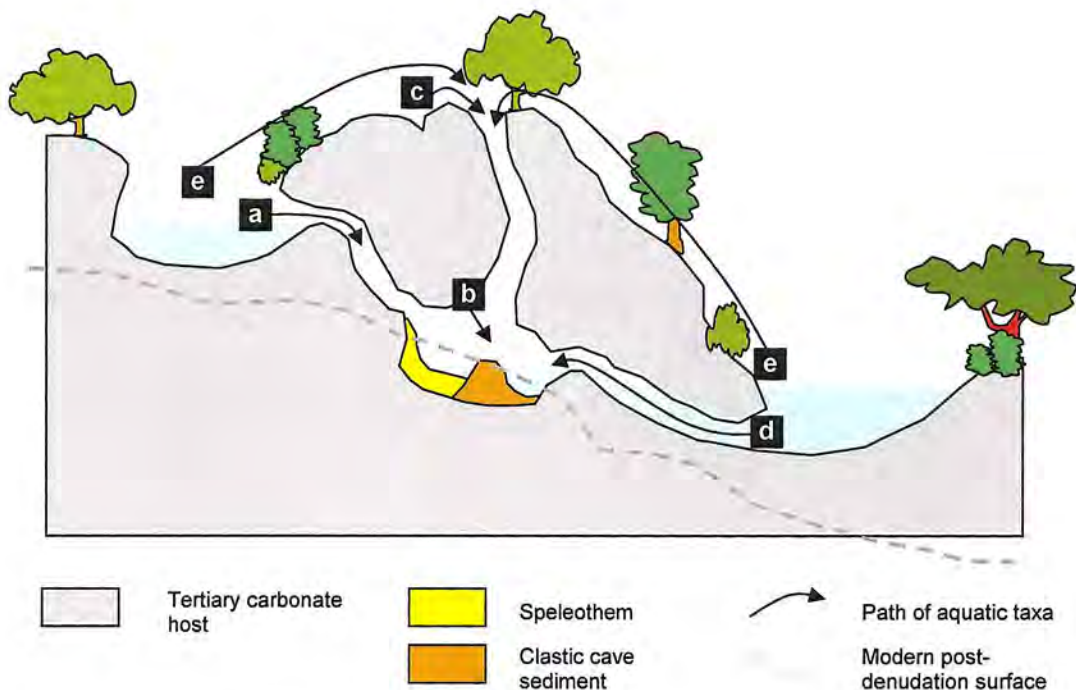
Figure 5.44: Entirely plausible scenarios allowing aquatic taxa to have been preserved in cave deposits at Riversleigh that would have been sufficiently far from the Miocene surface to avoid destruction by denudation (until the present). a) Aquatic taxa or remains of taxa enter via cave passages from a perched pool environment close to the surface that is normally inhabited by aquatic taxa. Deposits formed (and fossils preserved) in this source environment would have subsequently been lost to denudation. b) Remains of aquatic taxa are brought into the cave environment by other animals (i.e. bats). c) Remains of aquatic taxa at the surface (prey items, otherwise stranded) enter by normal clastic processes, or by flood. d) Taxa enter from surface pools/streams via phreatic passages. e) Aquatic taxa from surface pools/streams travel over land and enter cave environments either deliberately or by accident (i.e. crocodilians, turtles, platypuses, lungfish), or eggs are transported into cave environments by bats or birds (i.e. fish).

While the presence of abundant and diverse aquatic taxa in Riversleigh faunal assemblages could be considered indicative of tufagenic depositional conditions, many assemblages from cave environments at Riversleigh contain a variety of aquatic vertebrates including crocodilians, chelid turtles, neopterygian fish and lungfish. Diversity and abundance of these taxa is usually relatively low compared to faunas from primary host deposits. The remains of aquatic taxa could be incorporated into cave assemblages in the following ways:

1. Aquatic taxa could enter and inhabit cave systems via phreatic passages supporting phreatic conditions. Parts of such environments may have been enough to the surface to allow sufficient light and input of nutrient to support habitation, and deposition of bones could have occurred in other parts of the system that were sufficiently far from the surface to escape destruction by denudation until the present.

2. These taxa may have lived in perched cave pools. Caves could be colonised by crocodilians, turtles and lungfish travelling over land, and fish eggs could be transported into cave environments by birds or bats.

3. The remains of aquatic taxa could be introduced into caves by predators or scavengers, i.e. as prey items of Ghost Bats such as at Gotham City Site (Hand 1990, 1996).

4. Living aquatic taxa and the remains of dead aquatic taxa could enter cave environments from the surface during flood.

5. The remains of aquatic taxa at the surface (i.e. victims of predation or died while travelling over land) could enter caves by normal clastic processes. Occasional live aquatic taxa (i.e. crocodilians, turtles and lungfish) could conceivably become trapped in this way.

These scenarios are illustrated in Figure 5.44.

5.3.5 Representative cave deposit: AL90 Site

Aspects of the geological interpretation and depositional history of the AL90 Site deposit were described and discussed by Arena and Black (1997; Appendix E). The deposit is the largest cave deposit that has been excavated at Riversleigh, having a sub-
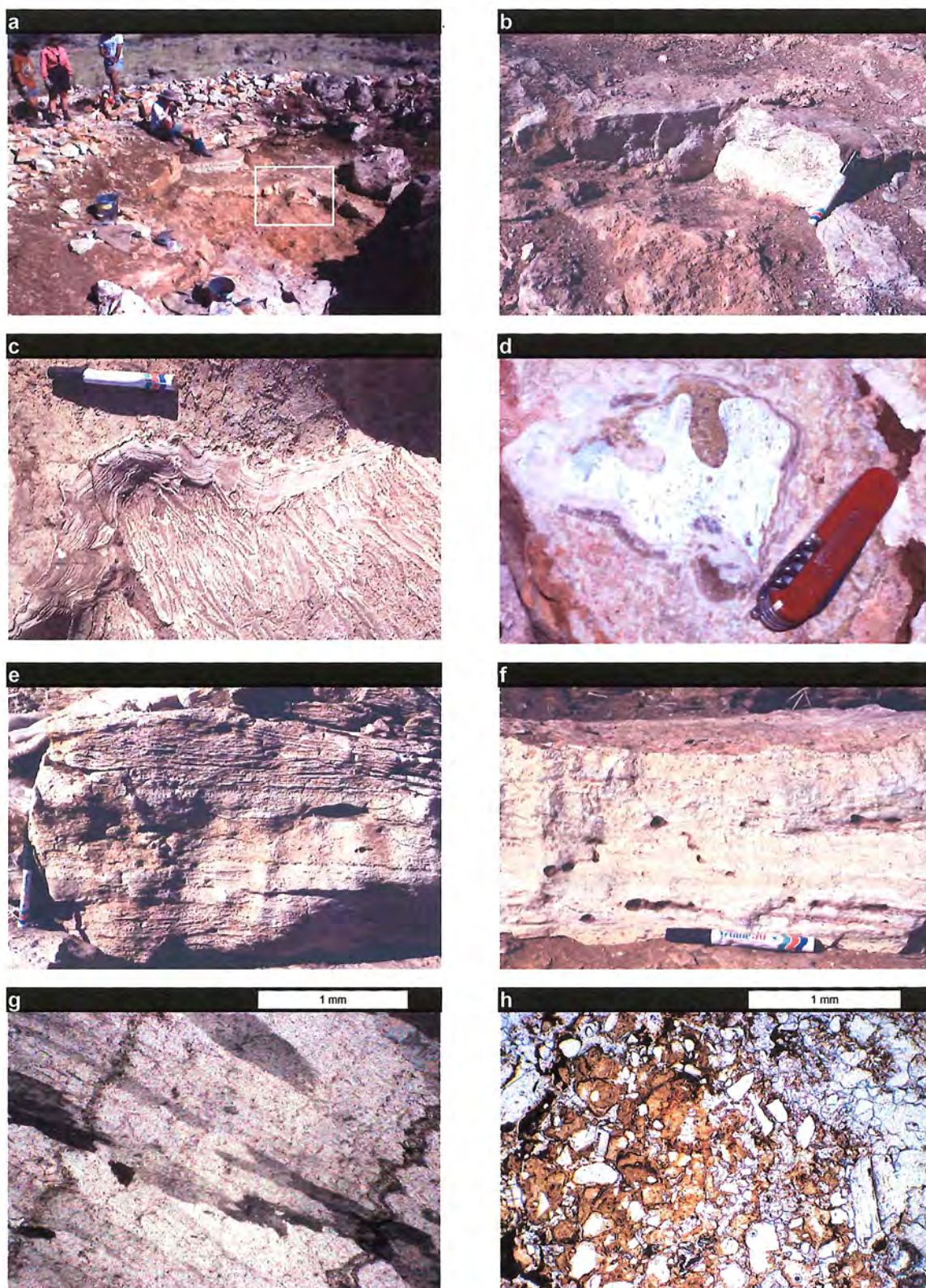
Figure 5.45: Geology at AL90 Site. a) Excavation pit showing flowstone layers and clastic cave fill rich in bone fragments and phosphatic textures. Region in 5.45b is outlined. b) Detail of flowstone (white) apparently unconformably overlying younger fill (brown). c) The deposit is clearly delineated by flowstone coating the intraclast tufa host rock (top). Later generations of flowstone (oriented vertically) onlap the primary coating. d) Section through the distal end of the tibiotarsus of a large bird with a lump of sediment adhering to the articular processes. A coating of flowstone surrounds the entire object. e) Profile view of thick flowstone on an excavated weathered block. f) Profile of freshly broken flowstone block. g) Flowstone lithotexture (XP; RA2003-9B). h) Phosphatic lithotexture (PP; RA2003-6).

circular plan pattern with the longest dimension approximately 8m (Figure 5.37). The deposit has so far been excavated to a depth of 2m from the surface.

The complex structure and lithology of the deposit, and the vertebrate taphonomy and faunal composition are typical of deposits and assemblages formed in the inner environment of the upper vadose zone where influence of surface conditions that affect entrance environments is limited, allowing the development of speleothem, pooling of water, accumulation of well-preserved vertebrate material, an abundance of cave-dwelling bats and formation of associated phosphate-rich sediments. Variations in the distribution and composition of lithotypes in the deposit are indicative of the dynamic conditions that characterise this type of cave environment.

These lithotypes vary in composition throughout the deposit including thick flowstone; flowstone interleaved with fine pink sediment, haphazard accumulations of shelfstone; and massive pink, brown and yellow cave sediment deposits rich in detrital crystals and phosphatic lithotextures (Figure 5.45). Representative sections of the excavated profile are illustrated in Figure 5.46.

The host rock contact is clearly marked by a coating of flowstone several layers thick. Subsequent onlapping flowstone deposits are oriented roughly perpendicular to the wall-coating. This suggests that during the deposition of the cave infill films of water may have initially run down the walls, forming coatings; and at a later time flowstone was deposited by sub-horizontal flow over top of material that had partially filled the cave to that level.

The accumulations of shelfstone and detrital crystals (i.e. derived from calcite rafts) indicate that at times standing water was present within the cave environment. Reworking of shelfstone, which may exceed a centimetre in thickness, may have been due collapse of structures that had grown to very large size, and/or destructive forces associated with the influx of clastic material and organic debris, including animals. Structures resembling dessication cracks in cave sediment (Figure 5.41f) may indicate that water availability may have fluctuated within the cave environment, allowing drying and cracking of some sediment.
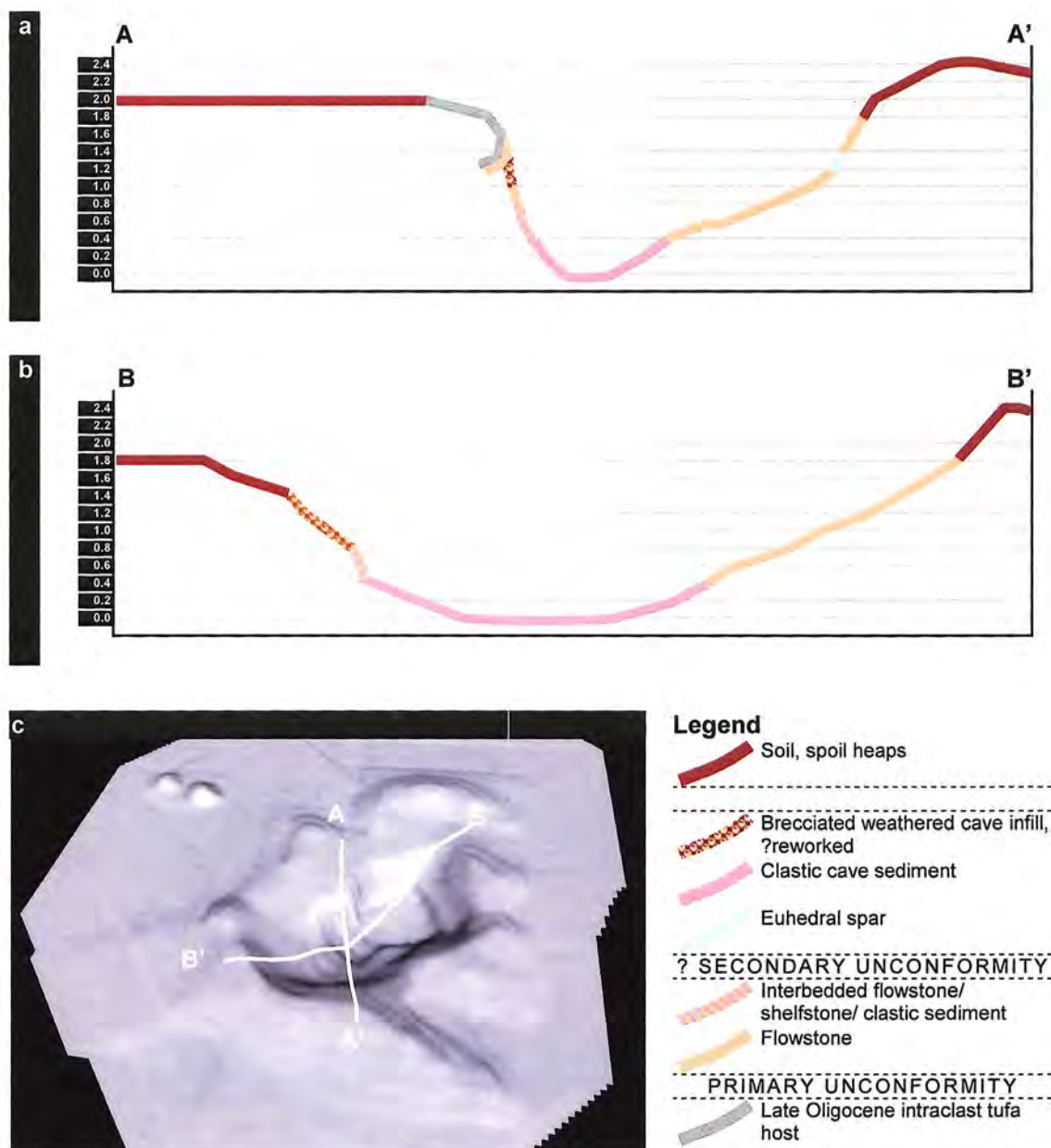
Figure 5.46: Simplified representative sections through the cave deposit at AL90 Site. Facies are complex with a high degree of lateral and vertical variation. a) North west to south east section spanning overhanging host rock with intact primary wall (primary unconformity). b) North to south section spanning breccia, cave sediment and primary flowstone deposits. c) Reconstruction of excavation pit from survey data looking northwest. Fossiliferous flowstone and cave sediments appear to unconformably contact clastic sediment at the lower part of the profile. The brecciated infill contains reworked flowstone, cave sediment and host rock and contains fossil vertebrates that may be relatively younger than those from the primary fill. This could be interpreted as a stratigraphic reversal resulting from a secondary dissolution and infill event. Locality model is approximately 30m wide, section elevations are measured from an arbitrary datum, no vertical exaggeration.

A possible stratigraphic reversal *sensu* Osborne (1984), has been recognised in the deposit. Flowstone overlying pink cave sediment appears etched on the contact surface, and layering within the flowstone at this interface does not conform to the morphology of the underlying sediment (Figure 5.45b). The contact between the two lithotypes is abrupt, with no apparent alteration interface caused by dissolution. It is therefore possible that the vertical succession represents a secondary cavity in the flowstone formed by dissolution and subsequently filled with clastic material.

Related to this secondary unconformity is brecciated infill, composed of both reworked host rock and reworked cave material, including flowstone. The relationships between this breccia and the other components of the deposit are not clear, however the physical relationships suggest this may be a later infill. There are indications that fragmentary faunal remains collected from this material could be younger than vertebrates collected from the rest of the deposit (i.e. flowstone-dominated material), however further investigation is required. Even if the unconformity is related to subsequent dissolution and infill, these events could all date from the same time period and faunal distinction need not be marked. Alternatively, the breccia may be related to more recent weathering.

Euhedral spar coatings several centimetres thick also appear to coat partially dissolved primary flowstone. This type of deposit is considered to have formed under subaqueous conditions (Osborne 1986, Ford 1988, Hill and Forti 1997a). It is not clear whether the formation of this material is related to dissolution and inundation events that occurred during the depositional history of the deposit, or dissolution and reprecipitation at a later time related to ongoing weathering.

Vertebrate fossils occur in varying densities in both flowstone and cave sediments. The latter are often rich in very small vertebrate material. Vertebrates from this locality, particularly those preserved in flowstone are often very well preserved, with very fragile material such as bat skulls, articulated skeletons and closely associated skeletal parts all being relatively common. Sometimes, horizontally-oriented bone-rich layers occur. Some slabs of flowstone were observed to contain layers of bat skulls with complete internal moulds of each brain cavity. The AL90 fauna is listed in Faunal List 10.

Faunal List 10: AL90 Site Local Fauna
Source locality: AL90 Site

CHORDATA
 ARCHOSAUROMORPHA
  STRUTHIONIFORMES
   DROMORNITHIDAE
    Indet.
 LEPIDOSAUROMORPHA
  SQUAMATA
   SERPENTES Family indet.
    Indet.
 MAMMALIA
  DASYUROMORPHIA
   THYLACINIDAE
    Nimbacinus dicksoni
  DIPROTODONTIA
   MACROPODIDAE
    Ganguroo bilamina
    Genera indet. spp.
   PHALANGERIDAE
    Indet.
   DIPROTODONTIDAE
    cf. Neohelos
    Nimbadon lavarackorum
    Nimbadon sp.
  PERAMELEMORPHIA
   Genera indet. spp.
  CHIROPTERA
   HIPPOSIDERIDAE
    Genera indet. spp.
    Archerops annectens

References for this list: Archer *et al.* (1997), Black (1997a), Hand and Kirsch (2003), Kear *et al.* (2001), Wroe and Musser (2001).
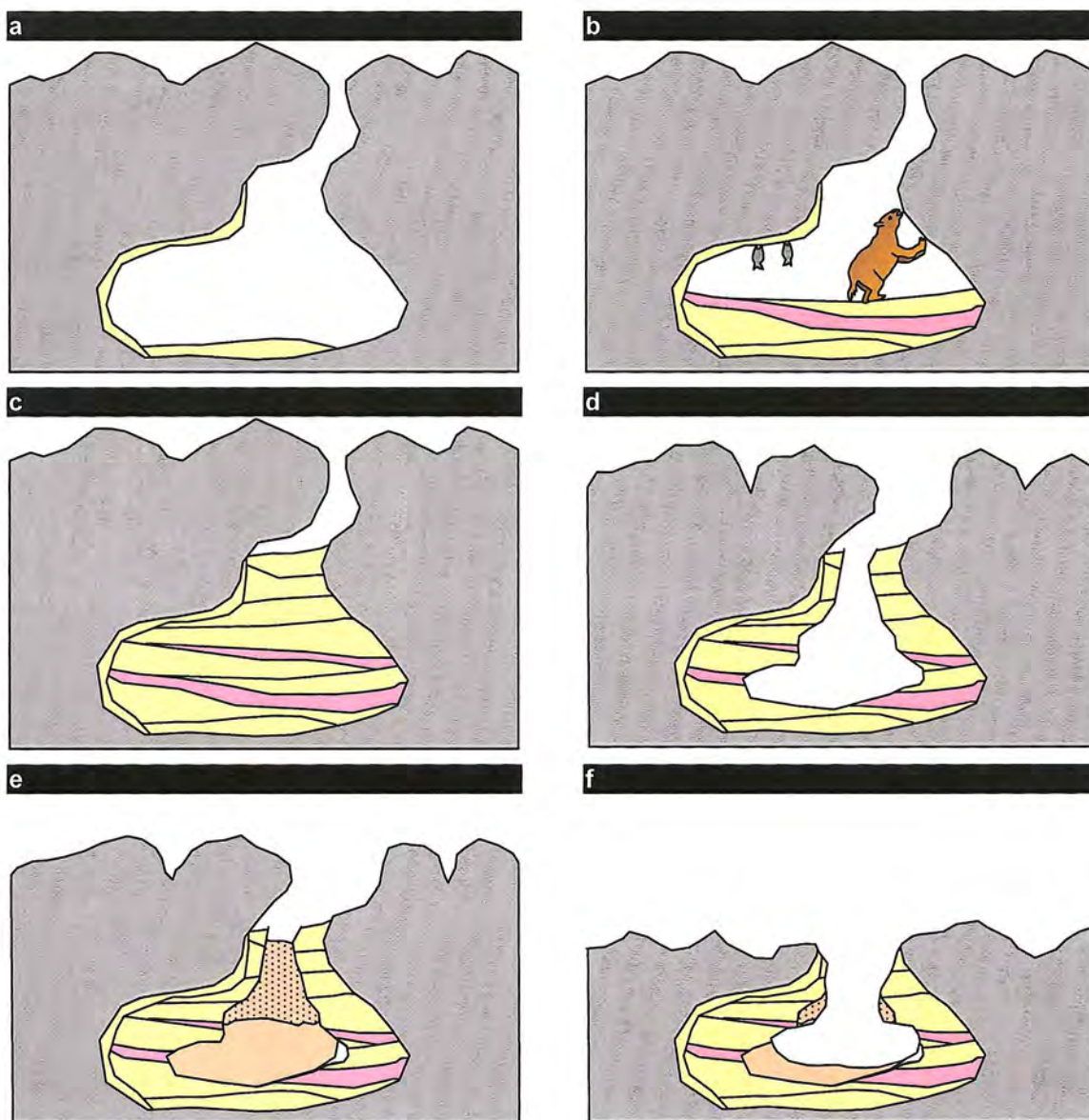
Figure 5.47: Simplified reconstruction of the possible depositional history of the cave deposit at AL90 Site (not to scale). a) Flowstone coating form on host rock surfaces in primary cave. The cave environment accesses the surface through vertical opening(s) in the epikarst b) Formation of fossiliferous primary infill comprised of flowstone and cave sediment rich in phosphatic lithotexture. Entrapped animals provide articulated skeletons and bats provide abundant skeletal material and phosphate. c) Primary deposition complete. d) Dissolution of primary cave deposit. e) Infill with secondary fossiliferous phosphatic clastic sediment and breccia and minor euhedral spar. f) Modern surface and excavation exposing primary and secondary fill with reverse stratigraphy.

Remains of crocodilians and other aquatic taxa have not been found. Bats are a dominant component of the vertebrate fauna, and several species occur. *Archerops annectens* is a hipposiderid bat with modern relatives that inhabit deep caves and fissures in rainforested limestone terrain in the tropics of New Guinea (Hand and Kirsch 2003). There is a distinctive abundance of the zygomaturine diprotodontid *Nimbadon lavarackorum*. Skeletal components of this sheep-sized herbivore are often articulated, suggesting that the animals entered the cave environment intact (i.e. alive or shortly after death) and post-mortem disturbance was limited. Similarly a small bandicoot-sized polyprotodont marsupial skeleton and a skeleton of the fox-sized thylacinid *Nimbacinus dicksoni* were almost completely articulated. While fragmentary and isolated elements of various taxa including kangaroos, dromornithid birds and snakes also occur, indicating that accumulation of material by typical clastic processes probably occurred, the abundance of articulated skeletons of a variety of taxa may indicate that the cave at AL90 Site occasionally acted as a kind of pitfall trap from which living animals were unable to escape once they had entered, either deliberately or by accident. Scavenging omnivores including bandicoots and thylacinids may have been lured into the environment by entrapped prey and associated food items. It is therefore possible to speculate that the cave environment may have had a vertically oriented entrance, perhaps in the ceiling, through which escape was difficult.

According to interpretation and observations made so far, the depositional history of the AL90 Site deposit can thus be reconstructed as possibly having had two stages of infill (Figure 5.47). The primary deposition was characterised by the deposition of flowstone, cave sediment and subaqueous accumulations of detrital crystals and shelfstone. Vertebrates may have been entrapped in this environment, resulting in the abundance of articulated remains. The primary deposit may then have been partially dissolved and a secondary infill of phosphatic cave sediment and reworked breccia, which may contain a different fauna, was formed.

5.4 The presence of faults at Riversleigh

Using aerial photographs, Megirian (1992) mapped a number of faults in Tertiary deposits at Riversleigh. However, they have not been detectable in the field. There is little evidence of displaced geology. While visible lineaments do exist, they are not

necessarily faults. In some cases, lineaments mapped as faults by Megirian (1992) have been found to be well-worn animal tracks.

If faults existed in the Tertiary carbonates, they would tend to be targets of solution and recrystallisation, because karst processes focus on areas of weakness and are often controlled by fault and joint patterns (Ford and Williams 1989, Klimchouk 2000, Klimchouk and Ford 2000a, 2000b). Faults in the Tertiary carbonates would thus be expected to be marked by deep corrosion. Clear evidence of joint patterns, which would be expected to be associated with faulting and folding, are also markedly absent from the Tertiary carbonates at Riversleigh. By comparison, the Cambrian limestones in the area exhibit well-developed vertical and horizontal joint patterns and bedding planes, which are clearly marked by corrosion and contribute to distinctive weathering morphology.

Some lineaments that are mapped as faults by Megirian (1992) are marked by the presence of drainage channels, however there is no other reason to presume that these are faults. They may be randomly distributed solution structures.

An extensive lineament marked by weathering and drainage patterns is illustrated in Figure 2.6. This could be also be considered a fault, however there is no other evidence to support this interpretation, such as detectable displacement of geology. The pattern of outcrop evident can be adequately explained without invoking tectonic activity.

The most recent major tectonic event known to have occurred in the region was the Pine Creek Upwarp (Smart *et al.* 1980), which is here considered contemporaneous with the late Oligocene deposits at Riversleigh. There otherwise appears to be little evidence of subsequent faulting at Riversleigh. While the possibility of faulting is discussed in the following depositional models, faulting need not be invoked to formulate parsimonious models.

Chapter 6

The 4-phase model of geological development of the Riversleigh terrain during the middle Tertiary

6.1 Distinction and timing of depositional phases

Interpretations of the depositional environments of the major lithofacies from Riversleigh, age relationships of deposits determined by vertebrate biocorrelation and understanding of processes occurring in karst systems can be used to divide the events during the middle Tertiary geological development of Riversleigh into a chronological sequence.

The karst stratigraphic units *period* and *phase* can be used to divide events in the history of a karst system (Bosák *et al.* 1989). A karst period is the major span of time during which a host rock is subject to karst processes after deposition. Different events and processes occurring during a karst period, such as different modes of deposition or terrain development mediated by tectonic movement or climatic change, may be assigned to karst phases. The broad divisions of facies at Riversleigh are considered here to be formed by different modes of deposition during successive karst phases.

The oldest middle Tertiary deposits at Riversleigh were formed during a major and relatively prolific tufagenic depositional event and contain late Oligocene faunas of Riversleigh Faunal Zone A. These deposits host vadose cave deposits containing faunas that are distinct and post-date the late Oligocene faunas. This faunal and depositional distinction defines the primary late Oligocene tufagenic depositional episode of Phase 1 which would have occurred during a period of high water table level (phreatic) and the subsequent low water table conditions indicated by the vadose cave deposits containing early Miocene Zone B faunas during Phase 2.
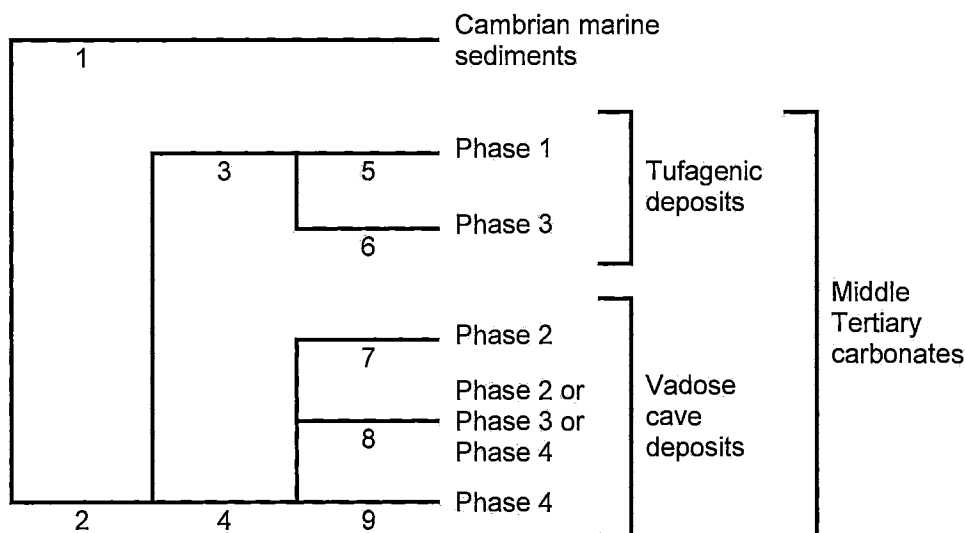
Figure 6.1: Classification of Riversleigh lithofacies and their karst stratigraphic relationships.
Characters at numbered nodes:

1. Massive limestone, dolomite, chert layers and massive bedded chert.
2. Heterogeneous carbonate, reworked Cambrian chert lithoclasts, abundant Tertiary molluscs and ostracods, Tertiary vertebrate fossils.
3. Abundant reworked tufaceous intraclasts, dominant micritic, intraclast, bio-precipitated, peloidal, arenaceous lithotextures with open fabrics, occasional Cambrian chert lithoclasts (more abundant in basal facies), laterally and vertically extensive geometrically unrestricted deposits, normal grading and lenticular profiles may be observed, relatively greater abundance and diversity of fossil aquatic vertebrates.
4. Presence of flowstone and other speleothem, relatively lower abundance and diversity of aquatic vertebrates, abundant and diverse fossil bat faunas, associated and articulated fossil skeletal parts more common, depositional geometry restricted and clearly delineated by facies change, dominance of crystalline and phosphatic lithotextures.
5. Late Oligocene (Zone A) vertebrate faunas.
6. Middle Miocene (Zone C) vertebrate faunas.
7. Early Miocene vertebrate faunas (Zone B), deposits hosted by Phase 1 deposits.
8. Early Miocene or Middle Miocene vertebrate faunas (ages uncertain), deposits occur within Phase 1 deposits.
9. Middle Miocene to early-Late Miocene (Zone C) vertebrate faunas, deposits occur within Phase 1 and Phase 3 deposits.

Age-range (Archer et al. 1997)	Biozone	Depositional phase	Dominant depositional process
Middle to early-Late Miocene	Riversleigh Faunal Zone ('System') C	Riversleigh Depositional Phase 4	vadose cave
		Riversleigh Depositional Phase 3	tufagenic/ ?vadose cave
		? ⇧ ? ⇧ ?	? ⇧ ? ⇧ ?
Early Miocene	Riversleigh Faunal Zone ('System') B	Riversleigh Depositional Phase 2	vadose cave
Late Oligocene	Riversleigh Faunal Zone ('System') A	Riversleigh Depositional Phase 1	tufagenic

Table 6.1: Riversleigh age-ranges, biozones, depositional phases and the dominant process characterising deposits formed during each depositional phase.

The tufaceous deposits of Gag Plateau contain Zone C faunas of middle Miocene age that post-date the Zone B faunas from deposits of Phase 2. These Phase 3 deposits which would have formed during a period of high-water table level, are in turn post-dated by cave deposits containing younger Zone C faunas. These youngest cave deposits were formed during the vadose conditions of Phase 4.

These 4 depositional phases alternate between tufagenic-dominated and vadose cave-dominated deposition that can be interpreted as having had occurred during alternating periods of phreatic and vadose dominance respectively (i.e. periods of high and low water table level). These relationships are summarised in Table 6.1, and the relationships of the broad divisions of Riversleigh lithotypes to depositional phases is shown in Figure 6.1.

The 4-Phase model of middle Tertiary deposition and terrain development at Riversleigh is illustrated in Figure 6.2.

The primary tufagenic phase appears to have generated most of the deposits at Riversleigh. These constitute the host for the vadose cave facies produced in the second phase. Phase 3 is marked by a return to phreatic tufagenic conditions that formed tufagenic deposits on Gag Plateau. Some vadose cave deposits may also have formed during this period. Vadose cave deposits of Phase 4 formed in cave environments on the Gag and Southern Gag Plateaux. The Encore Site local fauna is the youngest fauna from this period and is considered to be early-late Miocene in age (Archer *et al.* 1997, Myers *et al.* 2000).

At this stage it is unclear from vertebrate faunal biocorrelation whether some vadose cave deposits containing Zone C faunas from Gag and Southern Gag Plateaux were deposited before or after the tufagenic event of Phase 3. Establishing clearer age relationships between Zone C faunas from definite Phase 4 spelaean deposits that were deposited in caves within Phase 3 tufaceous deposits (i.e. Gotham City Site), Zone C faunas from cave deposits hosted by Phase 1 deposits on Southern Gag Plateau (including local faunas from AL90 Site, KCB Site, Dome Site, Jim's Carousel Site; not the early-late Miocene Encore Site LF) and Zone C faunas from the tufagenic Phase 3

a Oligocene late Bulimba Cycle weathered surface

b PHASE 1 – late Oligocene

c PHASE 2 – early ?to middle Miocene

d PHASE 3 – middle Miocene

e PHASE 4 – middle to late Miocene

f Modern surface
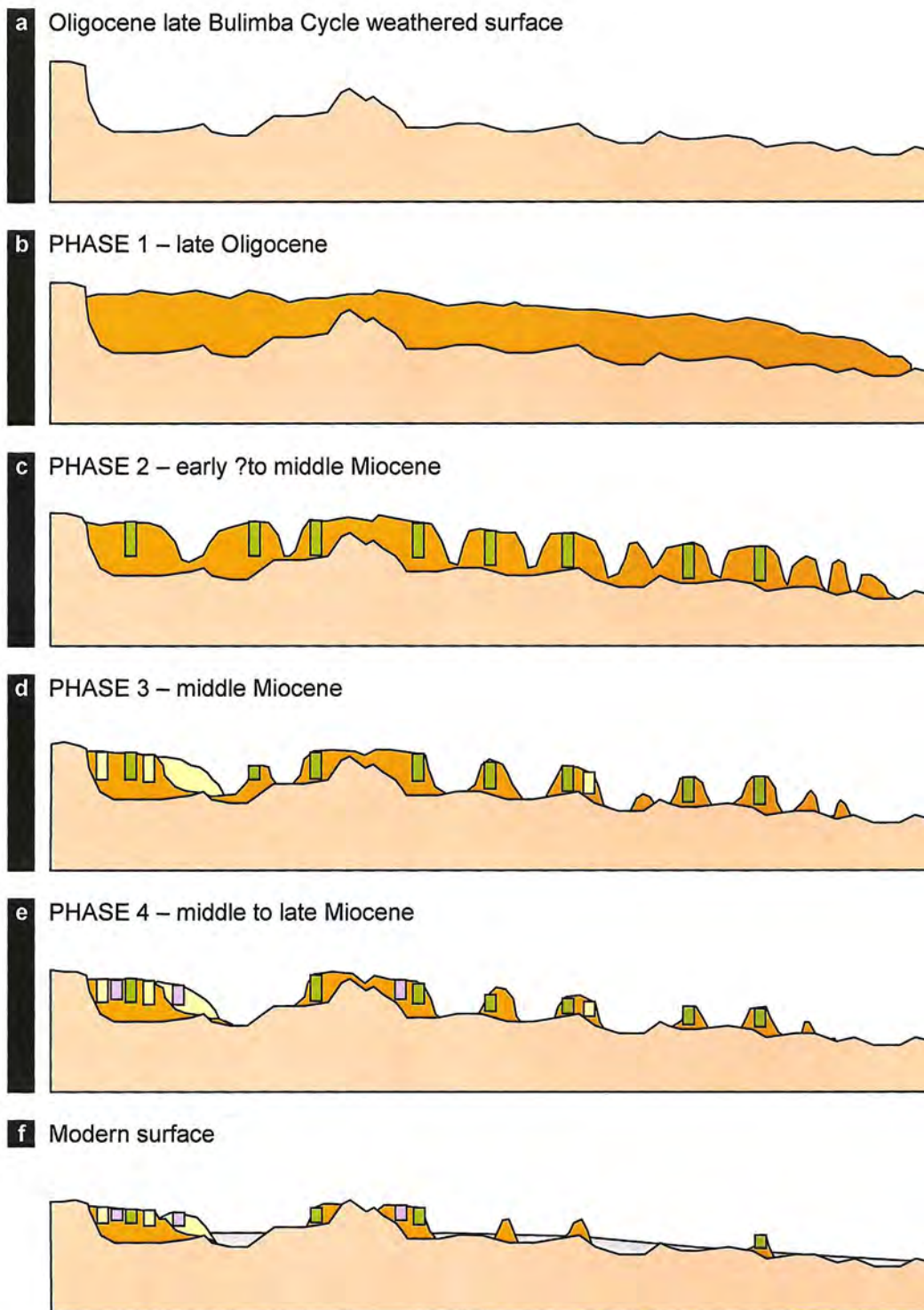
Legend

Cambrian and Proterozoic basement sediments	Middle Miocene: Phase 3 tufaceous and vadose cave deposits
Late Oligocene: Phase 1 tufaceous deposits	Middle to early-late Miocene: Phase 4 vadose cave deposits
Early to ?middle Miocene: Phase 2 vadose cave deposits	Plio-Pleistocene to Recent: alluvium and colluvium

Figure 6.2: The 4-phase model of geological development of the Riversleigh terrain during the middle Tertiary. Schematic diagrams are not to scale. a) Cambrian and Proterozoic basement. b) Phase 1: formation of tufaceous deposits in fluvial barrage systems. Vertebrate fossil assemblages containing late Oligocene vertebrate faunas accumulate in barrage pond infill deposits. c) Phase 2: onset of karst terrain

development dominated by corrosion and dissection by major drainage channels. The resulting young karst landscape is characterised by a high degree of topographic variation. Early Miocene faunas and possibly some early-middle Miocene faunas accumulate in vadose cave deposits accessing the surface at high-points. c) Phase 3: raised water table floods the vadose zone and localised fluvial barrage deposition occurs. These conditions may be related to the relatively extreme greenhouse conditions of the middle Miocene optimum. Middle Miocene faunas accumulate in tufaceous barrage pond deposits, some vadose cave deposits containing middle Miocene faunas may have formed during this period if the water table fluctuated and allowed vadose processes to continue. By this time, the development of the karst landscape has resulted in the gradual expansion of low-points and retraction of high-points. Ongoing denudation has caused an overall loss in relief. d) Phase 4: water table has lowered and vadose cave deposits containing middle to early-late Miocene faunas are formed. Terrain low-points widen and merge, high-points recede to form residual highs. f) Modern landscape: modern highs are remnants of original high-points, with cave deposits preserved. Colluvial and alluvial deposits are formed in the low areas in the Plio-Pleistocene and Holocene.

deposits on Gag Plateau would clarify whether Phase 2 conditions persisted into the early-middle Miocene.

6.2 Riversleigh Depositional Phase 1: late Oligocene

The primary phase of deposition at Riversleigh involves two main aspects:

1. Recognising mechanisms responsible for the onset of depositional flow during the late Oligocene.

2. The development of tufagenic depositional environments in this system that formed the deposits characterising this phase.

6.2.1 Modelling of processes contributing to the onset of depositional flow

Mechanisms for the onset of the first depositional phase have not been previously modelled. The Gregory River Valley probably pre-dates the late Riversleigh Oligocene deposits (Day *et al.* 1983, Megirian 1992, see Figure 2.1), so some fluvial processes probably occurred during the early Tertiary prior to Phase 1.

Ongoing processes in this drainage system in the area are unlikely to have contributed to the onset of depositional flow. This is because Riversleigh primary deposits are apparently restricted to the late Oligocene. If the system were previously capable of deposition at that scale, some older deposits would be expected to exist.

For the deposition during Phase 1 to have been initiated, there must have been some change to the depositional regime, either to the rate or nature of flow into the area or to the nature of the environment near to, or in which, deposition took place, such as tectonic processes.

There is no geological or palaeoclimatic evidence for processes such as climatic change producing high rainfall that could have increased flow of the palaeo-Gregory output from the karst terrain near Riversleigh. Because there are no older deposits known from Riversleigh that could have been formed by earlier exsurgences or fluvial processes, it is possible that sufficient karst outflow had not previously occurred at Riversleigh during

the Tertiary. The karst drainage regime that now feeds the Gregory and O'Shanassy Rivers and their tributaries from permanent exsurgences in the Barkly Tableland may have been initiated during the late Oligocene.

The onset of outflow at Riversleigh could have been related to the tectonic uplift along the extension of the Pine Creek Upwarp that raised the Barkly Tableland and formed the south-western margin of the Karumba Basin (Doutch 1976, Grimes 1979, Smart *et al.* 1980, Day *et al.* 1983). This occurred when interaction between the Australian and Pacific plates caused warping in northern Australia and orogeny and terrane accretion that contributed to the formation of Eastern New Guinea (Doutch 1976, Grimes 1979, Smart *et al.* 1980, Day *et al.* 1983, Veevers 2000). Uplift of the Barkly region could have affected the aquifers and flow gradients in the drainage system, with the following consequences:

1. Gradients of surface drainage systems might have increased by dipping toward Riversleigh to the northeast, increasing the erosion rates. Resulting incision of Proterozoic highs to the north east of Riversleigh (Figure 6.3f) could have further contributed to an increased flow gradient. This could have increased the rate of removal of Jurassic marine sediments capping the Cambrian limestone in the Barkly area.

2. Displacement of aquifers confined by Proterozoic sediments below and Jurassic sediments above could have increased outflow toward Riversleigh from the karst system.

3. Greater exposure of Cambrian limestone by the removal of Jurassic cover could have increased capture and resulting outflow from that karst system.

4. Subsurface drainage flow toward the northeast might have increased with dipping of the system that direction.

The overall effect could have been an increase in the outflow of carbonate-rich water from the Cambrian karst in the Riversleigh area. This increase may have been sufficient to support the prolific deposition of large amounts of tufaceous carbonate during the late Oligocene. The upwarp model of depositional flow at Riversleigh during the late Oligocene is illustrated in Figure 6.3.

SW BARKLY TABLELAND AREA   RIVERSLEIGH AREA   NE

a LOW FLOW GRADIENT

b HIGH FLOW GRADIENT

c

d

e

f
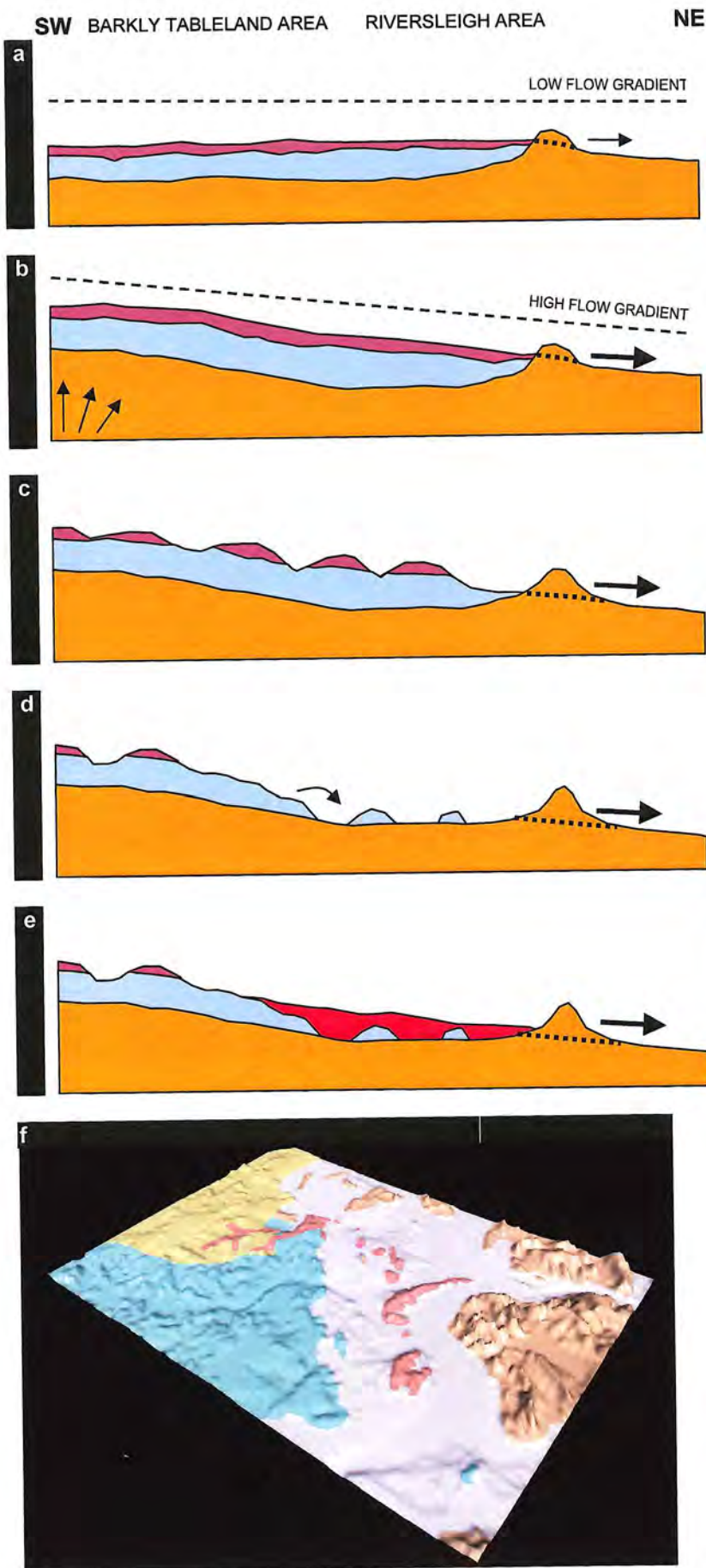
Figure 6.3: The upwarp model of depositional flow at Riversleigh during the late Oligocene. Schematic diagrams not to scale. a) Hypothetical setting prior to the Pine Creek Upwarp, with low flow gradient toward the northeast. Cambrian marine sediments are overlain by more complete Jurassic cover. b) Uplifting of the Barkly Tableland in the southwest increases flow gradient to the northeast. c) Rapid stripping of the Jurassic cover commences. Overall high flow gradient is maintained by incision of the Proterozoic high to the northeast. d) The combination of increased capture by the exposed Cambrian karst and increased drainage flow into the Riversleigh area result in prolific outflow (underground and/or on the surface) of carbonate-rich waters at Riversleigh. e) Deposition of carbonates occurs at Riversleigh. f) Modern Riversleigh setting looking northwest showing incised Proterozoic high to the northeast and residual Tertiary carbonate outcrops lying upon and adjacent to Cambrian sediments.

Legend

☐ ?Pliocene alluvium and colluvium

🟥 Tertiary carbonates

🟪 Jurassic sediments

🟦🟨 Cambrian sediments

🟧 Proterozoic sediments

········ Incised valley

Day *et al.* (1983) consider this upwarping event to have occurred during the late Oligocene. Northern Australian volcanics attributed to this period of tectonic movement date from this time (*ibid.*). Doutch (1976) recognised that the Pine Creek Upwarp triggered the onset of the deep weathering of the Aurukun and Tennant Creek Surfaces in affected areas. This weathering is regarded by Smart *et al.* (1980) to mark the final stage of the Bulimba Cycle, which they consider to have occurred at the end of the Oligocene. These speculative ages conform to the age-range of biocorrelated vertebrate faunas from facies at Riversleigh deposited during this time (Riversleigh Zone ('System') A, late Oligocene; Archer *et al.* 1997).

6.2.2 Late Oligocene fluvial barrage deposition

The Tertiary-basal contact at Riversleigh is undulating. The basal surface probably formed when the later stages of the Bulimba Cycle produced gently undulating surficial deposits and planation surfaces throughout northern Australia prior to tectonic upwarping of the late Oligocene (Grimes 1979, Smart *et al.* 1980, Day *et al.* 1983).

As increased outflow from the south west entered this landscape and formation of fluvial barrages commenced, an anastomosing, low-energy system would have developed .Siliceous surficial lag deposits could have been preserved by tufagenesis *in situ* or locally reworked, rather than transported very far. This formed extraclast tufa ('basal conglomerate') and some minor beds of fine calcarenite formed by localised reworking of fine siliclastics.

Fluctuating conditions in this dynamic environment, and the random occurrence of cyclic damming, fill and incision would have resulted in the dispersal and deposition of reworked intraclasts, producing texturally varied intraclast tufa deposits. In most cases reworked material would have been trapped in adjacent barrage basins immediately downstream, localising dispersion of reworked material.

Constant ample supply of carbonate in solution and as reworked material filled successive basins quickly with micritic tufa rich in intraclasts, gastropods, ostracods and occasionally vertebrate material (normally graded intraclast and micritic tufa). This then

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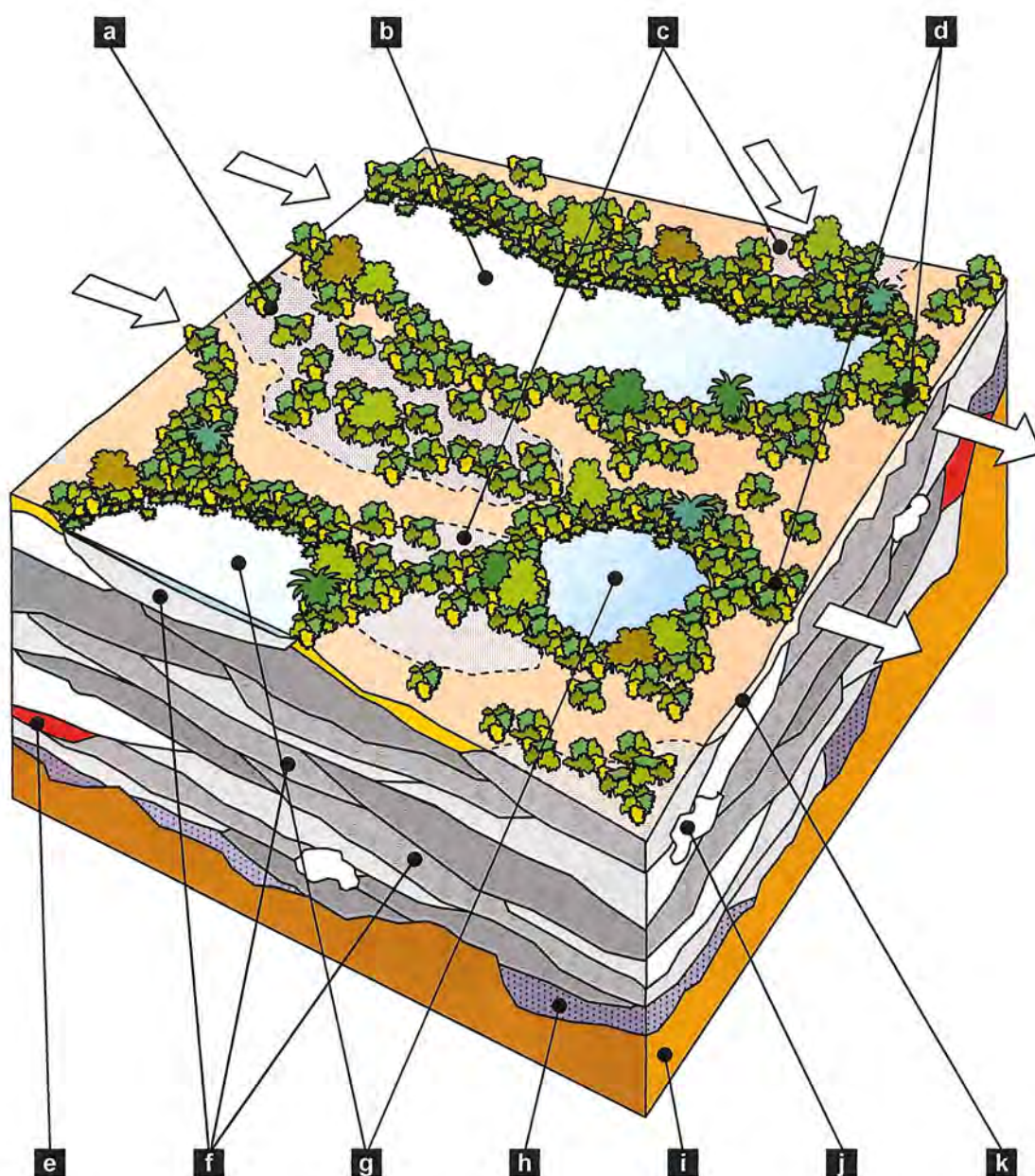
Figure 6.4: Reconstruction of part of Phase 1 terrain at Riversleigh during the late Oligocene. During this time the water table is very high, and prolific outflow of carbonate-saturated water from the Cambrian karst to the southwest contributes to the development of successive fluvial barrage systems in an anastomosing drainage system. a) Relict barrage infill deposit and channel. Exposed deposits are fragmented, corroded and denuded, and will supply reworked material for subsequent deposition occurring at that position in the landscape. b) Large barrage lake. This type of large aquatic environment may have produced deposits that extend for tens to hundreds of metres. c) Relict barrage infill deposits being reworked by active channels. Tufaceous intraclasts are transported and deposited into barrage basins downstream. d) Active drainage channels in an anastomosing system throughout which barrage systems form. e) Pedogenic facies such as palaeosol or relict alluvium. These deposits may eventually form calcrete or altered silicate facies. f) Successive barrage infill deposits comprised of micritic and intraclast tufa with occasional vertebrate fossils. g) Active barrage ponds in which micritic and intraclast tufa deposits form. These low-energy aquatic environments are inhabited by crocodilians, fish, lungfish and turtles, giving rise to vertebrate assemblages characterised by relatively abundant and diverse aquatic taxa. h) Basal facies comprised of extraclast tufa and calcarenite. i) Undulating late Bulimba Cycle surface of Cambrian/Proterozoic basement sediments. j) Syngenetic cave formed by diffuse recharge below water table level while depositional systems are still active. k) Unconsolidated alluvium and soil, mainly not preserved, although occasionally producing pedogenic facies.

resulted in incision by the destructive forces of overflow and material was reworked to the next barrage pond downstream.

As time progressed, the anastomosing flow pattern would have continued to develop these barrage pond systems at random points through the area, some at basal level, some adjacent to and on top of older barrage pond deposits (Figure 5.28) in an areal pattern similar to that which has been developing along Louie Creek since the late Pleistocene (Figure 4.28).

Flow energy in most of the system would have been low, because of the effect of barrages formed ponded environments throughout. If the transport potential in the source area (at the spring-line or points of exsurgence) was high enough to transport Cambrian lithoclasts from there, this material would have been trapped behind the most proximal barrages, and not distributed further into the system, resulting in the conspicuous absence of these clastic element from most of these deposits. The low-flow energy throughout the system was apparently not sufficient to form flow structures in deposits. Flow energy and conditions appear to have permitted the dispersal of sand-sized rounded quartz grains and occasional chert pebbles throughout the system.

Occasional deposits with a higher siliclastic clastic content may have been formed by non-tufagenic alluvial processes and by deviations in flow over non-carbonate terrain. These unconsolidated deposits were either eventually eroded away, or if exposed for long enough were calcretised, or if overlain by ongoing tufagenesis might have been altered to amorphous silicates by consistent hydration in the phreatic zone.

Over a long period of time, these processes formed the primary heterogeneous intraformational tufa deposits and related facies (i.e. calcrete) of up to 75m in thickness (or more) across the Riversleigh area. Based on projected rates of tufa accumulation estimated in Section 4.4.5, coverage of 100-400km^2 at Riversleigh could have occurred over a period of perhaps 4-10 Ma, especially if flow in the area occurred in more than one channel.
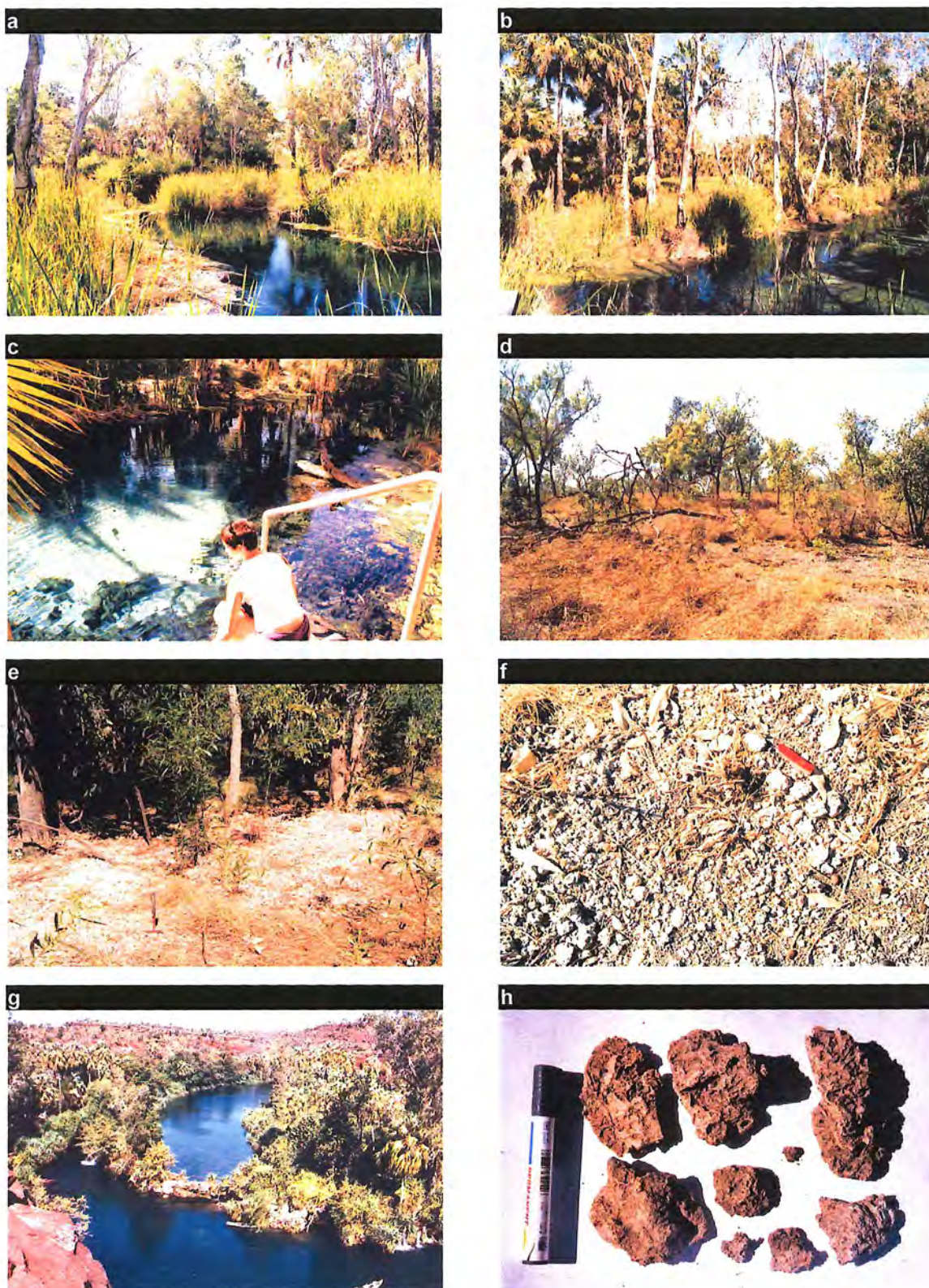
Figure 6.5: Examples of modern tufagenic environments that may be analogous to aspects of the Phase 1 environment at Riversleigh during the late Oligocene. a-f) The source of the Roper River at Bitter Springs, Elsey NP, Mataranka, Northern Territory is an exsurgence of warm, mineral-rich water. Note the lush vegetation (a, b) and abundant algae and aquatic plants (c). Relict tufa deposits are evident and reworked fragments of tufa are common throughout the area (e, f). Aquatic vertebrate taxa include crocodiles, turtles, fish and birds. The system occurs in an otherwise seasonally very dry environment (d). g) The fluvial tufa barrage at Indarri Falls, Lawn Hill NP, Queensland is an example of an active tufa barrage in a fluvial system. h) Reworked tufa fragments collected at Indarri Falls are considered analogous to reworked intraclasts in the Tertiary tufaceous carbonates at Riversleigh.

Depositional flow may have ceased because of a subsequent change in conditions at Riversleigh. The development of subsurface drainage and deepening valleys may have resulted in a drop in water table level. Phreatic flow would have continued away from the surface. Incision of the primary deposit by the development of major drainage channels might have restricted flow patterns and may no longer have supported widespread tufagenesis. Tufagenesis may have continued downstream from Riversleigh, deposits formed by this processes were mapped as Tertiary by Megirian (1992), however there is not enough data from these deposits to determine their age relationships. They could contain fossil faunas that post-date Zone A late Oligocene faunas of Phase 1.

Aspects of the tufagenic system Bitter Springs at the source of the Roper River at Elsey National Park, Mataranka, in the Northern Territory, may be considered analogous to of aspects of the late Oligocene depositional system at Riversleigh (Figure 6.5a-f). The system is fed by an exsurgence of warm, mineral–rich water the low energy flow which is regulated by the gradient of the low relief terrain and fluvial tufa barrages downstream. Relict and reworked tufa is abundant on the surface, indicating that dynamic flow and depositional conditions have resulted in cyclic episodes of tufagenesis throughout the system in the past. While the region is seasonally very dry, there is an abrupt transition of habitat around the flow channel where the permanently wet conditions support lush and diverse vegetation for a radius of about 50 m and algae and aquatic plants are abundant in the aqueous environment. Aquatic taxa present include crocodiles, turtles, fish and birds, and a relatively high diversity of terrestrial animals are attracted to the area.

The fluvial barrage system at Indarri Falls, in the Lawn Hill Gorge, near Riversleigh may also be an example of an analogous system. Tufa deposits accumulate in the low-energy barrage lake upstream of the main barrage, and tufaceous intraclasts are reworked and transported downstream (Figure 6.5g, h).

6.3 Riversleigh Depositional Phase 2: early Miocene karst terrain development

Facies at Riversleigh containing early Miocene faunas of Zone B are exclusively vadose cave deposits. Some of these deposits appear to have formed in well-developed caves. The dominance of vadose facies in cave deposits indicates that the water table must have fallen by this time, because these facies are unlikely to have formed when the water table was high and tufagenic conditions prevailed.

During the early Miocene, 'greenhouse' conditions prevailed and were approaching a middle Miocene peak (McGowran and Li 1994), global temperature was approximately $2^{\circ}C$ warmer than today (Barrett 2003) and Riversleigh was moving north between warm-temperate and subtropical latitudes at between $30^{\circ}S$ and $28^{\circ}S$ (see Table 2.1, Figure 2.19). These circumstances are considered indicative that climate at Riversleigh was relatively warm and wet. Karst terrain development processes including the formation of topographically variable (i.e. polygonal) karst, are usually associated with warm and humid climates, particularly sub-tropical and tropical climates (Ford and Williams 1989, Ahnert and Williams 1997; see Section 4.3.3). Under the climatic conditions prevailing at Riversleigh during this period, the initiation of a sequence of karst development characterised in its early stages by the formation of a deeply corroded topographically variable karst terrain similar to modern young karst terrains in humid climates during the early Miocene is considered very likely.

Once dissolutional drainage systems controlling the pattern of surface flow and corrosion had developed, key processes affecting subsequent terrain development would have been initiated. The development of fissures and dolines in the epikarst, controlled initially by topography and random variations in the solubility of Phase 1 deposits, would have resulted in the formation of the drainage and surface flow patterns that characterise karst terrains. Flowing water on the surface (i.e. including depositional flow) may well have been irregularly distributed, restricted deeply incised channels or absent, because the epikarst would have captured runoff by draining surface water directly into the phreatic zone. Here, accumulation and movement of water would to a large degree have remained subsurface processes at water table level. Valleys and

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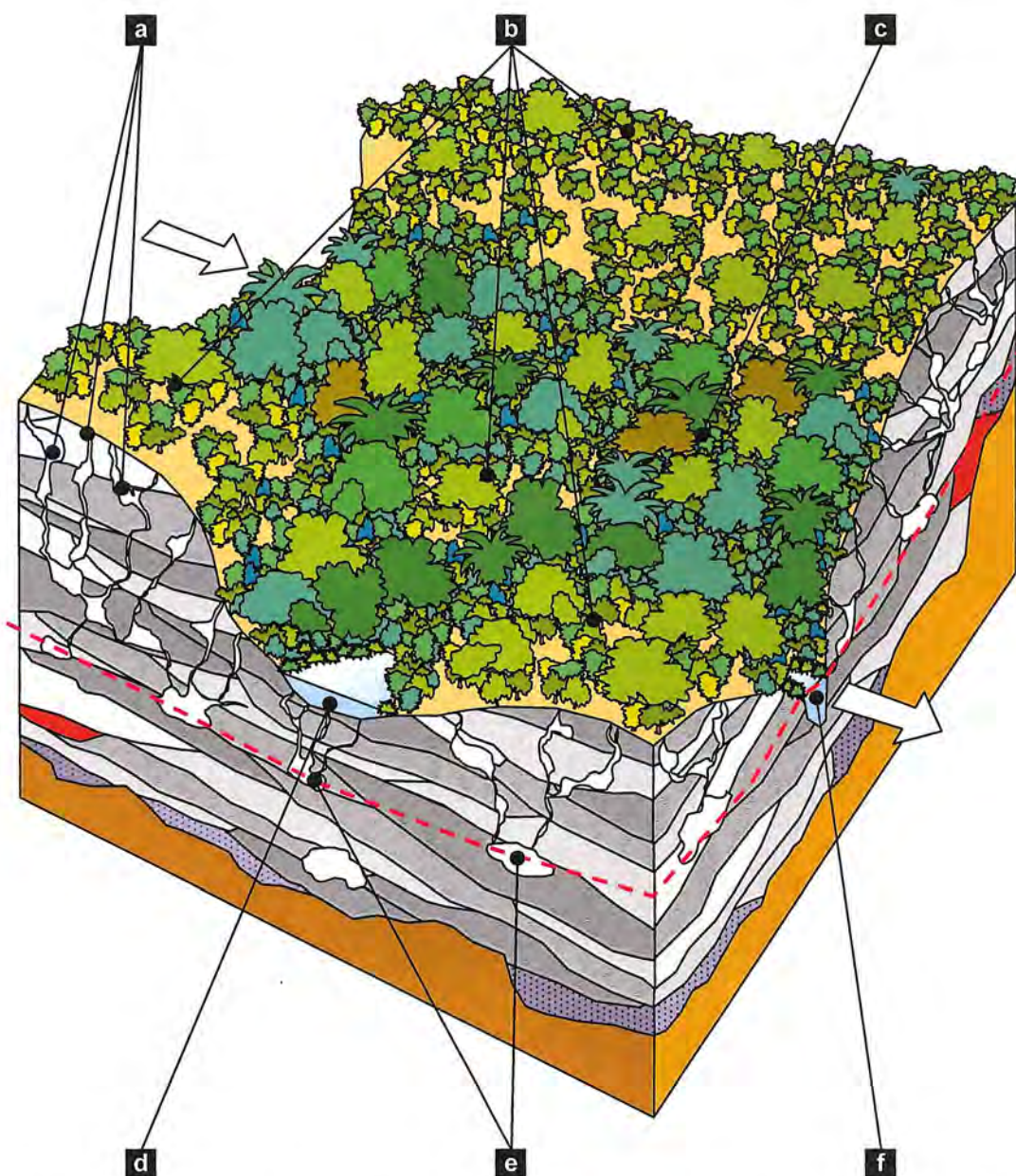
Figure 6.6: Reconstruction of part of the terrain at Riversleigh during Phase 2 in the early Miocene. The level of the water table has lowered (red dashed line) allowing dissolution and vadose depositional processes to dominate. The tertiary carbonates are here given an initial relief of 50-70m. Dissection, denudation and deep corrosion may have contributed to a high degree of topographic variability, which is typical of young karst terrains in warm and humid conditions. A well-developed epikarst keeps the surface well-drained and allows gravitational transport of clastic material, including vertebrate bones, into caves. Vegetation during this relatively warm, humid time in modern subtropical latitudes may have been comparable to forms of modern rainforest. The variable distribution of 'upper' and 'lower' distinction environments with characteristic humidity, soil and vegetation attributes may have been at its climax. a) Epikarstic speleogenesis provides access to lower cave environments and forms new cave environments. Vadose processes dominate in caves above the level of the water table. b) 'Upper' environments dominate high points. These are characterised by relative dryness, lower plant diversity, higher representation of shrubs and crevice-dwelling plants, disrupted soil and canopy cover and a greater degree of exposed rock. c) 'Lower' environments dominate low points. These environments are more humid, have thicker more continuous soil cover and a higher diversity and abundance of plant taxa. d) Perched pond forms aquatic environment in closed depression with blocked drainage system. e) Subsurface drainage forms caves by vadose/phreatic flow at the water table level. f) Main drainage channels occur in deeply incised valleys at the level of the water table.

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solution dolines would have acted as drains and discharge points to the basement. These structures would have become a dominant influence over topography and the formation of surface flow patterns, rather than only processes associated with erosional drainage channels that characterise non-carbonate terrains. Denudation and corrosion would have been the primary processes that shaped the terrain at this time.

These processes could have contributed to a typical pattern of karst terrain development (see Section 4.3.3). A karst developmental sequence at Riversleigh would most likely have been characterised by the following stages:

1. Early Miocene: early stage characterised by deep incision by doline formation main flow channels forming topographically variable karst terrain (Figure 6.2c).

2. Middle Miocene: middle stage characterised by ongoing expansion of low-points and retraction of high-points and the gradual expansion of surface drainage systems at basement level (Figure 6.2d).

3. Late Miocene to Recent: mature stage characterised by retraction of residual outcrops on the corrosion plain by ongoing denudation and erosional by the Gregory drainage system (Figure 6.2e, f).

If the Riversleigh terrain had been deeply corroded and incised by the early Miocene, the landscape would have been characterised by highly variable topography (Figure 6.6).

The approximate time period (i.e. perhaps 1-4 Ma) that separates the probable cease of late Oligocene tufagenic deposition and this vadose cave deposition in the early Miocene is comparable to the spans of time during which karst systems have developed under similar conditions in humid systems in more recent times. Aspects of these terrains may be analogous to conditions at Riversleigh in the early Miocene. The topographically-variable polygonal karst terrains of the Darai Hills, Mt Kaijende and the Emia Valley in New Guinea and the Lelet Plateau in New Ireland have formed on marine limestone terranes uplifted in the Pliocene (Williams 1970, 1971, Gillieson 1997). Given the pre-denudation surface could have been 5 to 30m higher than the modern surface, surface topography could have had relief of up to 50m which is within
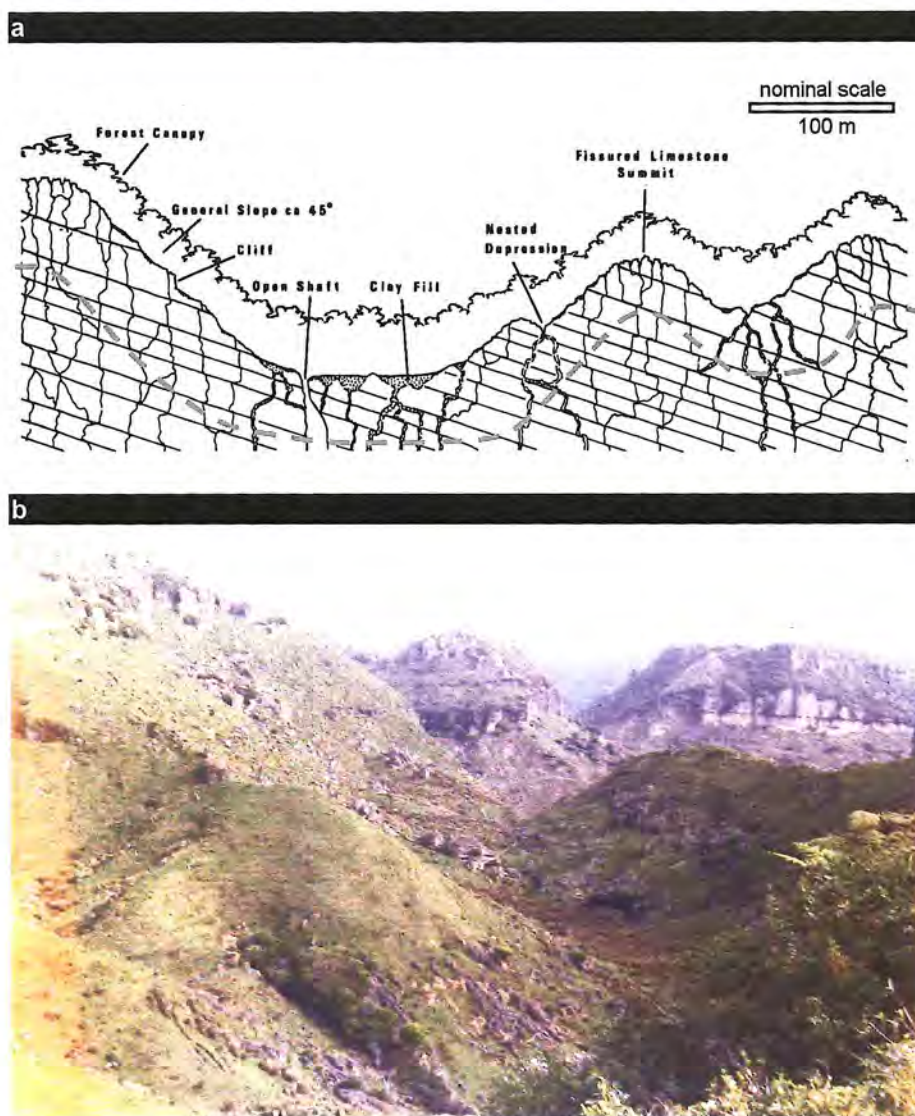
Figure 6.7: Examples of modern young karst terrains that may be comparable to aspects of the Phase 2 landscape at Riversleigh during the early Miocene. a) Typical profile of karst terrain in the Darai Hills, New Guinea. The host rock is dipping marine limestone with relief of 50-100m. The grey dashed line indicates the hypothetical position of the surface after denudation, analogous to the modern residual surface at Riversleigh. Note topographic high points are characterised by thinner canopy cover and open vertical fissures through the epikarst. Low-points are characterised by clay soils and thicker canopy cover. After Williams (1971). b) Karst terrain on uplifted Miocene marine limestone at Puna Paua near Mangarakau, South Island, New Zealand. Relief is approximately 50-70m. The undulating landscape is typical of topographic variability in young karst terrains. Caves and dissolutional drainage systems occur throughout the area. In the foreground is a closed depression. Exposed crests are evident on topographic highs in the foreground and background. Vegetation cover, which has been modified by sheep farming, was originally native forest characterised by pines, palms and ferns. Photograph by L. Farmer.

the ranges of relief in young karst terrains in New Guinea, West Malaysia and New Ireland (Williams 1970, 1971, Crowther 1982, Gillieson 1997).

In the earliest stages of karst development, there may have been little surface water at all because the phreatic zone would have been well below the surface. As time progressed and the surface lowered and dolines deepened, standing water may have occurred in perched lakes and at low points in the profile that were at basement level or water table level. These environments could have been inhabited by aquatic taxa. Exsurgences may have issued from these low points in the system.

This pattern of topography would have had significant implications for the distribution of surface environments and depositional environments in the terrain as development progressed, and at maturity. According to sequences of karst terrain development (i.e. Section 4.3.3), high points in the terrain would have retracted, while low areas expanded. These high points would have been the location of the epikarst that supplied clastic material to vadose cave deposits that were preserved and now outcrop at the surface of modern residuals at Riversleigh. Any deposits formed by processes in low points of the terrain would have since been lost to corrosion and denudation. The influence of the variable karst topography of on the distribution of environments is discussed in more detail below in Section 7.3.

The karst terrain at Puna Paua, New Zealand may exhibit some analogous characteristics to the early to middle Miocene landscape at Riversleigh (Figure 6.7b). This landscape is dominated by highly variable undulating topography with a relief of approximately 50-70 metres characterised by abundant closed depressions, exposed hill tops, caves and dissolution drainage systems, perched lakes and disrupted surface drainage patterns. The profile of the Darai Hills terrain (Williams 1971; Figure 6.7a) may also illustrate comparable features, including undulating landforms, fissured rocky crests in high-points and variations in soil type and canopy thickness with topography.

6.4 Riversleigh Depositional Phase 3: middle Miocene fluvial barrage deposition in a karst terrain

The tufagenic Gag Plateau deposits are similar to facies of Phase 1, yet they contain faunas that are distinct from those found in Phase 1 deposits. The Zone C faunas of Phase 3 are considered to be middle Miocene in age (Archer *et al.* 1997). Like those found in Phase 1 deposits, these faunas contain a higher abundance and diversity of aquatic taxa. These deposits mark a return of tufagenic conditions to Riversleigh in the middle Miocene.

By this time, ongoing attrition of the surface by a combination of denudation and erosional flow at the emerging basement level could have resulted in the expansion of valleys, dolines and other topographic lows, while high-points including interfluves and inter-doline areas would have regressed. This would have gradually shifted the balance of distribution of landforms from domination of high-points over depressions and valleys to a dominance of depressions and valleys over high-points. Overall relief would have been reduced by denudation since the early Miocene. Surfaces of low-points would have been characterised by scree, exhumed undulating basement (late-Oligocene surface), and ponded water or drainage channels. The hypothetical landscape at Riversleigh during this time is illustrated in Figure 6.10.

Tufagenic deposition at this time appears to have occurred adjacent to and upon Phase 1 deposits, which at this time were still perhaps 20m higher in maximum relief. The source of depositional flow may well have been from a proximal exsurgence in the Phase 1 limestone or flow in an incised channel, resulting in the formation of tufa barrage deposits with similar facies to those of Phase 1. This process may have been restricted to the Gag Plateau area, or deposits formed by this process elsewhere at Riversleigh have been lost to corrosion and erosion.

There are a number of vadose cave deposits on Gag and Southern Gag Plateaux that contain faunas that may be either early Miocene, middle Miocene or younger. Their relationships to the middle Miocene faunas from the tufaceous Phase 3 deposits of Gag Plateau, the early Miocene vadose cave deposits and the middle Miocene and early-Late
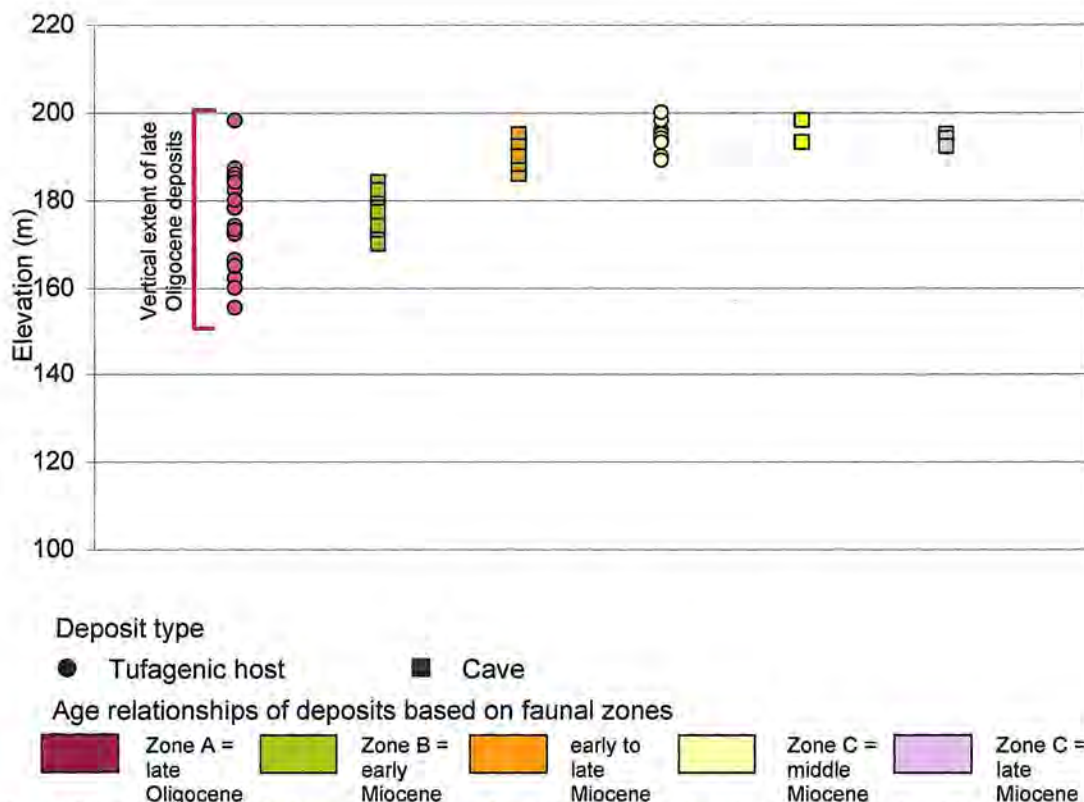
Figure 6.8: Elevations of selected fossil deposits at Riversleigh showing height relationships of deposits of different ages and types. The majority of carbonate deposits at Riversleigh are Phase 1 tufagenic deposits containing late Oligocene faunas of Zone A, and occur throughout the entire Tertiary profile (approximately 150m to 200m). These deposits are the 'host' for younger cave deposits that formed within them. Cave deposits containing Zone B and C faunas (early to early-late Miocene) are vertically restricted between approximately 165 and 200 m elevation. Tufagenic deposits of Phase 3 that contain middle Miocene Zone C faunas are positioned at heights equal to or higher than vadose cave deposits that may be of the same age, which has implications for the relative ages of tufaceous and vadose cave deposits from this period since vadose and phreatic deposits would not have formed at the same level in the profile at the same time. The vertical distribution of fossil localities containing Zone A faunas illustrates the important concept that position in the profile is not necessarily indicative of age relationships of deposits at Riversleigh, either within suites of tufaceous deposits (see depositional sequences in Figure 5.28) and between deposits from different phases that formed by different processes during successive stages of karst terrain development. Some elevations are from Creaser (1997).

Localities plotted are:
Zone A, Phase 1 tufagenic deposits: GILLESPIE'S GULLY, SMALL JAW, KJO, MARGAN'S IMMENSE MIGHT, IT, PA, LOW LION, HIATUS, HIATUS 2, BERNIE'S COOKING POT, COCO ROX, WHITE HUNTER, WHITE HUNTER WEST, BURNT OFFERING, VIP, SUE'S ROCKY ROAD, D, STICKY BEAK, MESA BONE LAYER, QUANTUM LEAP, UPPER BURNT OFFERING, DUNSINANE, CUSTARD TART, ALSITE, ANNA'S HORRIBILIS, BONE REEF, TWO GLOVES, BONE ATOLL, LOCKWOOD'S LINK.
Zone B , Phase 2 cave deposits: RSO, SOUVENIR, MIKE'S MENAGERIE, OUTASITE, PARISITE, ROBSON'S DELIGHT, STALAGMITE (aka 'sinter'), SEWER, RAT VOMIT, CREASER'S RAMPARTS, VIEW DELIGHTFUL, BOID SITE EAST, MILO SANDWICH, MIKE'S POTATO PATCH, BITESANTENARY, PANORAMA, BOID, CAMEL SPUTUM, WAYNE'S WOK, INABEYANCE, UPPER, OUTABEYANCE, DIRK'S TOWERS, NEVILLE'S GARDEN, MICROSITE, BITESANTENARY EAST.
Zone C, Phase 3 tufagenic deposits: QUENTIN'S QUARRY, LAST MINUTE, LD94, GAG, BOB'S BOULDERS, RINGTAIL, MAIN, GONE OVER HERE, BIRD BONE, COURTENAY'S CACHE, GROUP, GRIMES' GRIKE, SKULL, JAW JUNCTION.
Zone C, Phase 2 or 3 spelaean deposits (Middle Miocene faunas): HENK'S HOLLOW, MELODY'S MAZE.
Uncertain age, Phase 2 or 3 or 4 cave deposits (ages uncertain): ANGELA'S BAT PATE, ANTON'S PIXIE, CADBURY'S KINGDOM, WANG, TWO TREES, NICOLE'S BOULDERS, FILS FINE FLOWSTONE, NEVILLE'S RICHES, JIM'S JAW, JIM'S CAROUSEL, CAPTAIN ANDROGEN, PETER THE PILOT, NJC8, AL90, DOME, CLEFT OF AGES, KEITH'S CHOCKY BLOCK.
Zone C , Phase 4 cave deposits: BRER RICK'S BAT, GOTHAM NORTH, GOTHAM CITY, RICK'S RUSTY ROCKS, ENCORE.

Miocene vadose cave deposits of Phases 2 and 4 are unclear because not enough is known about their faunas to firmly establish relative ages. Figure 6.8 illustrates the relative heights of deposits from each phase that yield faunas of different ages. This is significant because the tufaceous deposits containing middle Miocene faunas are higher than most vadose cave deposits. Because tufagenic conditions and vadose karst conditions prevail under very different hydrogeological conditions this has implications for possible relative ages. Tufaceous deposits and vadose cave deposits at Riversleigh would not have formed contemporaneously at the same level in the profile because during times of tufagenesis, cave environments would have been inundated by the higher water table level, ceasing formation of subaerially-deposits speleothem and other vadose cave deposits, preventing bats and other animals from using the caves and possibly causing the dissolution and erosion of existing cave facies.

The relative heights of all of the vadose cave deposits at Riversleigh indicate that the vadose/phreatic boundary was between about 170m and 180m when they formed. The highest Gag Plateau tufaceous deposits outcrop at about 200m (Jaw Junction Site; Creaser (1997)). Either the tufaceous deposits of Phase 3 formed at and below this water table level and Gag Plateau is an uplifted remnant displaced by tectonic movement to a point higher than the vadose karst systems, or tufagenesis occurred *in situ* at the level where the deposits occur today level as the result of higher water table and the cave deposits in the area are therefore not contemporaneous because they would have been flooded at the time.

Thus, there are three possible scenarios that could explain the occurrence of the Gag Plateau tufa deposits high in the profile and the age-relationships of these deposits with vadose karst deposits on Southern Gag Plateau that contain faunas that may be early to middle Miocene in age:

1. The Gag Plateau tufa and the Gag and Southern Gag Plateaux vadose cave deposits are not contemporaneous because there was raised water table during tufagenesis.

2. The Gag Plateau tufa and the Gag and Southern Gag Plateaux vadose cave deposits are contemporaneous and tufa was deposited low in the profile then uplifted or surrounding areas subsided.

Figure 6.9: Depositional models illustrating the possible relationships between tufagenic deposits of Phases 1 and 3 and vadose cave deposits of Phases 2 and 4 by processes occurring in the middle Miocene during Phase 3. Both scenarios begin in a weathered karst landscape with a water table (vadose/phreatic boundary) below the level of vadose cave environments. Scenario 1 involves raised water table causing deposition of tufa (2). The water table returns to normal level and vadose processes resume in caves (3). In Scenario 2, tufagenesis occurs below the level of the water table (2) and would have been lost to ongoing karst processes, but uplift raises the deposit approximately to the level of the Phase 1 surface. (2a), where epikarstic development and vadose cave processes subsequently occur. Scenario 3 involves deposition by raised water table and uplift by tectonic movement, followed by epikarst development and vadose cave processes. In all scenarios, ongoing denudation produces the distribution of facies evident today (4). For simplicity, this model does not illustrate any deposition by vadose cave processes that may have occurred during Phase 3 if the water table was fluctuating.

3. The Gag Plateau tufa and the Gag and Southern Gag Plateaux vadose karst deposits are not contemporaneous because there was raised water table during tufagenesis and subsequent uplift or surrounding areas subsided.

These models are illustrated in Figure 6.9.

Scenarios 2 and 3 are considered very unlikely because there is no evidence of this type of tectonic movement (i.e. faulting). Taking denudation into account (i.e. original surface of Gag Plateau tufa deposits was higher), Gag Plateau would have been vertically displaced relative to karst deposits of Southern Gag Plateau by more than 25-30m if the deposits were formed below the water table level while the Southern Gag Plateau vadose system was active. There is a lineament marked partly by a deep gully trending southwest/northeast to the southeast of the plateau (Figure 2.6), but there is no reason to consider this a fault. Lineaments on airphotos mapped as faults by Megirian (1992) could be considered indicative of tectonic activity in the area, however these apparent 'faults' were mapped as underlying middle Miocene tufa deposits and thus would be older. Whether these really are faults is in doubt, because patterns of karst development would have been affected by their presence and the presence of any related joint systems, and because some fault-like lineaments have been observed not to be faults in the field (see Section 5.4).

In the absence of evidence of tectonic activity displacing deposits, raised water table is the most parsimonious explanation for the formation of the tufaceous deposits at that level. Climatic change involving increased rainfall, or blockage of the drainage system may have raised the water table, flooding vadose systems and discharging highly saturated waters into parts of the karst terrain, forming tufagenic deposits in which middle Miocene faunas were preserved. This is discussed in more detail below.

It is unclear whether tufagenesis occurred at Gag Plateau at more than one separate time during the middle Miocene. Myers (2002) grouped the Gag Site Local Fauna and the Henk's Hollow Site Local Fauna together in the Litokoala-Muribacinus palaeocommunity, which is here considered indicative of contemporaneity, however the Gag Site deposit is here considered to be tufagenic and the deposits at Henk's Hollow
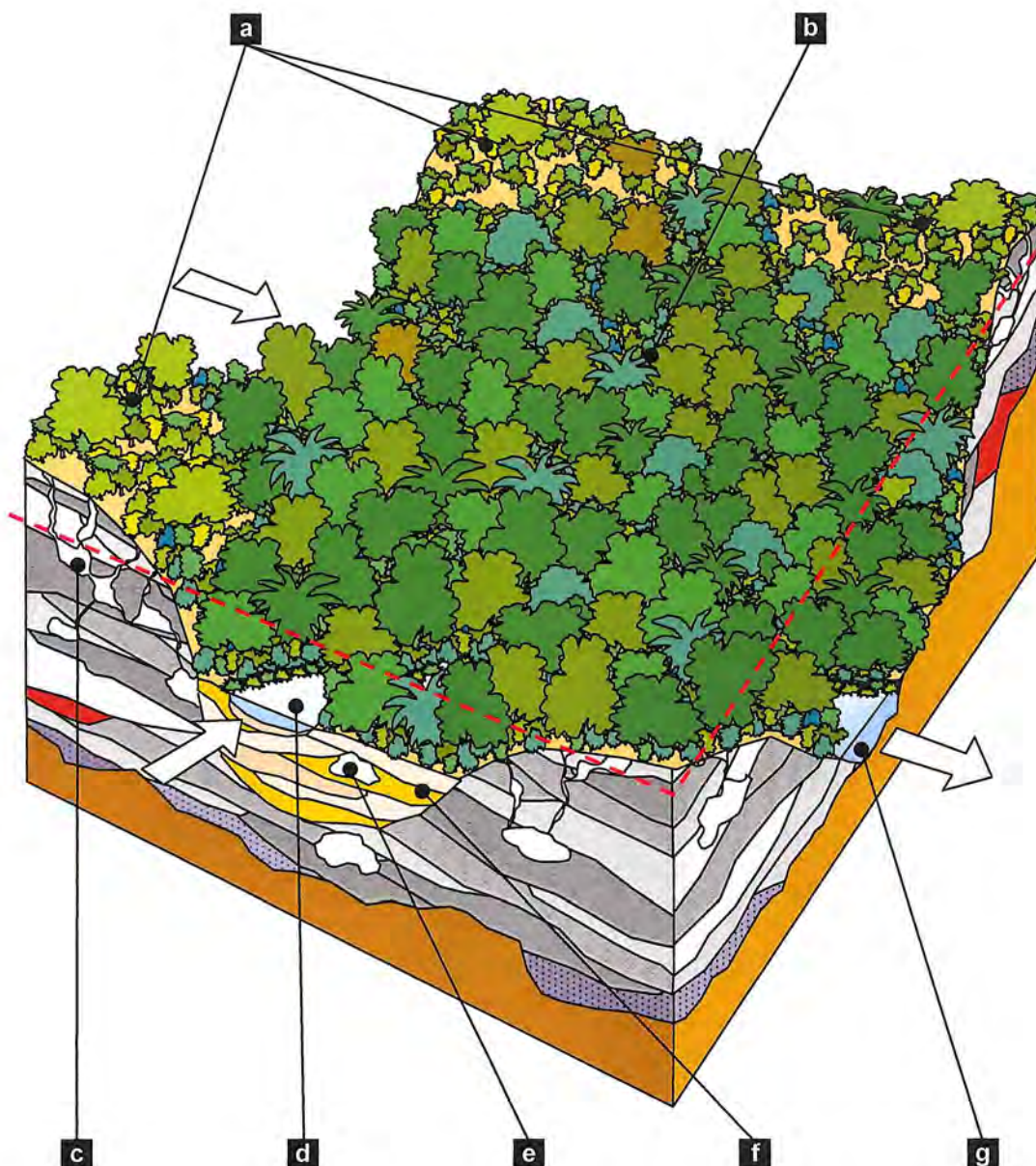
Figure 6.10: Reconstruction of part of Phase 3 terrain at Riversleigh during the middle Miocene. This phase is characterised by high water table level (red dashed line indicates hypothetical maximum elevation), which would have flooded the majority of cave environments and allowed tufagenic processes to occur on the surface, producing the barrage infill deposits on the northwest part of Gag Plateau. These events may coincide with the extreme 'greenhouse' conditions of middle Miocene climatic optimum of McGowran and Li (1994). Ongoing development of the karst terrain may have reached the medial phase in which lower areas begin to dominate as high-points retract. a) Topographic high-points with 'upper' environments are beginning to retract because of attrition by ongoing denudation and erosion. b) Expansion of topographic lows may have resulted in the domination of 'lower' environments. If extreme 'greenhouse' climatic conditions prevailed during this time, vegetation patterns typical of 'lower' environments may have proliferated, further diminishing the distribution of 'upper' environments, because differences between 'upper' and 'lower' environments are diminished in areas with very high rainfall. This could have contributed to an overall lowering of diversity in vertebrate communities. The hypothetical vegetation depicted here is comparable to modern tropical rainforest. c) Vadose processes cease in cave environments below water table level. d) Localised fluvial barrage systems form in surface drainage channels. Aquatic environments are inhabited by crocodilians, fish, lungfish and turtles, which are preserved in intraclast tufa deposits (i.e. Ringtail Site). e) Syngenetic caves form by diffuse recharge. f) Successive intraclast tufa deposits formed by fluvial barrage pond infill. g) Major channel draining the landscape has reached basement level. Erosion may make a significant contribution to landscape development at this time.

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Site is considered a cave deposits. This could indicate a problem with interpretation of these depositional environments, or the water table may have fluctuated between high and low levels during the Middle Miocene. Under these conditions, when the water table level was high tufagenesis would have occurred, and when the water table level was low vadose processes would have persisted.

The tufagenic episode(s) at Gag Plateau may have been relatively brief, in the order of 10^4 Ma, given the rate of accumulation for other deposits of comparable size (i.e. in Section 4.4.5). If the water table fluctuated rapidly, there may have been some temporal overlap of processes in vadose cave and tufagenic environments where fossils were preserved.

The geological relationships of deposits on Gag Plateau are complex and require further detailed investigation.

6.5 Riversleigh Depositional Phase 4: middle Miocene to early late Miocene

The final depositional phase of the middle Tertiary at Riversleigh, which appears to have persisted to the Holocene, is characterised by the return of vadose conditions and ongoing karst terrain development to a mature stage. No other tufagenic deposits containing faunas younger than middle Miocene age have been found at Riversleigh.

During this phase, infill of caves in Phase 1 deposits continued and this process also occurred in Phase 3 deposits. Cave deposits rich in bat material, speleothem and phosphatic textures hosted by middle Miocene Phase 3 deposits include Gotham City Site, and Brer Rick's Bat Site. The Encore Site deposit is a representative Phase 4 cave deposit hosted by Phase 1 tufagenic deposits on Southern Gag Plateau. Some other vadose cave deposits hosted within Phase 1 deposits on Southern Gag Plateau that are considered to contain middle Miocene, or younger, faunas may also have formed during this depositional phase.
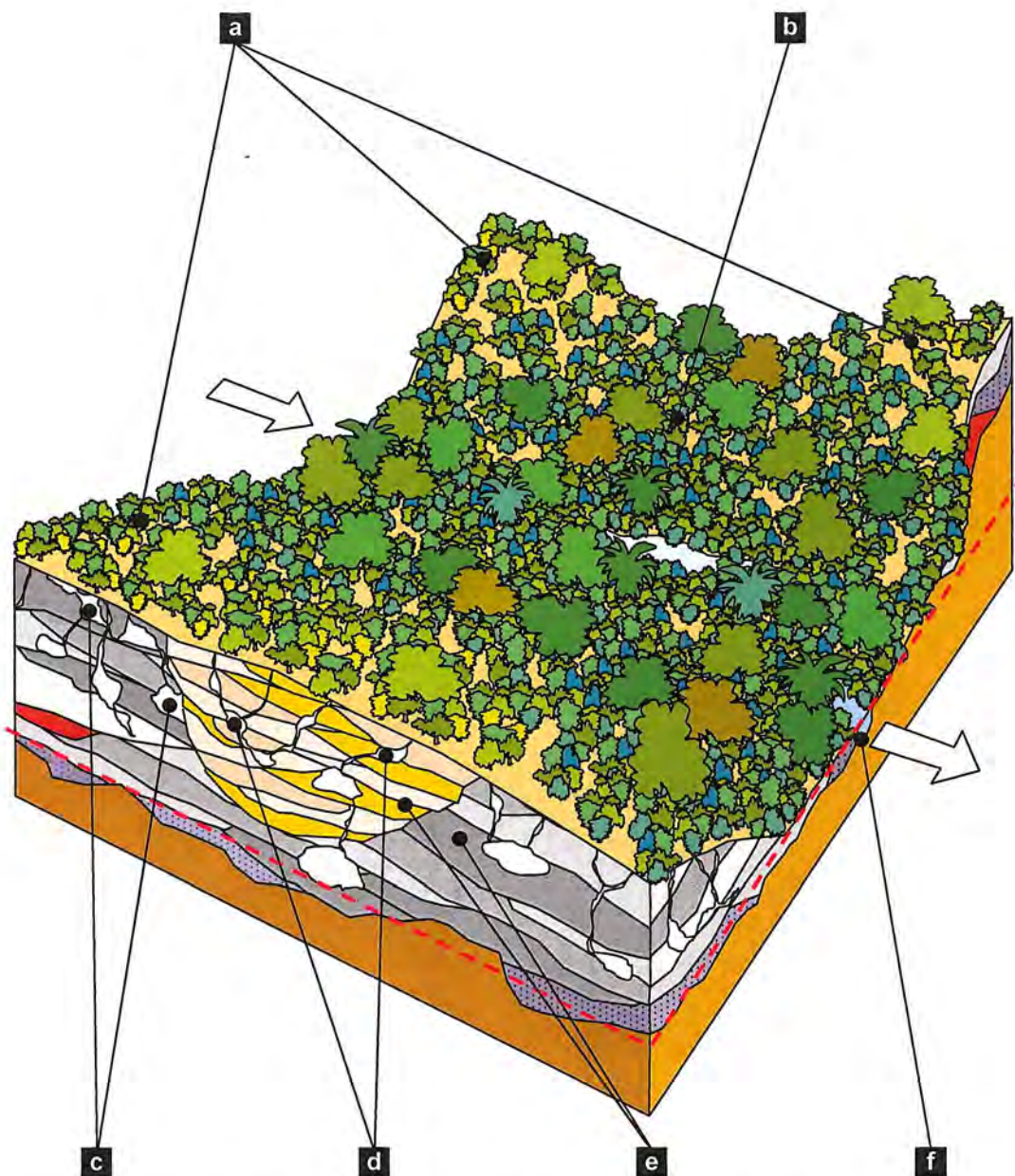
Figure 6.11: Reconstruction of part of Phase 4 terrain at Riversleigh during the middle to late Miocene. This period is characterised by low water table level (red dashed line), retraction of terrain high points, and the domination of topographic lows. Erosional processes by the Gregory River drainage system play a significant role in landscape development. Note that denudation has significantly lowered the overall relief of Tertiary carbonates since the early Miocene. a) Retracting high-points with 'upper' environments. Distribution of 'upper' environments is restricted and fragmented. b) Low-points with 'lower' environments dominate the landscape. Gradual changes in climate in Australia during this time may have contributed to changes to the vegetation patterns that had prevailed earlier in the Miocene. Hypothetical vegetation pattern here is of a more open cover that less comparable to modern tropical rainforest. c) Vadose cave depositional processes occur in caves above the water table. d) Epikarstic speleogenesis forms new cave environments and accesses deeper caves in the middle Miocene barrage infill deposits. e) Middle Miocene carbonates adjacent to late Oligocene carbonates. f) Drainage channel of the Gregory River system.

The terrain would have been characterised by the continuing expansion of low-points and the retraction of high-points to the isolated highs remaining today (see Figures 6.11 and 6.12). Ongoing denudation removed much of the upper part of Phase 1 and Phase 3 deposits, including the much of the epikarst and vadose cave deposits that had formed within them. Cave deposits found at the surface today are the lowermost remnants of the more extensive epikarst and cave systems of the early, middle and early-late Miocene.

The palaeo-Gregory River drainage system may have played an increasing role in erosion of middle Tertiary remnants in the middle to late Miocene. Perhaps by the Pliocene, areas at basement level had become fully interconnected and fluvial sediments were deposited by the palaeo-Gregory (Megirian 1992).
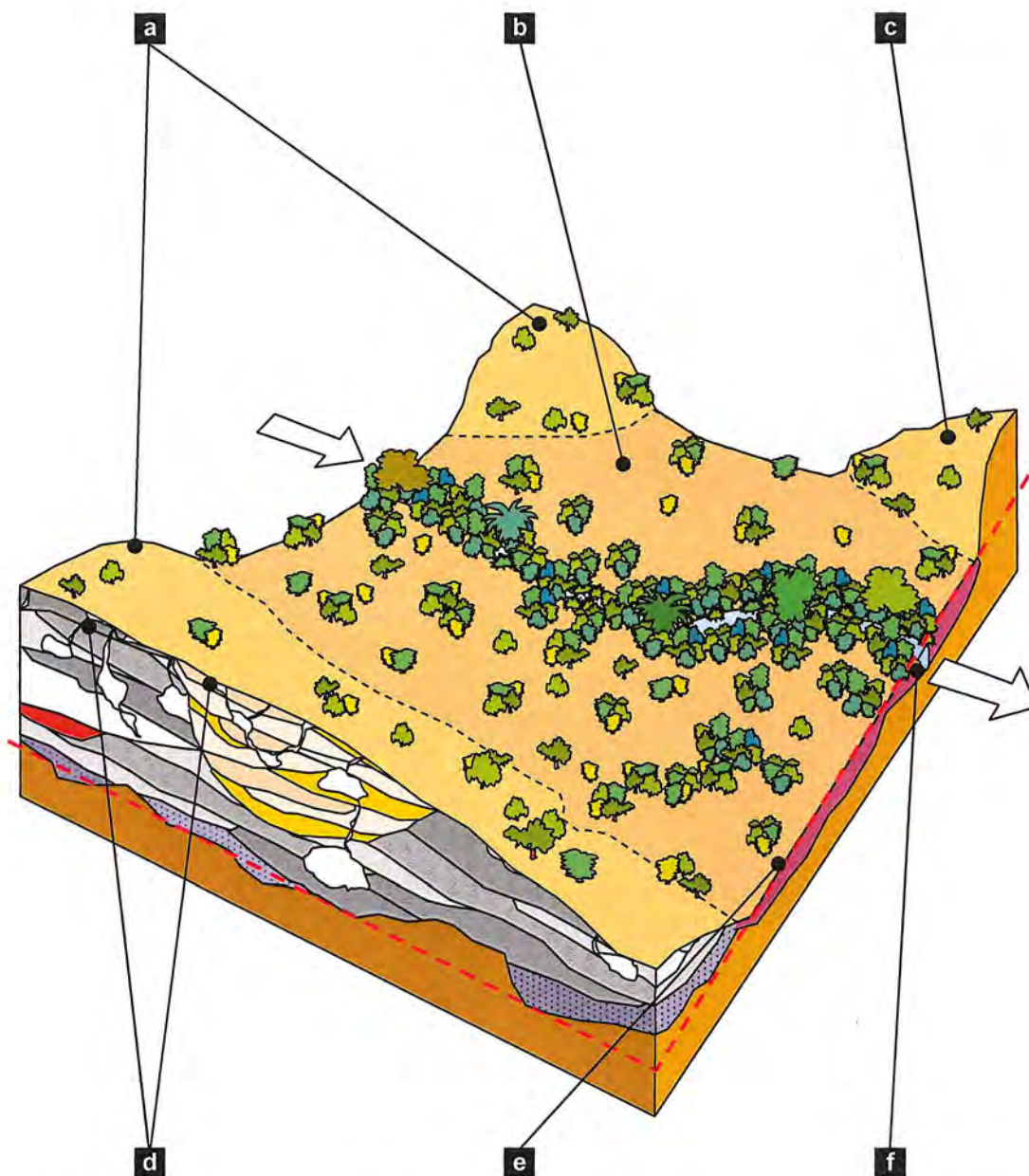
Figure 6.12: Representation of the modern terrain at Riversleigh in the seasonal tropics. Relief of Tertiary carbonate outcrops is 10 to 40 metres. Dry season water table marked by red dashed line. a) Residual Tertiary carbonate highs. These residuals had originally underlain the highest points in the middle Tertiary landscape. b) Corrosion plain dominated by grassland. c) Exhumed basement high-point. d) Early Miocene to early-late Miocene cave deposits outcropping at surface. e) ?Pliocene to Holocene alluvium and colluvium. f) Channel of the Gregory River system in which tufagenic processes are ongoing. Vegetation along drainage systems is relatively lush.

Chapter 7

Discussion of the Riversleigh 4-phase depositional model

The Riversleigh 4-phase model provides a sequential depositional framework to facilitate interpretation of geological processes that that occurred at Riversleigh during the middle Tertiary. The pattern of depositional processes occurring over time at Riversleigh can be useful for determining age relationships and aspects of palaeoenvironmental conditions at localities where fossil vertebrates occur.

Because the Riversleigh carbonates have undergone a sequence of karst processes that spans primary deposition in the late Oligocene to maturity in the Holocene, they provide an interesting opportunity to examine the sequence of karst processes occurring in a carbonate deposit which has apparently not experienced mesogenetic and telogenetic processes (*sensu* Klimchouk and Ford 2000b) such as burial, major lithological alteration, faulting, folding, uplift and gradual exposure. The Riversleigh Tertiary carbonates could thus prove useful for evaluation of the roles of mesogenetic and telogenetic processes in the development of karst systems, and analyses of processes including speleogenesis and landform development that have occurred at Riversleigh without mediation by the types of major lithological or structural changes over geological time that characterise other karst systems.

Aspects of the 4-phase model are useful for the purposes of correlation with palaeoclimatic and tectonic events in Australia during the middle Tertiary, interpretation of aspects of palaeoenvironmental conditions at Riversleigh and consideration of the effect of different processes occurring at Riversleigh throughout the middle Tertiary that may have affected the composition of, and relative differences between, vertebrate assemblages that formed during that period.

7.1 Palaeoclimatic implications of depositional models and correlation with the middle Tertiary record in Australia

Aspects of the Riversleigh 4-phase depositional model can be related to patterns of regional climatic, geological and tectonic processes that occurred in Australia during the

Time scale		Regional geology	Riversleigh geology and processes				Global processes		
Time (Ma)	Epoch	Karumba Basin cycles and processes	Faunal Zone (='System')	Depositional phase	Dominant depositional process	Karst terrain development	Riversleigh Palaeo-latitude (°S)	Southern oscillation 'Greenhouse' peaks	Global temperature curve (°C above present)
5.35	Late Miocene	Depositional — Wyaaba Cycle (Deposition of Wyaaba Beds)	C	Phase 4	Vadose caves	Mature	24-25		
7.1							(25-26)		
11.2	Middle Miocene			Phase 3	Tufagenic / ?vadose caves		(25-26)		
14.8									
15.4							(26-27)		
15.8				? ⇧ ? ?	? ⇧ ? ⇧ ?				
16.4			B	Phase 2	Vadose caves	Early	27-28		
17.5	Early Miocene								
18.6									
20.6							(28-30)		
22.5									
23.3				? ? ?	? ? ?	? ? ?			
23.8		Erosional — Late Bulimba Cycle	A	Phase 1	Tufagenic		(31-32)		
?	Late Oligocene								
25		Pine Creek Upwarp							
?							33-34		
30									

Figure 7.1: The 'Big Picture' of tentative correlation of events during the 4-phase model of geological development at Riversleigh with the regional geological record, palaeoclimatic cycles and global temperature changes during the middle Tertiary. The tufagenic event of Phase 1 is tentatively correlated with the Pine Creek Upwarp of the late Oligocene. Phase 3 is correlated with the extreme 'greenhouse' peaks of the middle Miocene optimum. Dashed lines indicate tentative correlations or temporal boundaries of events. Periods during 'greenhouse' peaks are marked in grey. Palaeolatitudes are as figured by Veevers (1984), inferred intermediate palaeolatitudes are in brackets. Time scale is from Berggren et al. (1995), faunal zones based on Archer et al. (1997), palaeolatitudes are from Veevers (1984), southern oscillation 'greenhouse' cycle peaks are from McGowran and Li (1994) and global temperature curve is modified to fit diagram after Barrett (2003).

Oligo-Miocene. These include tectonic processes during the Pine Creek Upwarp, the northward drift of the Australian continent into modern tropical latitudes and the 'greenhouse/icehouse' climatic fluctuations in the geological record (see Section 2.3). Relationships between events at Riversleigh and the Tertiary record are summarised in Figure 7.1.

McGowran and Li (1994) suggested that 'greenhouse/icehouse' fluctuations during the early and middle Miocene could correspond to processes occurring at Riversleigh because 'greenhouse' conditions were conducive to flourishing biotas and widespread deposition and 'icehouse' conditions characterised by depositional hiatus and relative loss in diversity of biotas. They regarded processes at Riversleigh as reflective of this trend because according to Megirian (1992) primary deposition had taken place in the Miocene during prevailing 'greenhouse' conditions. To accommodate the arid climate invoked by Megirian (1992), McGowran and Li (1994) suggested that climatic fluctuation within the overall Miocene climatic regime at a scale too small to be detected by the geological record was responsible for the occurrence of 'icehouse' conditions during a 'greenhouse' stage. Primary deposition was thus considered to have occurred during a relatively dry time and subsequent karst processes during more extreme 'greenhouse' conditions as the Miocene progressed.

However, Riversleigh vertebrate correlation indicates that the primary depositional phase occurred in the late Oligocene, which was characterised by 'icehouse' conditions, providing a more parsimonious interpretation of palaeoclimatic setting. Furthermore, tectonic activity during the Pine Creek Upwarp has been identified here as a process that may have played a key role in primary deposition, rather than climatic conditions.

The development of fluvial barrage systems is not restricted climatically. Modern systems occur in arid, temperate and tropical areas (Ford and Pedley 1996). Specific palaeoclimatic conditions need not be invoked to accommodate the Riversleigh fluvial barrage depositional model.

Pedley et al. (1996) recognised some morphological distinctions between fluvial barrage systems from cool temperate climates (Britain) and those from warmer, semi-

arid climates (Spain). Barrage systems in warmer drier climates are characterised by rapid growth of tall, narrow dams, deep barrage ponds, poor preservation of organics (including pollen) and absence of sapropel. In temperate climates barrages form more slowly generating wider dam profiles with broad bases, shallower barrage ponds and organics and sapropels are preserved well. Warm dry conditions promote rapid dam growth because of the combined effects of evaporation and higher metabolic rates of plants and algae mediating precipitation. More prolific flow in wetter conditions promotes more rapid infill and incision cycles (*ibid.*).

Carthew *et al.* (2003) showed that in seasonal tropical river systems such as the modern Gregory River, annual floods tended to flush infill accumulations from behind fluvial barrages, and thus that the presence of infill deposits in preserved barrage systems could be considered indicative of an absence of powerful flood conditions while the barrage system was active.

During the late Oligocene, the Australian climate was dominated by the relatively cooler, drier conditions of an 'icehouse' interval (McGowran and Li 1994), which is also reflected in the poor sedimentary record from the Karumba Basin from this period (Smart *et al.* 1980). Riversleigh was situated in the modern warm temperate zone at approximately between 31°S-34°S (see Figure 7.1).

The lithology of the late Oligocene Phase 1 deposits at Riversleigh suggests, when interpreted as fluvial barrage deposits, that cyclic infill and incision was a dominant process. The absence of indicators of deep lacustrine conditions, the poor preservation of organics and the abundance of reworked tufagenic material suggest that short-lived, relatively shallow barrage basins may have been dominant. Because barrage morphology has not been observed, it is not possible to ascertain whether barrages were broad or narrow. Possible reasons for the lack of recognition of barrages in the field discussed in Chapter 9. Prevalence of infill and incision processes could indicate ample flow contributing to rapid fill that characterises systems in temperate climates (i.e. maintained by relatively high precipitation), under stable low-energy conditions that were not punctuated by high-energy flow conditions that flush infill from barrage systems in the modern seasonal tropics. The lack of preserved organics could be

interpreted as indicative of drier climatic conditions. Given that the late Oligocene climate is considered to have been relatively cooler and drier, tectonic activity (of the upwarp model) is considered to be the process more likely to have initiated and regulated depositional flow rather than climatic conditions such as high rainfall.

Although relatively warm and wet conditions followed in the early Miocene, no surface deposits are known from this time, and the Riversleigh geological record during this period is dominated by vadose cave deposits, indicating a drop in water table level since the late Oligocene. While this is a reverse of the trend expected by McGowran and Li (1994), attrition outpacing surface depositional processes would be expected as conditions became more humid and the Riversleigh area entered latitudes equivalent to the modern sub-tropics. By the early Miocene Riversleigh was positioned at between 30°S and 28°S (see Figure 7.1). Furthermore, the development of karst hydrogeology, characterised by drainage of the surface by the epikarst to the subsurface system might be expected to restrict the capacity of surface flow regimes to form substantial deposits.

The middle Miocene Phase 3 deposits are structurally and texturally similar to those of Phase 1. A raised water table is considered to be the most likely cause of Phase 3 tufagenic deposition (see Section 6.4). While there is no evidence of contemporaneous tectonic activity in the region as in the late Oligocene, the middle Miocene is marked by the Miocene climatic optimum, during which 'greenhouse' conditions peaked at about 15-16Ma (McGowran and Li 1994) when Riversleigh was situated at approximately 28°S -25°S (see Figure 7.1), which is in the modern sub-tropical latitudes.

The tufagenic deposition of Phase 3 could be tentatively correlated with this event. Markedly increased rainfall could have raised the water table and initiated exsurgences from high points in the karst terrain. Alternatively, disruption of flow through the system by blockage of subsurface drainage with sediment and debris or damming of flow downstream by tufagenesis could also have caused raised water table level. However, because tufagenic deposits that post-date the late Oligocene are known only from the middle Miocene of Gag Plateau, this could indicate that Miocene tufagenesis at that level in the profile was a rare event that coincides with the extreme climatic conditions of the middle Miocene. Because middle Miocene deposits of this type have

so far only been identified at Gag Plateau, deposition during this period may have been limited by the relatively brief timing of the tufagenic episode(s), or because of physical restrictions of the karst terrain morphology.

Because middle Miocene Zone C faunas occur in both tufagenic and vadose cave deposits and their precise age relationships are uncertain, they may indicate that there was fluctuation between tufagenic and vadose karst dominated conditions. The twin-peaked middle Miocene optimum of McGowran and Li (1994; Figure 7.1) is characterised by oscillation of the extreme greenhouse conditions prevailing at the time, which may have affected the dominant depositional processes at Riversleigh by raising and lowering the level of the water table.

Relative to palaeoclimatic conditions occurring in the early Miocene, the occurrence of the tufagenic event in the middle Miocene follows the pattern of deposition expected by McGowran and Li (1994). Furthermore, only vadose cave deposits containing early-late Miocene Zone C faunas post-date this event, indicating a return to low water table conditions and limitation of net deposition at the surface. Combined with changes in the composition of vertebrate faunas from this time (Archer *et al.* 1994, 1997, 1999, Myers et al. 2000, Myers 2002), these conditions may be correlated with the gradual shift toward 'icehouse' conditions that prevailed throughout most of the Tertiary and Quaternary and conform to the expected pattern of depositional processes.

Frank (1975) discussed interpretation of palaeoclimatic conditions during the formation of cave deposits by recognising whether speleothems occur with dry clastic deposits (entrance facies) or with deposits indicating abundant water (i.e. subaqueous deposits; see Section 4.3). Cave deposits at Riversleigh contain combinations of deposits that characterise the interior of the upper vadose zone (*sensu* Osborne 1986) including clastic debris deposits, flowstones and other subaerially formed speleothem and subaqueous deposits. All of these facies types implicate the involvement of water during their formation. It is not possible to resolve palaeoclimatic conditions based on the available data from these deposits. Detailed study of individual cave deposits may provide further insight into conditions affecting depositional processes in caves at Riversleigh during the middle Tertiary. Further study of Riversleigh cave deposits may

determine whether the variations between deposits formed in vadose and phreatic conditions in the Miocene karst at Riversleigh could be considered as reliable indicators of changes in palaeoclimate during that time.

7.2 Pattern of karst terrain development at Riversleigh during the middle Tertiary

Landscape evolution processes in karst terrains have been modelled in systems dominated by solution doline development (Ahnert and Williams 1997) and fluvial drainage (Kaufmann 2002). These processes result in the development of complex, topographically-variable landscapes. Denudation is considered a significant process in the development of landforms and the rate of carbonate attrition which may occur at twice that of non-carbonates (Kaufmann 2002).

The original lateral extent of the primary carbonates at Riversleigh is difficult to determine with great certainty. The pattern of residual carbonate outcrops in the modern Riversleigh landscape can be interpreted as having been derived from an originally thicker and more laterally extensive outcrop of carbonate that has been subject to ongoing attrition by processes of corrosion and erosion by the Gregory drainage system since the cease of primary deposition.

Figure 7.2 is a hypothetical reconstruction of the pattern of attrition of the original distribution of Tertiary carbonate by these processes based on the distribution of residuals as indicators of patterns of erosional drainage channels and the solution-dominated karst terrain development models of Ahnert and Williams (1997) and Kaufmann (2002). By considering the modern residuals to be represent the axes of original topographic highs, a pattern of polygonal high and low points can be reconstructed. Increasing the lateral extent of carbonate around these high points at successive stages through time between the present and the late Oligocene (by an arbitrary amount) produces a sequence of landscape evolution dominated in the early stages by the development and expansion of large solution structures. The polygonal pattern is similar in scale and morphology to polygonal patterns of the Serranx karst in Belize and the Guilin karst in China (see Figure 4.21).
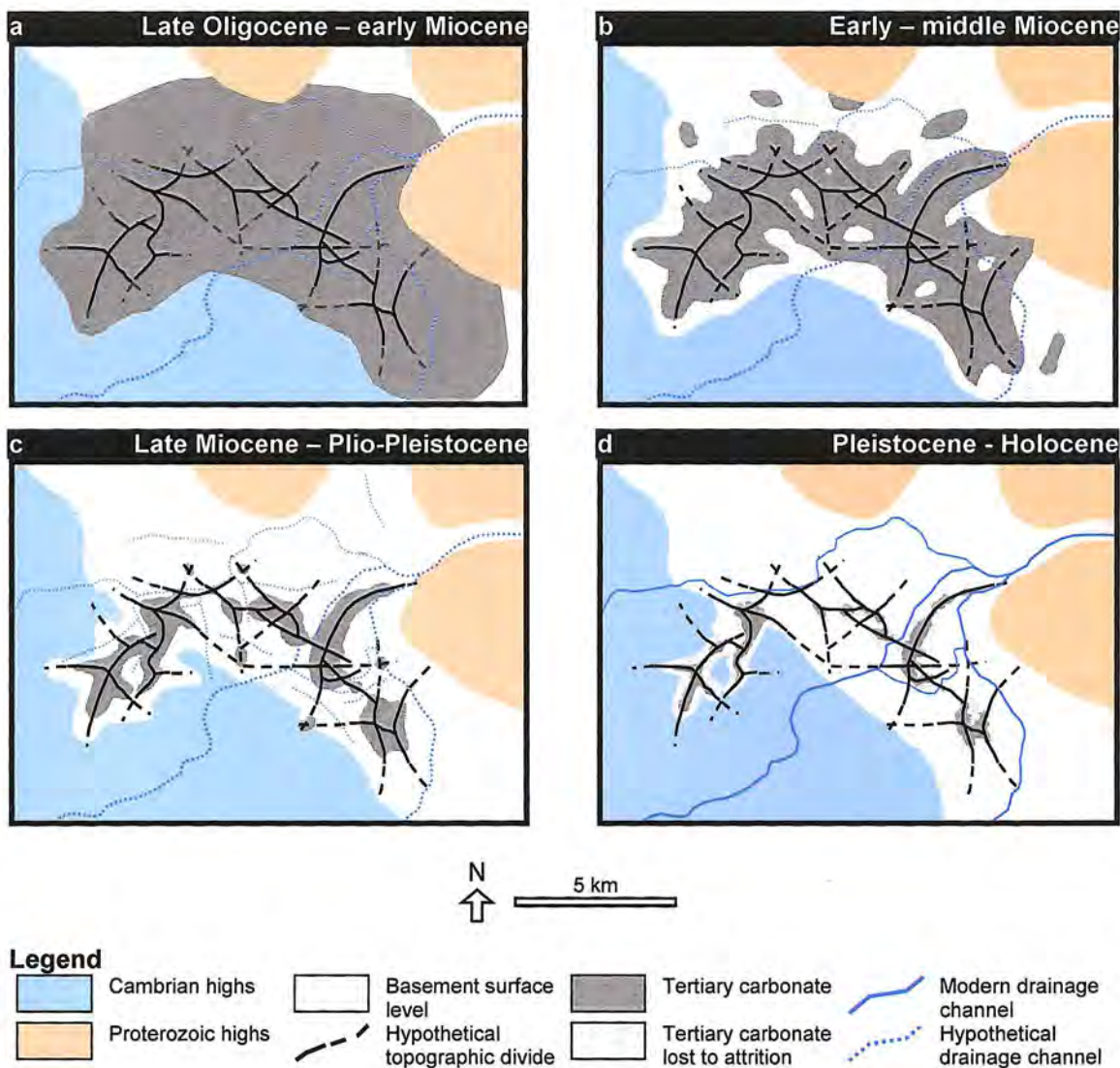
Figure 7.2: Simplified reconstruction of original extent of primary Tertiary carbonate at Riversleigh by hypothetical reversal of patterns of fluvial erosion and denudation. Modern residuals are interpreted as original high-points that were originally topographic divides, and the axes of these divides are reconstructed using solid and dashed lines. The modern drainage channels are considered to approximate paths of major surface channels that may have been active throughout the Tertiary. a) Original extent of carbonate of up to 70m thickness thinning toward the north and east and bounded to the south and west by Cambrian highs. During this time, only major drainage channels are considered to have occurred on the surface and the majority of drainage flow would have been underground. Corrosion would have been the dominant process shaping the landscape. b) Denudation causes deepening and lateral attrition of low points between topographic divides. Combined with erosion by surface flow, a topographically-variable dissected landscape is produced. During the early Miocene there may have been variability in topography may have peaked. The thinner parts of the Tertiary cover are reduced or lost by this time. c) Late Miocene to Plio-Pleistocene. Tertiary residuals are shaped by a combination of ongoing denudation and fluvial erosion by drainage channels in the emerging basement. Low points now dominate the landscape. Deposition of alluvial deposits occurs on the corrosion plane during the Pliocene. d) Pleistocene to Holocene dominated by ongoing erosion and alluvial deposition by the Gregory River system. As the drainage system has matured, the number of tributaries draining into the major channels has decreased.

According to this reconstructed estimate and the estimates of tufa depositional rates in Section 4.4.5, the original extent of deposits by the end of late Oligocene Phase 1 deposition could have been between 10-20km x 10-20km or 100 to 400 km^2. During the early Miocene, when the primary deposit was thicker and overland flow might have been more limited, solution may have dominated landscape development. The process of overland drainage capture in a subsequently solution-dominated landscape (i.e. Williams 1971, see Figure 4.20) could have influenced the early development of the karst terrain at Riversleigh. While the major drainage channels (i.e. palaeo-Gregory palaeo-O'Shanassy) might have deeply incised the primary deposit from the outset, lowering the water table and allowing vadose conditions to prevail in cave environments, most of the surface may have been relatively dry because the epikarst would have drained directly into a dissolutional drainage system which in turn drained into the major drainage channels.

By the middle to late Miocene, ongoing denudation would have resulted in the dominance of low-points in the landscape, and fluvial erosion by the developing surface drainage system may have played an increasing role in the shaping of the landscape as basement level was gradually exposed. The pattern of dissected remnants of the Tertiary carbonate may have been established by this time. Over time, as the Gregory River drainage system matured and the number of tributaries diminished, isolated residuals have been further reduced by ongoing denudation and erosion.

7.3 Effects of karst landforms and development patterns on palaeoenvironments and the accumulation of fossil faunas: the karst environment mosaic model

Archer *et al.* (1989, 1994, 1997) suggested that the composition of early Miocene faunas at Riversleigh, combined with relatively warm wet early to middle Miocene climatic conditions, were indicative that widespread vegetation comparable to modern wet forest or rainforest existed at Riversleigh. Archer *et al.* (1994) considered early Miocene faunas from Riversleigh to be comparable to faunas from modern rainforest because of the high diversity of species present, the presence of apparently complex feeding guilds of terrestrial and arboreal leaf eating mammals indicating high diversity

of resources and vegetation types, the dominance of browsing (and absence of grazing) marsupials and the presence of groups with modern representatives that are restricted to rainforest communities. While this scenario correlates with palaeoclimatic reconstructions of McGowran and Li (1994), there are no plant fossils from Riversleigh from this period that support this interpretation.

Habitats and depositional environments in modern karst landscapes are influenced by distinctive drainage, landform and development patterns that are related to the topographic variability of those terrains (see Section 4.3.4). This may have contributed to some of the differences between Riversleigh faunas that accumulated in vadose cave environments and tufagenic environments and may be particularly relevant to consideration of some of the possible causes of the apparent high diversity of early Miocene Zone B mammalian faunas compared to Zone A faunas and to the apparent decrease in diversity of mammalian faunas of Zone C throughout the middle to late Miocene. Processes occurring in topographically variable karst terrains that are relevant to differences between faunas from tufagenic and vadose cave deposits include:

1. The effect of variations in landform and topography on the distribution of different environments (i.e. comparable to 'upper' and 'lower' environments in modern karst landscapes).

2. The effect of the pattern of denudation and corrosion on the resultant distribution of landforms and associated environments.

3. The implications of denudation and landform development for the type of environment that supplied fauna to these cave deposits.

The extent of the effect (if any) of the patterns of distribution of different environments on the nature and distribution of components of vertebrate (particularly mammalian) faunas is not known. However the potential for such an influence should be recognised when considering issues of faunal composition and diversity during the Miocene at Riversleigh.

The karst environment mosaic model showing topographic control of the hypothetical distribution of adjacent environments and depositional environments in an early Miocene karst terrain at Riversleigh is illustrated in Figure 7.3 and Figure 7.4.
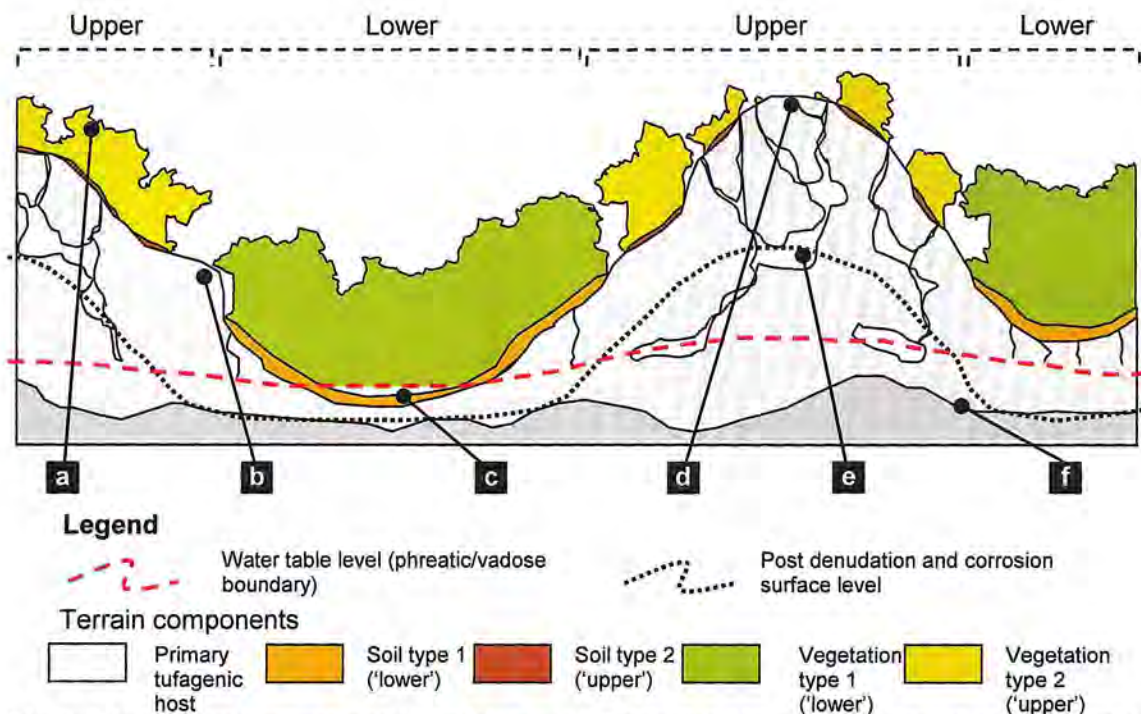
Figure 7.3: Karst environment mosaic model showing distribution of 'upper' and 'lower' environments in hypothetical young karst terrain at Riversleigh in the Miocene. 'Lower' environment is humid and wetter, with flowing and standing water available in low points at or below water table level; soil cover is thicker and more continuous with dominance of clay, vegetation cover is more continuous with dominance of certain tree species and presence of taxa that are uncommon or absent from upper environment. 'Upper' environment is characterised by thinner, more discontinuous soil cover different to soil of the lower environment, relatively drier surface conditions and vegetation is characterised by dominance of certain tree taxa and taxa favouring relatively dry conditions, with exposed rock surfaces favoured by shrubs, herbs and crevice-dwelling plants. a) More discontinuous canopy cover caused by stunted trees and discontinuous soil and vegetation distribution. b) Mid-slope cliff with exposed rock and associated vegetation. c) Drainage channel/standing pool of water fed by runoff or local exsurgences, inhabited by aquatic taxa. d) Exposed rocky crest with open fissures. e) Caves open to 'upper' environment via the epikarst. These deposits are preserved at the modern denuded surface level, whereas other components of the terrain would be lost to denudation and corrosion. f) Cambrian/Proterozoic basement.
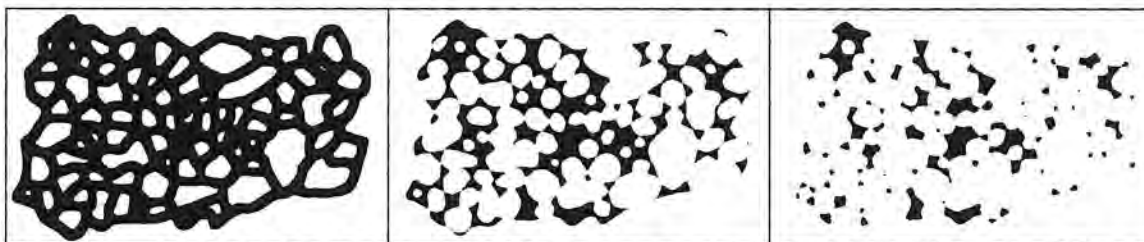
Figure 7.4: Diagram illustrating pattern of low point expansion and high-point retraction during advanced stages of karst terrain development and the effect on the distribution of associated 'upper' (black) and 'lower' (white) environments. The pattern of high-points is from the example polygonal karst pattern of the Darai Hills in New Guinea (Figure 4.20) from Ford and Williams (1989). The first stage could be comparable to a highly variable terrain at Riversleigh during the early Miocene, with more evenly balanced distribution of 'upper' and 'lower' habitats, supporting a diversity of communities. The second stage could represent a middle Miocene landscape in which doline expansion has caused low-points and their environments to dominate and high-point 'upper' environments have retracted and become fragmented, causing a possible decrease in diversity in mammalian faunas. The final stage represents a possible pattern of development from the late Miocene to Holocene, in which 'lower' environments are almost totally dominant and high-point areas become scattered remnants. Vadose cave deposits that were open to 'upper' environments are preserved in these residuals.

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7.3.1 Variations in landform and topography in karst

A complex mosaic of adjacent 'upper'/'lower' type environments could thus have developed in the early Miocene terrain at Riversleigh. Even if the vegetation cover was not wet forest or rainforest, the highly variable topography that is typical of young tropical and sub-tropical karst terrains may have supported a diverse array of adjacent communities.

According to this model, aquatic taxa and possibly certain types of other animals would have favoured lower environments because aquatic environments would have occurred in channels and doline bases close to basement level while higher parts of the profile were well-drained. The relatively lower abundance and diversity of aquatic taxa in vadose cave deposits could be interpreted as evidence of this pattern of distribution (some reasons for representation bias are discussed below).

Large ectotherms such as meiolaniid turtles that require direct sunlight for thermoregulation (White 1997) could have made use of thinly covered or exposed rock outcrops that tend to be more prevalent in upper environments. This also applies to smaller ectotherms including snakes and lizards. These taxa are all well-represented in vadose cave deposits. Similarly, open areas within the vegetation structure may have provided habitat for animals such as *Emuarius*, which is considered intermediate between modern cassowaries that live in thick rainforest and emus that inhabit open environments (Boles 1997b).

The distributions of different vegetation types in 'upper' and 'lower' environments, particularly dominance of certain plant taxa (i.e. certain tree species on crests, and herbs and shrubs in areas of exposed rock), could have supported different kinds and combinations of specialised terrestrial and arboreal herbivores and omnivores (such as bandicoots that may have specialised in feeding on fruits, fungi and invertebrates associated with certain plants) that favoured these environments.

Thus it is possible that the relatively high diversity of Zone B faunas that accumulated during the early stages of karst development at Riversleigh could be related to the presence of a diversity of adjacent communities in topographically variable polygonal-

type karst terrain, rather than a single diverse community comparable to communities in modern wet forest or rainforest ecosystems. Investigation of modern ecosystems in karst could determine whether diversity of faunas is higher in topographically variable terrains that support mosaics of adjacent environments.

7.3.2. Effect of the denudation and corrosion pattern on environment mosaics

While the early Miocene terrain at Riversleigh could have supported a mosaic of different habitat types, the ongoing process of karst landform development would have altered the balance of distribution of these environments over time.

The decrease in mammalian diversity in Riversleigh Zone C faunas in the middle to late Miocene, compared to early Miocene Zone B faunas, has been related to the changes in climate and the gradual shift in dominance from forests to open drier environments throughout Australia during the latter stages of the Cainozoic (Archer *et al.* 1997, Myers 2002).

While the presence of certain early-late Miocene taxa at Riversleigh indicate that this process was influencing environments and faunas by that time (Archer *et al.* 1997, Myers *et al.* 2000), the middle Miocene is characterised by the middle Miocene climatic optimum, which, if greenhouse conditions were prime factors in the high diversity of early Miocene faunas, would be expected to have supported an equally diverse range of faunas in the middle Miocene. However, middle Miocene faunas are considered relatively less diverse (*ibid.*).

Aspects of ongoing karst processes during that time at Riversleigh may have played a part in the apparent decrease in relative diversity in faunas in the middle Miocene:

1. The widening of low-points and resultant retraction of high-points would have resulted in the retraction of 'upper' environments and expansion of 'lower' ones that may have resulted in a net loss of diversity as lower environments became more dominant in the landscape (Figure 7.2, 7.4). This pattern of habitat change may also be related to the decline or local extinction of some groups in the Riversleigh area.

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2. If climatic conditions favoured high rainfall in the middle Miocene, which may
   be responsible for the deposits formed during the tufagenic event of Phase 3,
   then high precipitation may have diminished some of the relative differences in
   dryness and vegetation distribution between 'upper' and 'lower' type
   environments, causing an overall loss in diversity. Crowther (1982) found that
   vegetation distribution patterns in karst terrains in West Malaysia that
   experience constant high rainfall did not differ significantly from areas with
   seasonal dryness, whereas vegetation type did vary with this aspect of climate.

Complexity of landforms and associated environments may thus have peaked in the
early Miocene during the early stages of terrain development, followed by a decline in
complexity as low-point areas and associated environments gradually became dominant
during the middle and late Miocene.

7.3.3. Denudation and corrosion pattern and environments supplying faunas to cave deposits

Another significant aspect of the pattern of doline expansion and inter-doline retraction
during karst development is the resultant distribution of preserved vadose karst
environments and possible bias of faunas represented. Residual landforms in a mature
karst terrain, such as that at Riversleigh, represent those parts of the profile that were
previously underlying the highest points in the landscape (i.e. see Figures 4.22, 6.11).

This means that cave deposits outcropping on modern residuals contain sediment and
fossils that accumulated through epikarst that was open to the highest points in the
landscape (inter-doline areas), and thus potentially to 'upper' environments (Figure 7.3).
This epikarst has since been removed by denudation. Deposits that may have formed in
the lower parts of the terrain (within dolines or on lower slopes and valleys) would have
been lost to denudation and erosion and thus not preserved. This could result in biased
representation in assemblages of taxa that favoured 'upper' environments of high-points
and under-representation of taxa that favoured 'lower' environments. The presence of
aquatic taxa in most spelaean faunas, possible reasons for which are discussed in
Section 5.3.4, may indicate that this possible bias is not so significant.

7.4. Differences between Riversleigh depositional environments that may affect composition of faunal assemblages

Differences in abundance and in diversity in Riversleigh faunas may be related to the different factors affecting accumulation of assemblages in tufagenic and vadose karst depositional environments and to the length of the time span(s) during which each environment was active.

The most obvious differences between Riversleigh faunas from tufagenic and vadose cave depositional environments are the relative abundance and diversity of certain kinds of taxa. Diverse and abundant aquatic taxa are considered indicative of tufagenic aquatic systems in the surface, abundant bats are considered indicate of cave environments. Some differences in representation of other taxa may be related to their favouring either of these environments because of suitability of habitat, food availability, etc. occurring proximal to or in each kind of depositional environment. Further detailed study of the biology and ecology of taxa and faunas may identify these kinds of relationships between taxa and depositional environment. Differences in apparent diversity may also be related to habitat bias in depositional environments (described above).

Tufagenic systems may have accumulated fossil assemblages relatively quickly over short periods of time, resulting in apparently lower diversity of faunas. Depositional environments that favoured fossilisation of vertebrates in fluvial barrage systems at Riversleigh may only have existed for periods in the order of 10^2 to 10^3 years, given that other extensive accumulations of these types of deposits are known have formed within periods of thousands of years, such as at Caerwys and Louie Creek (Pedley 1987, Drysdale 1995), see Figures 4.28 and 4.29. Suites of related tufagenic deposits at Riversleigh, particularly the Gag Plateau deposits, may represent time periods in the order of 10^3 or 10^4 years.

However, cave environments may have gradually accumulated fossil assemblages over longer periods, resulting in higher apparent diversity. Some cave environments may have been active for periods exceeding 10^6 years, possibly the entire Miocene. These

cave environments at Riversleigh may have been active intermittently throughout the period deposition occurred, or some may have been active for single spans of time that still exceeded the length of time during which Phase 1 and Phase 3 tufagenic depositional systems were typically active. These longer periods of accumulation could have included changes in local habitat, climate, ecosystems and evolutionary changes in the biota that may have influenced the occurrence and diversity of certain taxa and may have resulted in relative differences in diversity between faunas from cave and non-cave deposits.

	Fluvial barrage infill deposits	Cave deposits
Depositional time span	Shorter discrete events of 10^2 to 10^3 years	Longer, 10^3 up to and exceeding 10^6 years, intermittent or continuous accumulation
Depositional processes	Poorer conditions for preservation: exposure, mechanical damage, scavenging etc.	Better conditions for preservation: exposure restricted; fragile bones, articulation and associated skeletal parts more common
Position in profile and possible habitat bias	Low points, 'lower environment'	High points, 'upper environment'
Possible bias in represented taxa	Aquatic taxa	Bats and other cave-dwelling taxa

Table 7.1: Summary of possible influences of different depositional environments on fossil vertebrate faunas.

Conditions prevailing in different depositional environments may also have affected preservation potential and resulting faunal composition and diversity. Vertebrate material accumulating under fluvial conditions, albeit low-energy conditions in barrage ponds, would be subject to a greater degree of exposure to elements, scavenging and mechanical damage than material in cave environments. This could have resulted in higher preservation rates in cave deposits, particularly of rare taxa or fragile material. The apparently high representation of taxa with fragile skeletal components such as lizards, frogs and non-dromornithid birds, and the more frequent occurrence of articulated and closely associated skeletal parts in Riversleigh faunas from cave deposits could be a result of better conditions for preservation in caves.

7.5. Stratigraphic concepts in the Riversleigh karst system

The manner in which tufagenic systems can form deposits and basins under non-basinal circumstances by precipitation can produce sequences of deposits that do not necessarily conform to the laws of superposition that govern the interpretation and recognition of sequences of stratigraphy. Normally superposed stratigraphic sequence at Riversleigh has been automatically assumed in the past (i.e. Archer *et al.* 1989, 1994, 1997, Creaser 1997). Figure 6.8 shows that deposits yielding late Oligocene faunas are found throughout the profile at Riversleigh. The depositional models of tufagenic processes of Golubić (1969) and Pedley (1987) show that deposits of the same ages can form at different levels in the profile, deposits of different age can occur at the same level (and be adjacent) and deposits of younger age can form lower in the profile than older deposits. This is reflected in the Riversleigh fluvial barrage model, that illustrates how it is possible for younger deposits (including basal facies) to occur at basal level and lower in the profile than older deposits, and that the overall random effect of successive tufagenesis, incision and reworking can produce a highly variable array of different sequences in adjacent parts of the profile that cannot be correlated by normal means or the assumptions of superposition (see the different observable sequences in Figure 5.28). Problems in the field with interpreting stratigraphy at Riversleigh, particularly in terms of tracing beds and 'strata' are certainly related to the asynchrony of successions formed by the tufagenic process modelled here that does not comply with the assumptions of superposition. This concept also applies to suites of deposits from successive regimes.

The profiles of modern weathering surfaces at Riversleigh, that can often exhibit apparent 'stratification' because of distinctive dissolution patterns, can produce resultant observable sequences that may be completely different to the true sequence in which deposition occurred at that point (see Figure 5.28). While true physical sequences of deposits, the type 'Sequences' of Creaser (1997) may not necessarily reflect the true depositional sequence or age relationships of deposits in that profile, and cannot be correlated with other profiles either in terms of lithology or 'stratigraphic level' of deposits.

Additionally, karst processes can produce new depositional environments that further complicate sequences by forming new depositional environment in which deposition can occur at lower levels (by the formation of dolines), and by the development of caves in which younger deposits can be emplaced within older ones, and can have very complex depositional histories of their own.

As a result, assumptions should not be made about age relationships of deposits at Riversleigh based primarily on apparent position in a sequence or position in the overall profile. Deposits occurring at the bottom of the profile or at basal level, need not necessarily be assumed to be the oldest, nor those occurring higher in the profile the youngest. At the moment, vertebrate biocorrelation is the most reliable form of relative dating at Riversleigh. The terms 'early' and 'late' should be used rather than 'upper' and 'lower' when referring to biostratigraphy and depositional phases at Riversleigh, since these latter terms do not really apply to deposits at Riversleigh.

Recognition of these karst stratigraphic concepts can simplify the lithostratigraphic sequence of Archer *et al.* (1994), illustrated in Figure 2.11. In that sequence, the 'host' rocks of Zone B (System B) age contain Zone B cave deposits. These 'host' rocks do not exist, as all Riversleigh deposits containing Zone B faunas are cave deposits hosted by late Oligocene carbonates (Zone A). However, this relationship cannot be expressed in a column with time as the vertical axis. Temporal relationships of Riversleigh Tertiary carbonates can thus be expressed in a simple column, in which spatial relationships are not expressed. Spatial relationships, but not temporal relationships, can be illustrated in a simple schematic diagram (Figure 7.5).
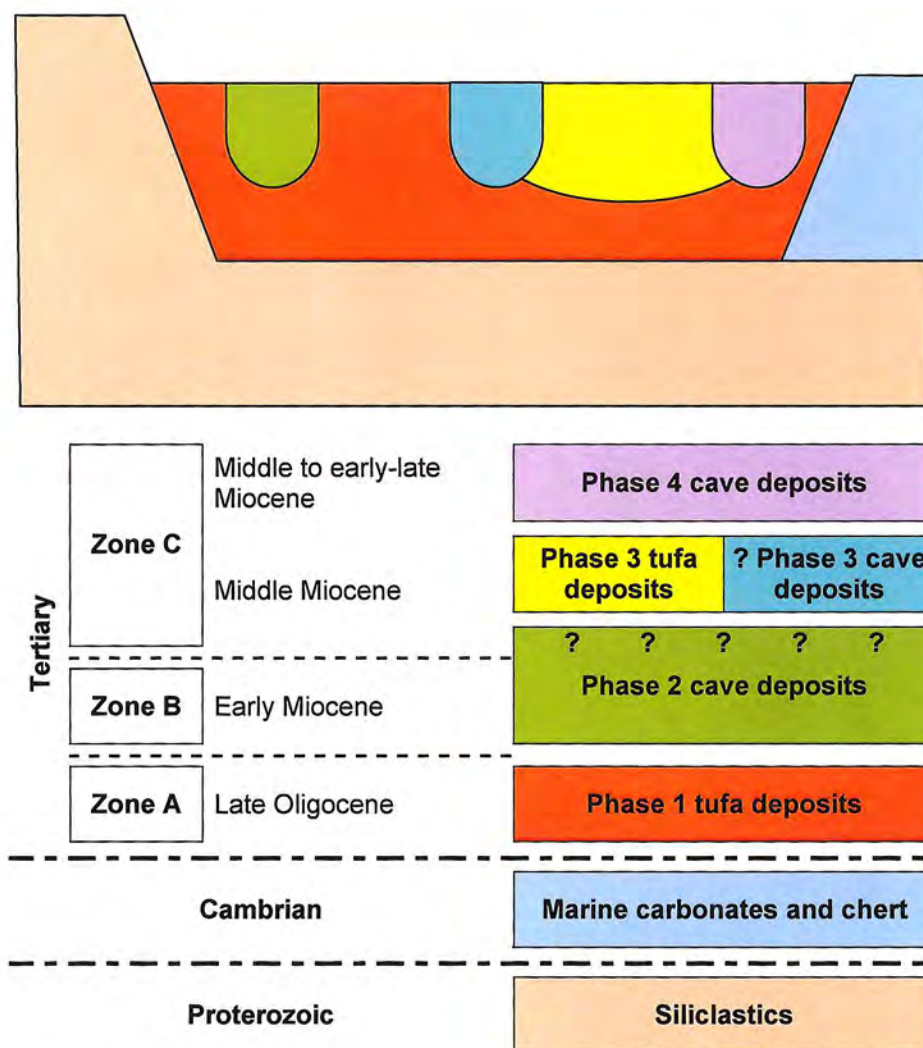
Figure 7.5: Revised spatial and temporal relationships of Riversleigh Tertiary karst stratigraphy. Schematic diagram shows physical interrelationships but not temporal relationships. The column shows temporal relationships based on vertebrate biocorrelation, but does not show spatial relationships (i.e. hosting of cave deposits within older deposits).

Chapter 8

Revised interpretation of the Carl Creek Limestone

The Riversleigh Tertiary carbonates were named by Jack (1896) as the Carl Creek Limestone. The Carl Creek Limestone is interpreted here as a freshwater carbonate deposit comprised primarily of intraclast and micritic tufa of late Oligocene age, and relatively limited outcrops of middle Miocene age; and cave deposits ranging in age from early to early-late Miocene (ages based on Archer *et al* 1997). Using the limestone classification scheme of Dunham (1962), these lithologies can also be interpreted as conglomerates and breccias comprised of calcarenites, calcwackes and calclutites (Megirian 1992). Outcrops of Carl Creek Limestone occur on Riversleigh Station west of the O'Shanassy River and south of Verdon Creek (these deposits are mapped as Riversleigh Tertiary carbonates in Figure 2.3). Because other carbonate outcrops mapped by Megirian (1992) occurring to the north of this area along the Gregory River have not been dated or sampled, it is unclear whether they belong to the Carl Creek Limestone or were formed by some other depositional events or process(es), such as more recent tufagenesis.

Chapter 9

Weaknesses of interpretations and models in this work

9.1 Restrictions of field conditions

Some of the interpretations and models presented in this work are restricted by the limitations of conditions in the field. Not all outcrops of Tertiary carbonates have been observed. Most work was restricted to outcrops within the Riversleigh World Heritage Area in the west of the Riversleigh area. The interpretation of the age and geology of the more easterly mesas relies upon Megirian (1992).

The constraints of field conditions have restricted extensive sampling of individual deposits for petrological analyses. Many outcrops are remote and difficult to access. Because individual deposits at Riversleigh contain diverse and complex lithologies, not all features of deposits may be represented.

9.2 Vertebrate biocorrelation

The ages of some Riversleigh faunas are not certain, there has been because insufficient sampling and because dating is based primarily on vertebrate correlation and stage of evolution comparison between taxa at Riversleigh and taxa from other fossil faunas in Australia. There is an inherent degree of uncertainty in these biocorrelation methods. Faunas and depositional events cannot be placed into a temporal framework with absolute confidence until some other form of independent method of dating can be implemented.

9.3 Fluvial barrage structures not observed

Although several lines of evidence including lithology, depositional structure and taphonomy are considered to indicate that tufagenic fluvial barrage systems were the dominant depositional mechanism at Riversleigh during Phases 1 and 3, tufa barrage structures or associated characteristic macrophytic and microphytic tufa facies have not been observed in the field. This absence of evidence is not considered a falsification of the model, especially when the strength of evidence leading to the interpretation is taken into account. The presence of relict barrage and pond structures is difficult to discern in

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the field. Drysdale (1995) stated difficulty discerning tufa facies in *in situ* Pleistocene tufa deposits that were well-preserved but no longer in depositional context. At Riversleigh, barrage structures may not be detectable or have not been recognised for the following reasons:

- Barrages may have been small and narrow, and are thus less likely to be detected. Because barrages can form ponds and lakes that are very large, they would comprise only a very small proportion of the entire deposit compared to infill facies.

- Barrages may have been eroded and denuded substantially after incision.

- Previous identifications of depositional structure of preserved fluvial tufa barrages (i.e. Pedley 1987) and travertine deposits (Chafetz and Folk 1984) were possible because of examination of extensive quarry faces that had been cut through the deposits. These deposits are also much younger that those at Riversleigh and retain a lot more detail of original structure and morphology. Lack of clear exposures of profiles and the obtuse intersection of depositional structures by modern weathered surfaces adds significantly to the difficulty of recognising primary depositional structures such as barrages.

- Barrage lithology may be very similar to the barrage pond fills (i.e. comprised of intraclast tufa rather than macrophytic and microphytic tufa) so that distinction between structures is not apparent by lithological variation.

- Post-diagenetic processes may have made lithology or structure difficult to identify by dissolution.

- The lithological interpretations and depositional model presented here are incorrect and there are no fluvial barrages.

While fluvial barrage systems have been interpreted as the depositional mechanism responsible for the accumulation of some extensive tufagenic deposits (Pedley 1987, 1993, Drysdale 1995), there is no precedent in the literature for fluvial barrage deposition at the scale depicted here for the middle Tertiary of Riversleigh. This may be related to the under-representation of tufagenic processes and deposits in the literature for reasons outlined in Section 4.4.6. Other deposits of similar or even larger scale could exist, but may have already been interpreted differently, as in the case of the fluvio-clastic interpretation of the Riversleigh carbonates of Megirian (1992), or have otherwise not been recognised.

The imperfection of the geological record and the nature of diagenetic and post-diagenetic processes in terrestrial carbonates may exclude the possibility of barrages being readily detectable in deposits of pre-Pleistocene age. Consideration should thus be given to the prospect that that the diagnosis of pre-Pleistocene fluvial barrage systems could be made on the basis of lithological, petrographic, depositional and faunal criteria used in this work, which does not include the identification of actual barrage structures.

Chapter 10

Conclusions

Viable lithological interpretations and modelling of depositional processes of the Riversleigh middle Tertiary carbonates can be formulated by the application of concepts and processes relating to karst systems. Previous interpretations that have regarded Riversleigh lithotypes and depositional processes as carbonate analogues of those occurring in siliclastic systems have faced serious challenges and inadequacies.

The Riversleigh 'System' biocorrelative concept of Archer *et al.* (1989, 1994, 1997) was developed in recognition of this difficulty, and has been revised here by division into a biostratigraphic faunal zone component and karst stratigraphic depositional phase component.

Diagnostic geological and palaeontological criteria have been recognised here that can be used to distinguish two major facies types at Riversleigh: primary heterogeneous carbonate host deposits and cave deposits. The interpretation of the primary heterogeneous carbonate host as forms of tufa, and the diagnosis of flowstone and speleothem in cave deposits play crucial roles in identifying these main kinds of deposits at Riversleigh.

Interpretations of the depositional environments of the major lithofacies from Riversleigh, age relationships of deposits determined by vertebrate biocorrelation and understanding of processes occurring in karst systems can be used resolve a chronological sequence of 4 depositional phases at Riversleigh throughout the middle Tertiary. These phases can be related to regional events including tectonics, climatic change and the northward drift of the Australian continent into sub-tropical and tropical latitudes.

Tufagenic deposits of Phase 1 are considered to have been deposited in a cyclic fluvial barrage system. This lithotype comprises the majority of deposits at Riversleigh and contains Zone A fossil vertebrate faunas from the late Oligocene. The fluvial barrage depositional process can account for the indicators of low-energy conditions in these

deposits, the abundance of reworked intraclasts as a function of cyclic infill and incision, and the absence of siliclastics from most of the system, apart from basal facies. Deposition may have occurred as a result of the raising of the Barkly Tableland by the Pine Creek Upwarp in the late Oligocene.

Deposits containing Zone B early Miocene faunas are vadose cave deposits, and indicate by the early Miocene the water table had lowered fluvial barrage depositional had ceased. The Riversleigh landscape might have been comparable to young karst terrains in the modern tropics and subtropics, where corrosion is a dominant force that shapes the landscape. Complex mosaics of environmental conditions, typical of these terrains, may have developed in the Riversleigh karst landscape, and could have contributed to the apparently high diversity of vertebrate faunas at Riversleigh from this time.

Limited outcrops of tufagenic deposits on parts of Gag Plateau that contain middle Miocene Zone C faunas are considered comparable to the Phase 1 fluvial barrage deposits of Phase 1. These Phase 3 deposits are interpreted as having been formed by high water table conditions, and may be tentatively correlated with the middle Miocene climatic optimum (McGowran and Li 1994). Some vadose cave deposits also appear to date from this time, indicating the possibility of complex processes involving raising and lowering of the water table during this time. These deposits require further detailed investigation.

Vadose cave deposits of Phase 4, and the apparent absence of tufagenic deposits that post-date the middle Miocene, indicate a return to stable low water table conditions until the Holocene. The pattern of karst terrain development might have progressed from a complex undulating dissected terrain in the early Miocene, to a landscape dominated by low-points as these areas expanded and topographic highs-retracted due to attrition by corrosion and fluvial erosion. These changes in the landscape, as well as ongoing climatic and environmental change in Australia, could have contributed to apparent changes in diversity and composition of vertebrate faunas at Riversleigh throughout the Miocene.

The recognition of depositional phases and their characteristic processes during the middle Tertiary at Riversleigh provides framework that is useful for the interpretation of individual fossil deposits, fossil faunas and environmental conditions throughout that time. The sequential patterns of depositional processes recognised here can be useful for temporal correlation of fossil deposits. Some of the differences in diversity and composition of faunas between faunas of different ages at Riversleigh may be attributed to differences between depositional environments (such as cave or non-cave) and changes in the karst terrain as the landscape developed over time from a topographically-variable young terrain comparable to modern young karst terrains in the tropics and sub-tropics, to a mature terrain characterised by isolated residuals on a corrosion plain. The most diverse Riversleigh faunas tend to originate from cave deposits, which may be the result of longer time periods during which accumulation occurred and better preservation potential than tufagenic deposits, from which relatively less diverse faunas tend to originate. Tufagenic depositional environments would have been characterised by shorter depositional time-span and poorer preservation potential.

The Riversleigh middle Tertiary deposits are very complex, and further study of both the wider geological picture and details of individual deposits and fossil vertebrate faunas is required in order to test, clarify and expand aspects of the patterns described here.

Chapter 11

Some recommendations for further research

Understanding of general depositional processes at Riversleigh during the middle Tertiary would benefit from more detailed investigation Riversleigh Tertiary deposits at a wider scale. More detailed mapping of geological boundaries and the distribution of basal facies would clarify the nature of the primary depositional environment. The observation of barrage structures should be attempted, while recognising the inherent difficulties of such a task. There may be clear diagnostic indicators of fluvial barrage processes occurring in modern systems that could be useful at Riversleigh in addition to those applied here other than the identification of barrage structures themselves. More detailed study of individual fossil deposits would be useful for testing and application of the depositional phase concept.

Investigation of lithology and whether fossil vertebrates are present in the carbonate outcrops to the northwest of Riversleigh that were mapped as Tertiary by Megirian (1992) would help determine whether they are of Tertiary age. A better understanding of these deposits could help clarify the processes that occurred in the Riversleigh area at that time and may extend the vertebrate fossil record.

The geology of Gag Plateau requires more detailed mapping and investigation in order to better understand the relationships and nature of deposits occurring there.

Accurate mapping of cave deposits could assist with understanding nature of speleogenetic processes that occurred at Riversleigh during the Tertiary, and may clarify aspects of processes and palaeoenvironmental conditions.

Faunal analyses may also clarify aspects of taphonomy and palaeoenvironments. It would be useful to attempt to quantify the qualitative concept of the apparent domination of certain faunas by aquatic taxa, which while based on the wisdom of experience, is in part based also on intuition. More detailed comparisons of faunal elements of similar and different ages can test the hypotheses that faunas reflect

palaeoenvironmental conditions related to both the mode of deposition and to prevailing karst processes in the landscape at the time of accumulation of assemblages.

The nature of any role of environmental variation in karst terrains in affecting the diversity of mammalian faunas would also be useful for the interpretation of Riversleigh palaeoecology and palaeoenvironments. For example, comparisons with possible modern analogues of the Riversleigh middle Tertiary landscape, such as the Darai Hills in New Guinea may provide useful data.

Understanding of Riversleigh faunas and geology would benefit greatly from absolute dating methods, which have been elusive so far. Geological processes occurring elsewhere that may have been contemporaneous with events at Riversleigh could provide tentative age-ranges. For example, dates obtained from volcanics related to the Pine Creek Upwarp may help provide a figure for tentative maximum age limit to Riversleigh Zone A faunas. Current methods of dating flowstone provide maximum age ranges that do not extend to the middle Tertiary. Investigation of whether detailed understanding of stratigraphy of cave deposits could be used to identify patterns from existing geological records, such as palaeomagnetism, could provide dating mechanisms.

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Appendix A

Supplementary petrography of representative Riversleigh middle Tertiary deposits.
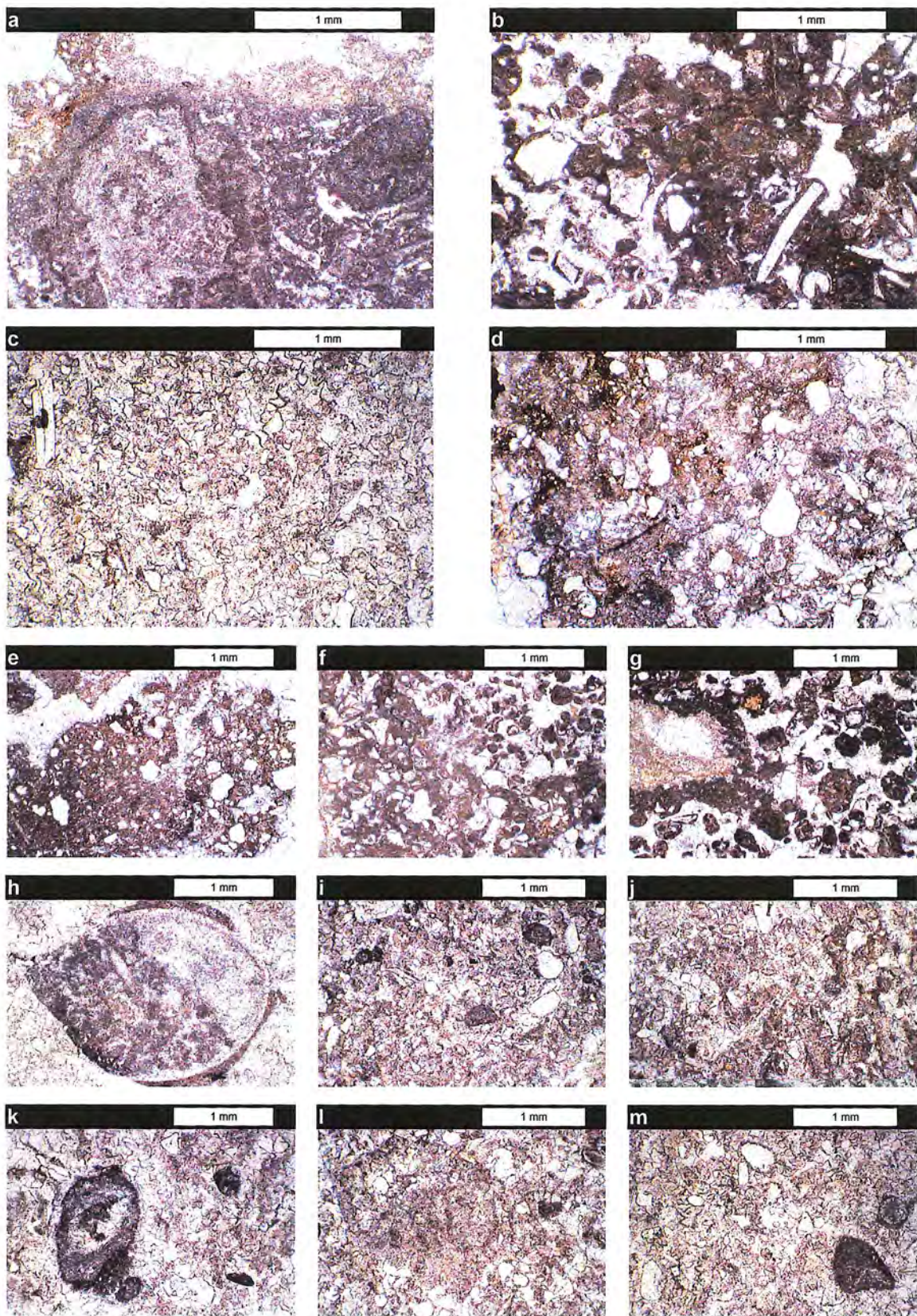
Figure A.1: Representative lithologies from the tufagenic deposit at White Hunter Site. a) Laminar micrite around intraclast with irregular voids (PP; EP74). b) Particles including intraclasts and shell fragments coated with micrite (PP; EP74). c) Arenaceous texture with siliceous sand and bone fragments (PP; R150). d-f) Arenaceous texture with siliceous sand grains (PP; EP74). h) Gastropod or ostracod partially filled and coated with bio-precipitated micrite in coarse crystalline matrix. The shell has been replaced with calcite 'ghost' that may indicate that this deposit has been weathered or recrystallised. i-m) Coarse crystalline texture with tufaceous intraclasts, sand and bone fragments and irregular voids.
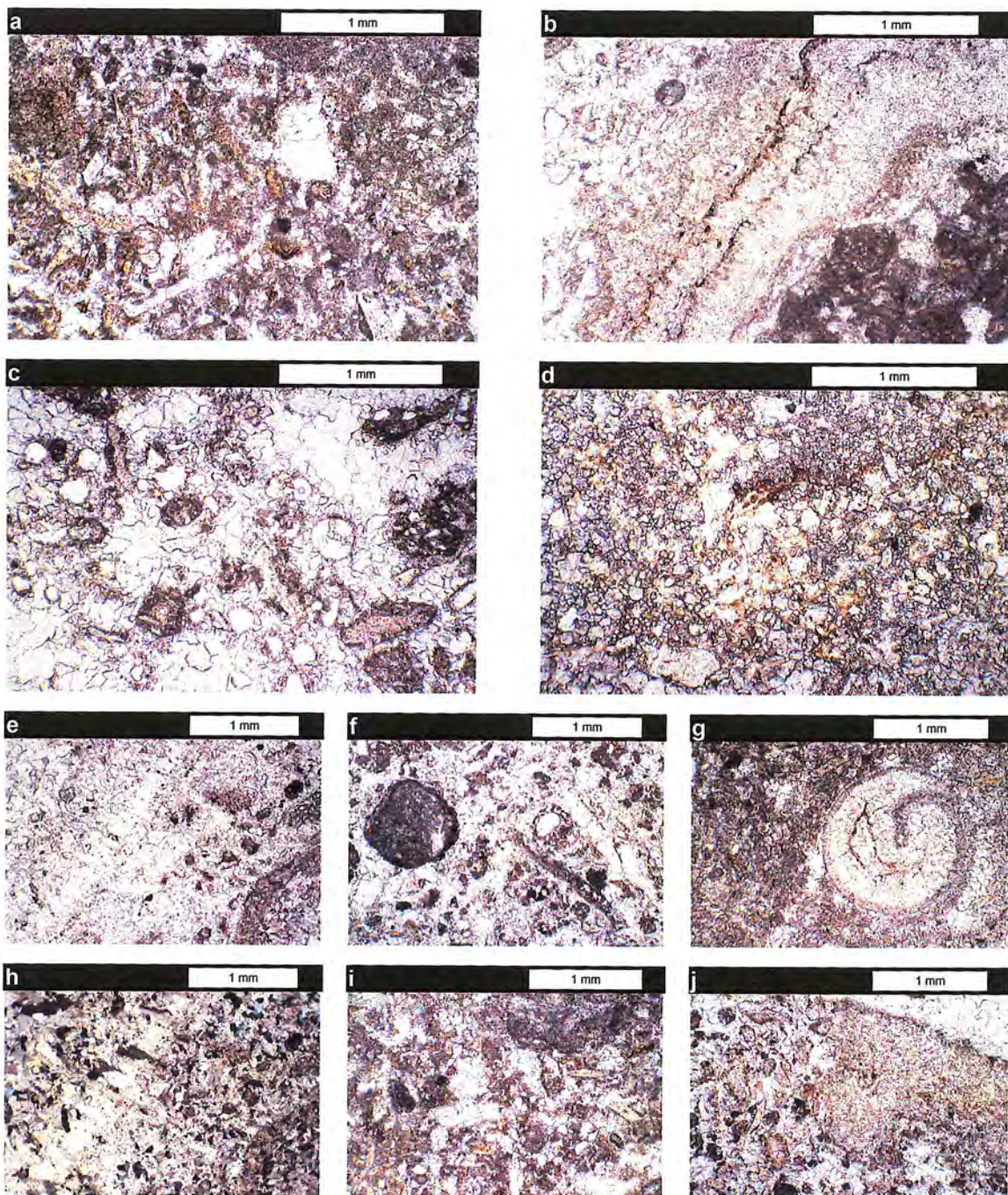
Figure A.2: Representative lithologies from the cave deposit at Wayne's Wok Site. a) Coarse detrital matrix with detrital calcite raft centre bottom (PP; R151A). b) Fine flowstone coating a tufaceous intraclast (PP; R151C). c) Coarse crystalline texture, possibly replacement of original micritic matrix (PP; R151C). d) Coarse/fine crystalline texture (PP; R151A). e/h) Fine flowstone. (PP/XP; R151B). f) Coarse detrital matrix with intraclast (PP; R151B). g) Fine crystalline matrix with 'ghost' of recrystallised ostracod or gastropod shell (PP; R151A). i) Coarse texture with detrital crystals and tufaceous intraclasts (PP; R151A). j) Coarse texture with reworked intraclast of fine crystalline matrix similar to A.2d (PP; R151B).
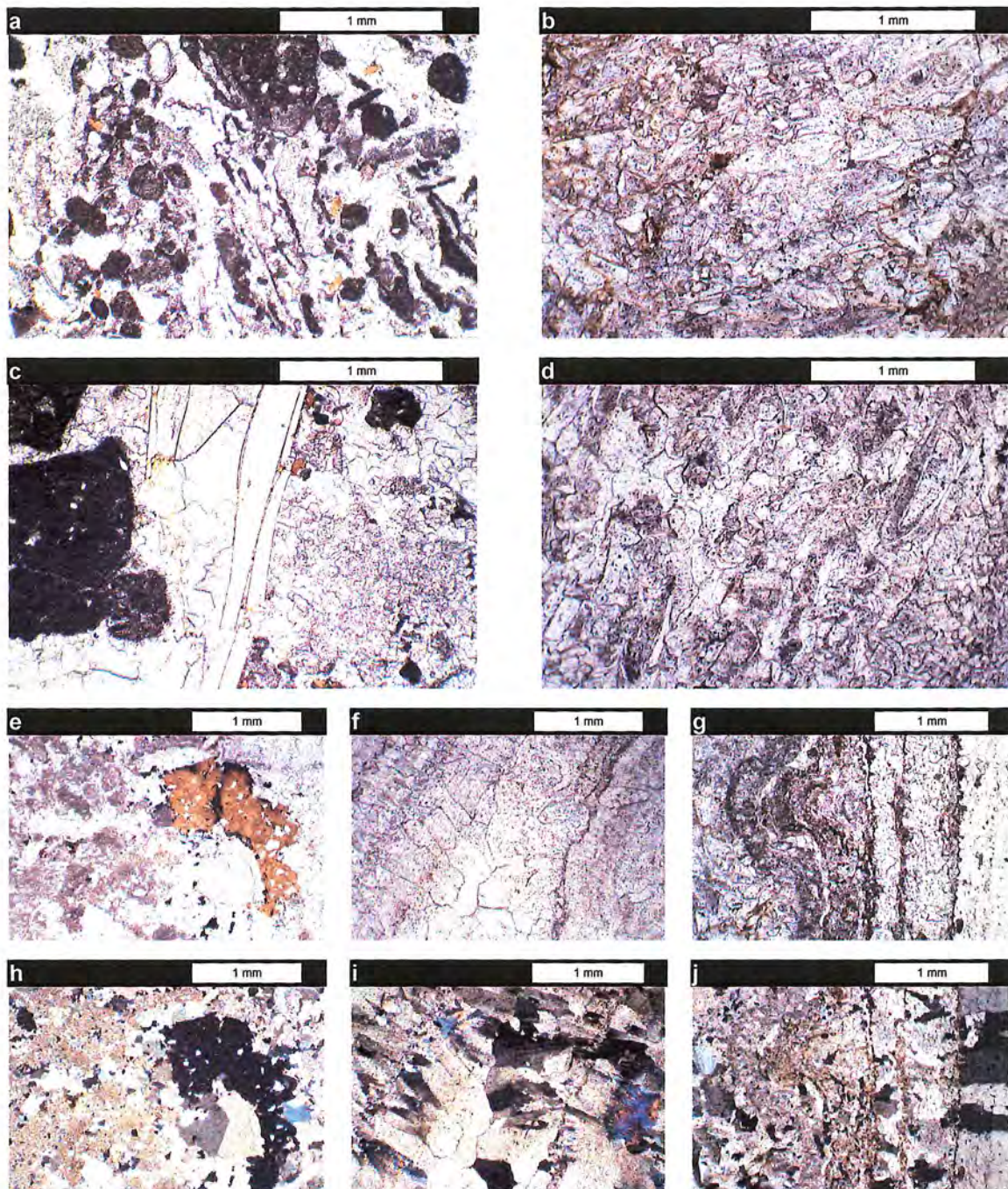
Figure A.3: Representative lithologies from cave deposits at Melody's Maze Site and Neville's Garden Site. a) Matrix composed of detrital crystals and intraclasts (PP; R119; Melody's Maze Site). b,d) Coarse crystalline matrix (PP; EP14; Neville's Garden Site). c) Bone and tufaceous intraclasts in crystalline matrix and spar (PP; R119; Melody's Maze Site). e/h) Clast of possible amorphous phosphate material that appears black under crossed polars (PP/XP; R119A; Melody's Maze Site). f/i) Flowstone (PP/XP; R120; Melody's Maze Site). h) Successive layers of fine flowstone coating a tiny particle with coarse crystalline matrix (PP; EP14; Neville's Garden Site).
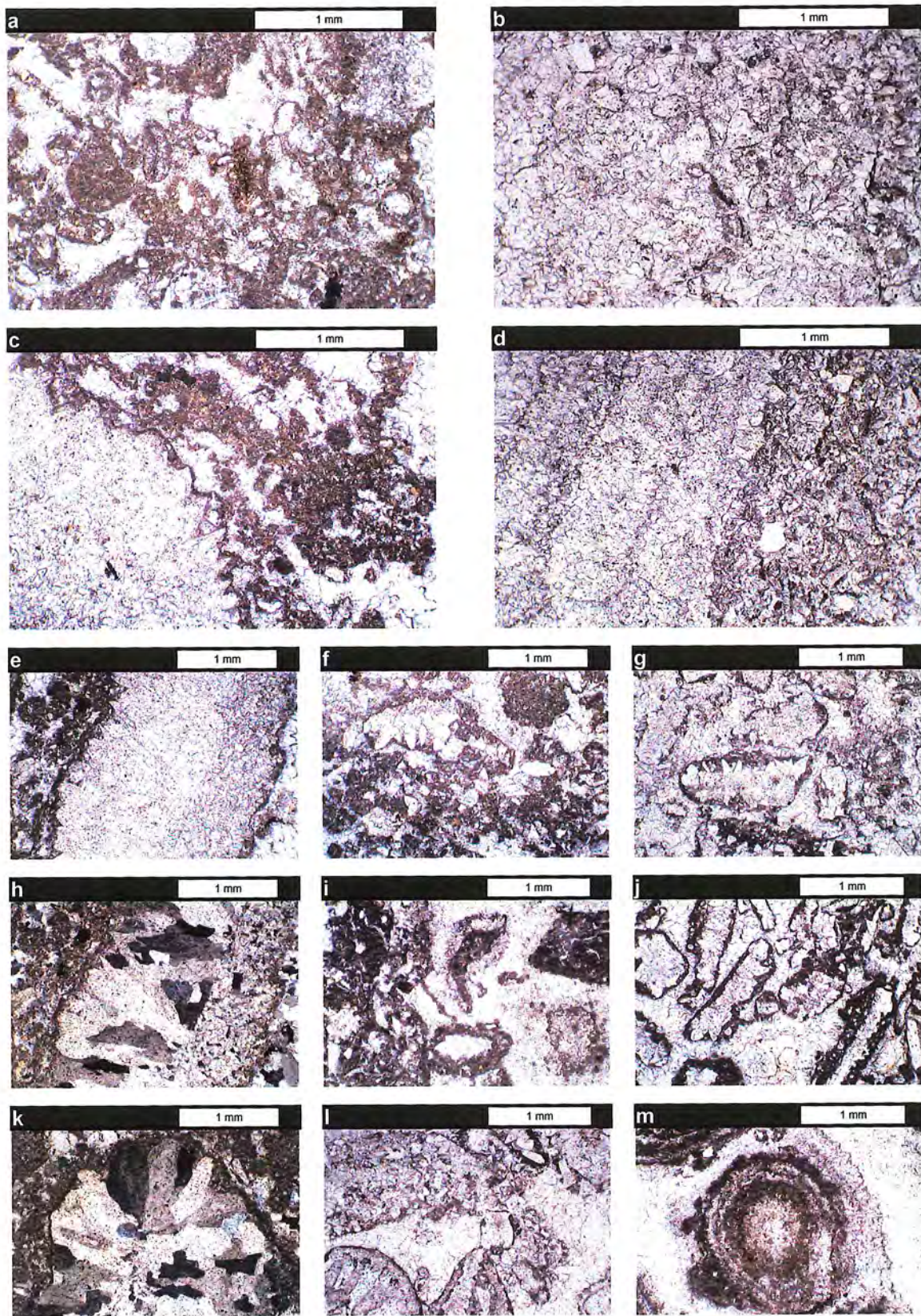
Figure A.4: Representative lithologies of cave deposits from Inabeyance Site and Mike's Menagerie Site on Godthelp's Hill. a) 'Porous cavity fill' comprised of globular micrite in crystalline matrix (PP; R158; Inabeyance Site). b,d) Crystalline matrix (PP; R154; Mike's Menagerie Site). c) Sparite clast in 'porous cavity fill' matrix (PP; R158; Inabeyance Site). e/h) Flowstone (PP/XP; R158; Inabeyance Site). f) Detrital crystalline texture composed of calcite rafts and tufaceous intraclasts with spar-filled voids. (PP;

R158; Inabeyance Site). g) Detrital crystals matrix with micritic coatings in spar (PP; R154A; Mike's Menagerie Site). i) Detrital crystals and tufaceous intraclasts with micritic coatings in sparite (PP; R154A; Mike's Menagerie Site). j) Detrital crystalline matrix with micritic coatings in spar (PP; R154; Mike's Menagerie Site). k) Tip of shelfstone (XP; R158; Inabeyance Site). l) Detrital crystals and bone with micritic coatings in spar (PP; R154; Mike's Menagerie Site). m) Laminar micritic structure resembling bacterially precipitated texture, see cave pearls in Figure 5.36 (PP; R154A; Mike's Menagerie Site).
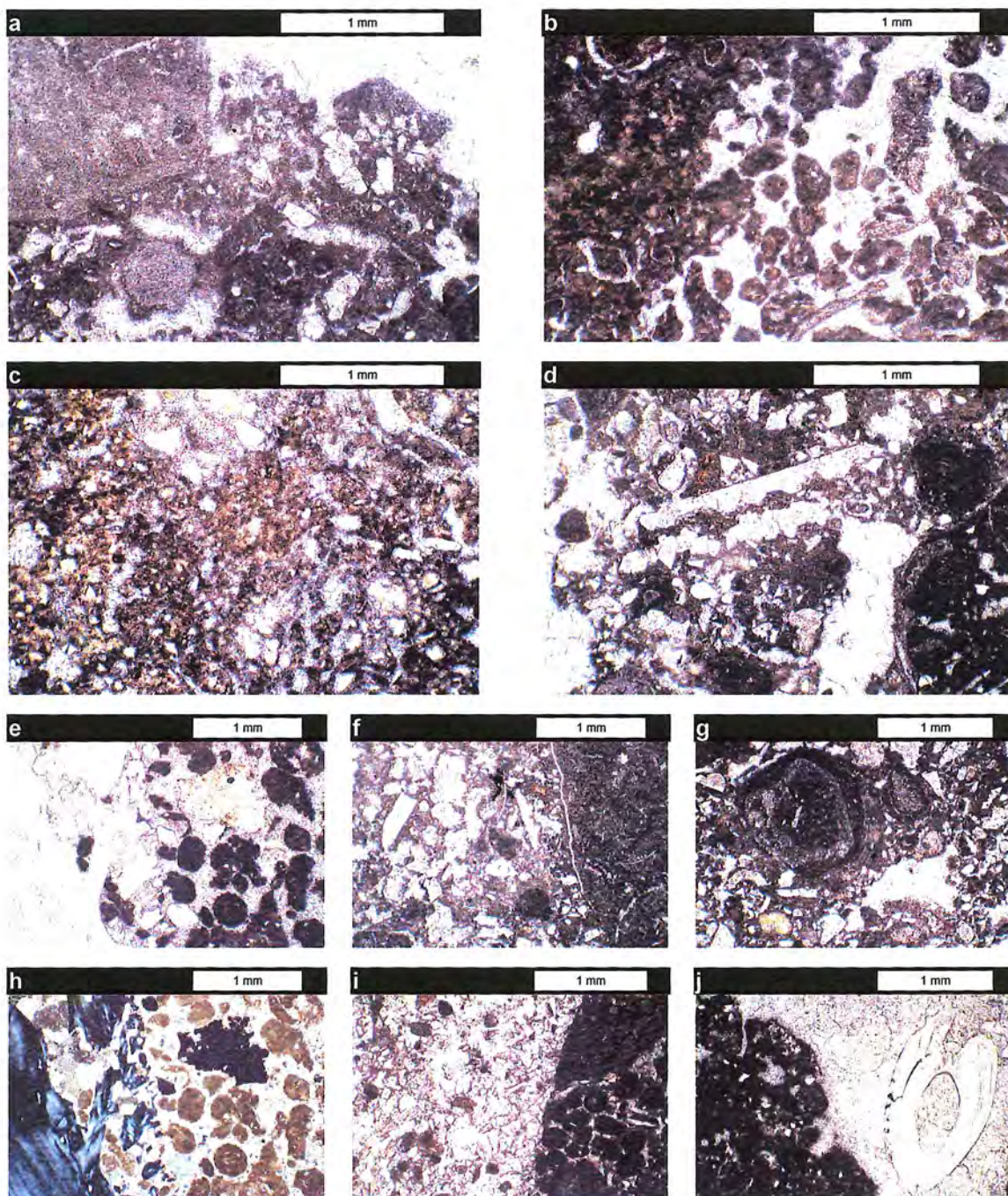
Figure A.5: Representative lithologies from Henk's Hollow Site. a) Tufaceous intraclasts and detrital crystals in micrite with spar-filled irregular voids (PP; R109A/2). b) Globular texture, possibly 'porous cavity fill' (PP; EP28). c) Detrital particles in micritic matrix (PP; EP28). d) Detrital crystals and intraclasts in micrite, calcite raft at centre (PP; R109). e/h) Bone and bone fragments and possible amorphous phosphate particle (black under crossed polars) in possible 'porous cavity fill' (PP/XP; EP28). f) Detrital crystals and tufaceous intraclasts in micrite (PP; R109). g) Detrital crystals and tufaceous intraclasts with laminar micritic coatings in micrite (PP; R109A/3). i) Detrital crystals and tufaceous intraclasts (PP; R109A/1). j) Tufaceous intraclast and bone in crystalline matrix (PP; EP28).
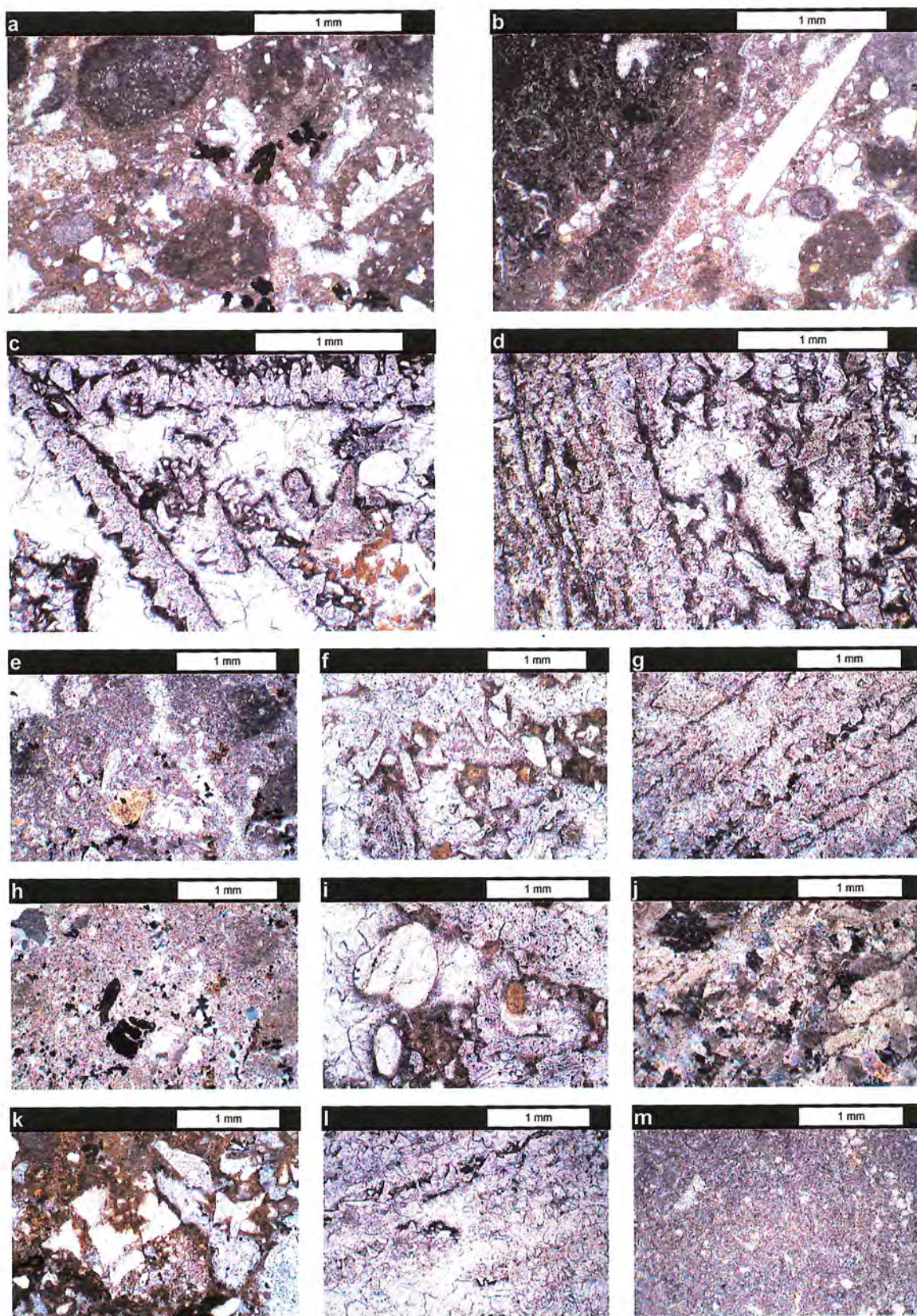
Figure A.6: Representative lithologies from Gag Site. a,b) Tufaceous intraclasts, detrital crystals and bone in micrite (PP; EP24). c) Detrital crystals texture comprised of micrite-coated calcite rafts in spar (PP; R118A). d) Detrital crystals texture (PP; EP26). e/h) Particle that appears black under crossed polars, similar to amorphous phosphates; in micritic matrix (PP/XP; EP24). f) Detrital crystals texture (PP; R118A). g/j) Texture resembling both detrital crystals and altered/disrupted flowstone (PP/XP; EP26). i) Detrital crystals in spar with rounded siliceous sand grains (PP; 118A). k) Detrital crystals in micrite (PP; R118B). l) Texture resembling both detrital crystals and altered/disrupted flowstone (PP; R118C). m) Fine crystalline matrix (PP; EP24).
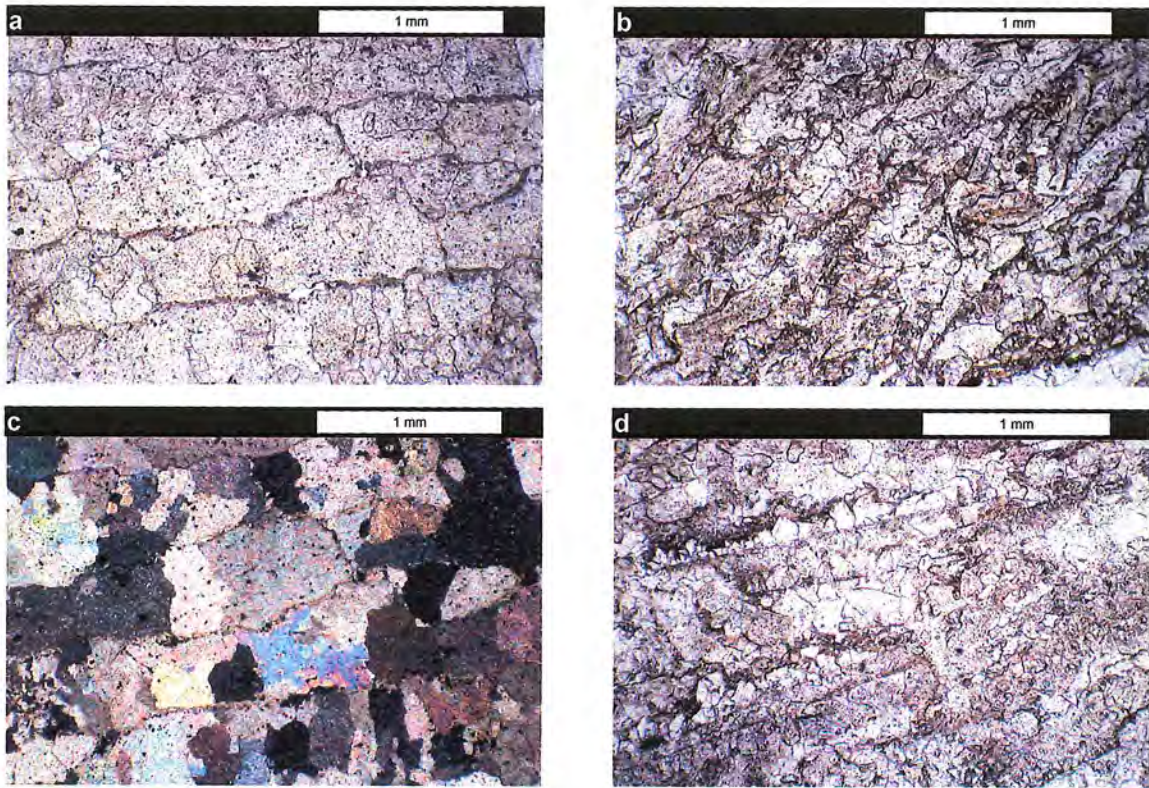
Figure A.7: Lithotextures of crystalline cave deposits in Ray's Amphitheatre at Riversleigh (referred to as 'the flowstone layer' by Archer *et al.* (1994, 1997). a/c) Layered crystalline texture interpreted as altered flowstone (PP/XP; R136; Ray's Amphitheatre). b) Dense detrital crystals texture (PP; R136A; Ray's Amphitheatre). d) Detrital crystals texture with calcite rafts (PP; R136A; Ray's Amphitheatre).

Appendix B

Supplementary faunal lists from Riversleigh.

CHORDATA
 ARCHOSAUROMORPHA
  PELECANIFORMES
   PHALACROCORACIDAE
    Genus indet. sp. indet.
  PASSERIFORMES
   [Indet.]
   ORIOLIDAE
   [Indet.]
  STRUTHIONIFORMES
   DROMORNITHIDAE
   [Indet.]
  CROCODILIA
   [Indet.]
 LEPIDOSAUROMORPHA
  SQUAMATA
   AGAMIDAE
    Genus indet. sp.
    Physignathus sp.
    Sulcatidens quadratus
   SCINCIDAE
    Egernia sp. cf. *E. striolata*
    Sphenomorphus spp. attenuate type
    Sphenomorphus Group genus indet. sp. small insectivore
   VARANIDAE
   [Indet.]
   PYTHONIDAE
   [Indet.]
   BOIDAE
   [Indet.]
   MADTSOIIDAE
    [*Yurlunggur* sp.]
    [*Wonambi* sp.]
 MAMMALIA
  DASYUROMORPHIA
   DASYURIDAE
    [*Barinya* sp. 3]
   THYLACINIDAE
   [Indet.]
  PERAMELEMORPHIA
   YARALIDAE
    [*Yarala burchfieldi*]
    [New genus 1 new sp. 2]
    [New genus 1 new sp. 3]
    [New genus 2 new sp. 1]
    [New genus 3 new sp. 1]
    [New genus 5 new sp. 1]
  DIPROTODONTIA
   BURRAMYIDAE
    Burramys brutyi
    Cercatetus new sp.
   BALBARIDAE
    Balbaroo gregoriensis
    Ganawamaya ornata
    Nambaroo sp. 2
    Nambaroo sp. 3

Nambaroo sp. 4
Nambaroo sp. 5
Nambaroo sp. 6
Wururoo sp. 2
[*Nambaroo* ?new sp. 3]
MACROPODIDAE
 Bulungamaya delicata
 Ganguroo bilamina
 Nowidgee matrix
 Wabularoo naughtoni
HYPSIPRYMNODONTIDAE
 [*Ekaltadeta ima*]
PHALANGERIDAEIDAE
 [*Ilungalya aletes*]
 [*Onirocuscus silvacultrix*]
PETAUROIDEA incertae sedis
 Djaludjangi yadjana
PSEUDOCHEIRIDAE
 Marlu kutjumarpensis
 Paljara nancyhaywardae
 Paljara tirarensae
 [New genus 1 new sp. 1]
 [*Marlu* sp. 1]
 [*Pildra* sp. 4]
 [*Pseudocheirops* sp. 2]
EKTOPODONTIDAE
 Ektopodon sp. cf. *E. serratus*
PETAURIDAE
 [Genus 1 sp. 1]
 [Genus 2 sp. 1]
MIRALINIDAE
 Durudawiri inusitatus
DIPROTODONTIDAE
 Neohelos tirarensis
PALORCHESTIDAE
 Propalorchestes ponticulus
WYNYARDIIDAE
 Namilamadeta new sp.
NOTORYCTEMORPHIA
 NOTORYCTIDAE
  [*Notoryctes* sp.]
CHIROPTERA
 MYSTACINIDAE
  Icarops aenae
  Icarops paradox
 MEGADERMATIDAE
  [*Macroderma* sp.]
 VESPERTILIONOIDEA
 [Indet.]
TEMNOSPONDYLI
 ANURA
  LEPTODACTYLIDAE
   Crinia presignifera
   Lechriodus intergerivus
   Limnodynastes antecessor

DIPNOMORPHA
DIPNOI
[Indet.]

CRUSTACEA
MALACOSTRACA
ISOPODA
Genus indet. sp. 1

References for this list: Archer *et al.* (1994), Bassarova *et al.* (2000), Black (1997a), Boles (1997a), Brammall and Archer (1997), Brammall (1998), Cooke (1992, 1997a, 1997b), Covacevich *et al.* (1990), Crosby (2002a, Crosby and Archer (2000), Hand *et al.* (1998), Hutchinson (1992), Murray *et al.* (2000), Pledge *et al.* (1999), Tyler (1989, 1990, 1991a), Tyler *et al.* (1990).

CHORDATA
  TESTUDOMORPHA
    TESTUDINES
      MEIOLANIIDAE
        Meiolania sp.
        Meiolania sp. cf. *M. platyceps*
        ?*Warkalania* sp.
  ARCHOSAUROMORPHA
    APODIFORMES
      APODIDAE
        Collocalia buday
    GRUIFORMES
      RALLIDAE
        Genus indet cf. *Gallinula* sp.
    PASSERIFORMES
      [Indet.]
    PELECANIFORMES
      PHALACROCORACIDAE
      Indet.
    STRUTHIONIFORMES
      DROMORNITHIDAE
      [Indet.]
      CASUARIIDAE
        Emuarius gidju
    CROCODILIA
      [Indet.]
  LEPIDOSAUROMORPHA
    SQUAMATA
      AGAMIDAE
        Genus indet sp.
        Physignathus sp.
      SCINCIDAE
        Egernia sp cf. *E. frerei*
        Eugongylus Group genus indet. spp.
        Sphenomorphus spp. attenuate type
        Sphenomorphus spp. robust type
        Sphenomorphus Group genus indet. sp. durophagous taxon
        Sphenomorphus Group genus indet. sp. small insectivore
      PYTHONIDAE
      [Indet.]
      BOIDAE
      [Indet.]
      MADTSOIIDAE
        Nanowana godthelpi
        Nanowana schrenki
        [*Yurlunggur* sp.]
        [*Wonambi* sp.]
  MAMMALIA
    DASYUROMORPHIA
      DASYURIDAE
        [*Barinya* sp. 2]
      THYLACINIDAE
        Ngamalacinus timmulvaneyi
        Wabulacinus ridei
    DIPROTODONTIA

ACROBATIDAE
  [Indet.]
BURRAMYIDAE
  Burramys brutyi
BALBARIDAE
  Balbaroo gregoriensis
  Ganawamaya acris
  Nambaroo sp. 5
  Wururoo sp. 2
HYPSIPRYMNODONTIDAE
  Hypsiprymnodon new sp.
  Ekaltadeta ima
MACROPODIDAE
  Bulungamaya delicata
  Ganguroo bilamina
  Nowidgee matrix
  Wabularoo naughtoni
PETAUROIDEA incertae sedis
  Djaludjangi yadjana
PSEUDOCHEIRIDAE
  Paljara maxbourkei
  Paljara nancyhaywardae
  [*Marlu kutjumarpensis*]
  [*Marlu* sp. 3]
  [*Pildra* sp. 2]
  [*Pseudocheirops* sp. 2]
PHALANGERIDAE
  Wyulda asherjoeli
  [New genus 1 new sp. 2]
  [New genus 3 new sp. 4]
  [New genus 3 new sp. 1]
  [New genus 3 new sp. 2]
PILKIPILDRIDAE
  [Indet.]
PETAURIDAE
  [Genus 2 sp. 1]
PHASCOLARCTIDAE
  Nimiokoala greystanesi
DIPROTODONTIDAE
  Neohelos tirarensis
PALORCHESTIDAE
  Propalorchestes ponticulus
WYNYARDIIDAE
  [*Namilamadeta* sp.]
THYLACOLEONIDAE
  [*Priscileo* sp.]
PERAMELEMORPHIA
  YARALIDAE
    Yarala burchfieldi
    [New genus 1 new sp. 1]
    [New genus 1 new sp. 2]
    [New genus 1 new sp. 3]
    [New genus 2 new sp. 1]
    [New genus 3 new sp. 1]
    [New genus 3 new sp. 2]

[New genus 5 new sp. 1]
YALKAPARIDONTIA
  YALKAPARIDONTIDAE
    Yalkaparidon coheni
NOTORYCTEMORPHIA
  NOTORYCTIDAE
    [*Notoryctes* sp.]
CHIROPTERA
  HIPPOSIDERIDAE
    [Indet.]
TEMNOSPONDYLI
ANURA

HYLIDAE
  Litoria magna
  [*Litoria rubelliformis*]
LEPTODACTYLIDAE
  Crinia presignifera
  Lechriodus intergerivus
  Limnodynastes antecessor
  Limnodynastes cf L. tasmaniensis
DIPNOMORPHA
  DIPNOI
    [Indet.]
UNIRAMIA
  [Indet.]

References for this list: Archer *et al.* (1988, 1994), Bassarova *et al.* (2000), Black (1997a), Black and Archer (1997a), Boles (1992, 1997a, 2001), Brammall and Archer (1997), Brammall (1998), Cooke (1992, 1997a, 1997b), Covacevich *et al.* (1990), Crosby *et al.* (2001), Crosby (2002a), Gaffney *et al.* (1992), Hutchinson (1992), Menu *et al.* (2002), Muirhead (1997), Muirhead and Filan (1995), Murray *et al.* (2000), Scanlon (1997), Tyler (1989, 1990, 1991a, 1991b), Tyler *et al.* (1990), Wroe (1996).

Faunal List B3: Rat Vomit Site Local Fauna
Source locality: Rat Vomit Site

CHORDATA
 TESTUDOMORPHA
  TESTUDINES
   CHELIDAE
    Indet.
 ARCHOSAUROMORPHA
  CROCODILIA
   CROCODYLIDAE
    Indet.
 LEPIDOSAUROMORPHA
  SQUAMATA
   SCINCIDAE
    Indet.
   MADTSOIIDAE
    Indet.
 MAMMALIA
  DIPROTODONTIA
   PSEUDOCHEIRIDAE
    Indet.
   PHASCOLARCTIDAE
    Nimiokoala greystanesi
  PERAMELEMORPHIA
    Indet.
  CHIROPTERA
   HIPPOSIDERIDAE
    Genera indet. spp.
    Miophyllorhina riversleighensis
    Rhinonicteris tedfordi
   MOLOSSIDAE
    Indet.
   VESPERTILIONIDAE
    Leuconoe sp.

References for this list: Black and Archer (1997a), Hand (1997b, 1997c), Menu *et al.* (2002).

Faunal List B4: Gag Site (Dwornamor) Local Fauna
Source locality: Gag Site

CHORDATA
 TESTUDOMORPHA
  TESTUDINES
   CHELIDAE
    Chelodina sp.
 ARCHOSAUROMORPHA
  CICONIIFORMES
   ?Ciconia sp.
  STRUTHIONIFORMES
   CASUARIIDAE
    Emuarius gidju
 LEPIDOSAUROMORPHA
  SQUAMATA
   AGAMIDAE
    Indet.
   SCINCIDAE
    Egernia sp. cf. E. frerei
    Egernia sp. cf. E. striolata
    Sphenomorphus spp. attenuate type
    Sphenomorphus spp. robust type
    Sphenomorphus Group genus indet. sp durophagous taxon
    Sphenomorphus Group genus indet. sp small insedivore
    Tiliqua pusilla
   BOIDAE
    Morelia riversleighensis
 MAMMALIA
  DASYUROMORPHIA
   THYLACINIDAE
    Muribacinus gadiyuli
    Thylacinus macknessi
   DASYUROMORPHIA incertae sedis
    Joculusium muizoni
  DIPROTODONTIA
   BURRAMYIDAE
    Burramys brutyi
    Cercatetus new. sp.
   HYPSIPRYMNODONTIDAE
    Hypsiprymnodon bartholomaii
    Ekaltadeta ima
   MACROPODIDAE
    Bulungamaya delicata
    Ganguroo sp. 2
    Wanburoo hilarus
    [Wanburoo wulugu]
   PSEUDOCHEIRIDAE
    Paljara nancyhaywardae
    [Marlu kutjumarpensis]
    [Marlu sp.1]
    [Marlu sp.2]
    [Marlu sp.5]

[New genus 2 new sp.1]
[New genus 2 new sp.2]
[Indet.]
[Pildra sp.1]
[Pildra sp.2]
[Pildra sp.5]
[Pseudocheirops sp.2]
[Pseudocheirops sp.4]
PILKIPILDRIDAE
 Djilgaringa gillespiae
PHALANGERIDAE
 [?New genus 1 sp. 1]
 [New genus 2 sp. 1]
PHASCOLARCTIDAE
 Litokoala kanunkaensis
DIPROTODONTIDAE
 Neohelos spB
 Nimbadon lavarackorum
PALORCHESTIDAE
 Propalorchestes ponticulus
PERAMELEMORPHIA
 YARALIDAE
  [Yarala burchfieldi]
  [New genus 1 new sp. 1]
  [New genus 2 new sp. 1]
  [New genus 3 new sp. 1]
  [New genus 3 new sp. 2]
  [New genus 5 new sp. 1]
  [New genus 4 new sp. 2]
 YALKAPARIDONTIA
  YALKAPARIDONTIDAE
   Yalkaparidon jonesi
 CHIROPTERA
  MEGADERMATIDAE
   Macroderma godthelpi
   Genus indet. Dwornamor variant sp.
  HIPPOSIDERIDAE
   [Indet.]
TEMNOSPONDYLI
 ANURA
  HYLIDAE
   Litoria magna
  LEPTODACTYLIDAE
   Lechriodus intergerivus
   Limnodynastes antecessor
MOLLUSCA
 GASTROPODA
  [Indet.]

References for this list: Archer et al. (1987, 1988, 1994), Archer and Flannery (1985), Bassarova et al. (2000), Black (1997a), Black and Archer (1997a), Boles (1992, 1997a, 1997b), Brammall and Archer (1997), Cooke (1999), Covacevich et al. (1990), Crosby (2002a), Flannery and Archer (1987a, 1987b), Gaffney et al. (1989), Hand et al. (1993), Hand (1985, 1990, 1996), Hutchinson (1992), Kear et al. (2001), Muirhead (1992), Murray et al. (2000), Myers et al. (2001), Myers (2002), Scanlon (2001), Shea and Hutchinson (1992), Smith and Plane (1985), Tyler (1989, 1990, 1991b), Tyler et al. (1990), Wroe (1996a, 1996b, 2001).

Faunal List B5: Henk's Hollow Site Local Fauna
Source locality: Henk's Hollow Site

CHORDATA
ARCHOSAUROMORPHA
  PASSERIFORMES
    [Indet.]
  CROCODILIA
    [Indet.]
LEPIDOSAUROMORPHA
  SQUAMATA
    AGAMIDAE
      [Indet.]
    SCINCIDAE
      Sphenomorphus spp. attenuate type
      Sphenomorphus spp. robust type
      Sphenomorphus Group genus indet. sp. small insectivore
    BOIDAE
      Morelia riversleighensis
MAMMALIA
  DASYUROMORPHIA
    DASYURIDAE
      Barinya wangala
      [*Dasylurinja* new sp.]
    THYLACINIDAE
      Muribacinus gadiyuli
      Nimbacinus dicksoni
  DIPROTODONTIA
    BALBARIDAE
      Balbaroo sp. 4
    MACROPODIDAE
      Ganguroo sp. 2
      Wanburoo sp.
    POTOROIDAE
      Bettongia moyesi
    BURRAMYIDAE
      [*Burramys brutyi*]
    ACROBATIDAE
      [Indet.]
    PETAUROIDEA incertae sedis
      Djaludjangi yadjana
    PSEUDOCHEIRIDAE
      cf. *Pseudocheirops* sp.
      [*Marlu kutjumarpensis*]
      [*Marlu* sp. 1]
      [*Pseudocheirops* sp. 1]
      [*Pseudocheirops* sp. 3]
    PHALANGERIDAE
      [New genus 2 sp. 1]
      [New genus 2 cf. New genus 2 sp. 1]
    PETAURIDAE
      [Indet.]

    PILKIPILDRIDAE
      [Indet.]
    PHASCOLARCTIDAE
      Litokoala kanunkaensis
    DIPROTODONTIDAE
      Neohelos spB
      Nimbadon lavarackorum
    PALORCHESTIDAE
      Propalorchestes novaculacephalus
    THYLACOLEONIDAE
      [*Wakaleo vanderleuri*]
  PERAMELEMORPHIA
    YARALIDAE
      [*Yarala burchfieldi*]
      [New genus 1 new sp. 1]
      [New genus 2 new sp. 1]
      [New genus 3 new sp. 1]
      [New genus 5 new sp. 1]
  CHIROPTERA
    MEGADERMATIDAE
      Macroderma malugara
      Macroderma sp.
      Genus indet sp.
    HIPPOSIDERIDAE
      [Indet.]
TESTUDOMORPHA
  TESTUDINES
    [Indet.]
TEMNOSPONDYLI
  ANURA
    LEPTODACTYLIDAE
      Lechriodus intergerivus
      Limnodynastes antecessor
DIPNOMORPHA
  DIPNOI
    [Indet.]
MOLLUSCA
GASTROPODA
  [Indet.]

References for this list: Archer *et al.* (1994), Black (1997a), Black and Archer (1997a), Boles (1997a), Brammall and Archer (1997), Brammall (1998), Cooke (1997), Crosby (2002a, Flannery and Archer (1987a, 1987c), Hand *et al.* (1993), Hand (1990, 1996), Hutchinson (1992), Muirhead and Archer (1990), Murray *et al.* (2000), Scanlon (2001), Smith and Plane (1985), Tyler (1989, 1990), Tyler *et al.* (1990), Wroe (1996, 1999).

Appendix C

Sample	Description	Locality	Calcite	Fluorapatite	Goethite	Quartz	Kaolinite	Amorphous P₂O₅
A1	Fossiliferous nodule	Dunsinane Site		A	A			
A2	Crystals in fossiliferous nodule	Dunsinane Site	S	A	A			
A3	Clay in fossiliferous nodule	Dunsinane Site	S				D	
A4	Fossiliferous nodule	Dunsinane Site	S	A	A			
B1	Pisolitic rock	Near Dunsinane Site			D	T		
B2	Brown crystalline concretion	Dunsinane Site	A	M	S			
B3	Pisolitic rock	Near Dunsinane Site	A/M		A/M	A/M		
B4	Brown concretion	Dunsinane Site	A/M	A/M	M	S		
B5	Orange crust	Dunsinane Site	A	S	M		T	
B6	Pisolitic rock	Near Dunsinane Site			M	A	T	
B7	Red clast	Dunsinane Site	A	T?	M	M	M	
B8	Orange clast	Dunsinane Site	A	M	A	S	S	
B9	Cambrian quartzite	Near Dunsinane Site				D		
B10	Fossil mammal bone in carbonate matrix	Dunsinane Site	A	M	S/T	M	S/T	
B11	Fresh carbonate matrix	Dunsinane Site	A	M		M	S	
B12	Intraclast tufa	Overlying Dunsinane Site	A		M	S		
B13	Isolated mammal bone	Dunsinane Site surface	S	D	S			
B14	Isolated fossil wood fragment	Dunsinane Site surface	S	D	S			
B15	Fossil mammal bone	White Hunter Site	A	A				
AL90-1	Cave fill	AL90 Site	A			A		S

Table C.1: Summary of X-Ray diffraction test results showing mineralogical composition of samples. D = dominant (>60%), A = abundant (40-60%), M = moderate (20-40%), S = small (5-20), T = trace (<5%).

Appendix D

Arena, D., 1997. The palaeontology and geology of Dunsinane Site, Riversleigh. *Memoirs of the Queensland Museum,* 41(2): 171-179.

Appendix E

Arena, R., and Black, K., 1997. An early-mid Miocene cave deposit at Riversleigh. *Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics, Sydney, July 1997, Abstracts*: 10-11.

AL90 Site is significant among Riversleigh's Oligo-Miocene fossil deposits for the potential of its rich taxonomic, taphonomic and geological resources to provide detailed insights into some of Riversleigh's Oligo-Miocene communities and environments. The deposit is primarily travertine which, in addition to the prevalence of well-preserved bat material, indicates the presence of cave conditions. This cave may have acted as a natural pitfall trap that accumulated a relatively high number of skeletal parts in close association and in some cases, articulation. The rich and diverse terrestrial vertebrate assemblage includes balbarine and balungamayine kangaroos, bandicoots, a ringtail possum, snakes, bats, a large diprotodontid (possibly *Neohelos*), a thylacinid and the sheep-sized diprotodontid *Nimbadon lavarackorum*. The geology of the deposit records the history of an early to mid-Miocene primary cave system followed by later secondary cave formation and infill which is characterised not only by contrasts in geology, but also in the associated fossil faunas.

Appendix F

Archer, M., Arena, R., Bassarova, M., Black, K., Brammall, J., Cooke, B., Creaser, P.,
Crosby, K., Gillespie, A., Godthelp, G., Gott, M., Hand, S. J., Kear, B.,
Krikmann, A., Mackness, B., Muirhead, J., Musser, A., Myers, T., Pledge, N.,
Wang, Y., Wroe, S., 1999. The evolutionary history and diversity of Australian
mammals. *Australian Mammalogy*, 21:1-45.

THE EVOLUTIONARY HISTORY AND DIVERSITY OF AUSTRALIAN MAMMALS

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Palaeodiversity and relationships of all groups of Australian mammals are reviewed. The fossil record spanning this time is of variable quality. 'Dark Ages' about which nothing is known in terms of Australian mammal evolution include the late Triassic to late Jurassic, late Cretaceous to late Paleocene and middle Eocene to middle Oligocene. Very little is known about the early Cretaceous and late Miocene. The late Oligocene to middle Miocene record documents the highest levels of biodiversity known for the continent, comparable to that which characterises the lowland rainforests of Borneo and Brazil. Order Monotremata spans at least the last 110 million years and includes four families. The enigmatic *Ausktribosphenos* from 115 million-year-old sediments in Victoria may represent an archaic monotreme, specialised peramurid or previously undocumented order of mammals but is unlikely to represent a placental as suggested in the initial description. Order Microbiotheria is represented in the early Eocene (~55 mya) by two genera similar in morphology to early Eocene taxa from Argentina. Order Peramelemorphia spans the early Eocene to Holocene and includes at least five families. Order Dasyuromorphia spans at least the late Oligocene to Holocene and includes at least three families. Other dasyuromorphian-like marsupials are indeterminate in terms of family-level affinities. Order Notoryctemorphia spans the early Miocene to Holocene with one family. Order Yalkaparidontia spans the late Oligocene to middle Miocene with one genus. Order Diprotodontia spans the late Oligocene to Holocene, represented throughout by three major groups: Phalangerida (eight families), Vombatomorphia (seven families) and Macropodoidea (at least three families). A possible placental condylarth (*Tingamarra*) has been recorded from the early Eocene. An archaeonycteridid bat (*Australonycteris*) is known from the early Eocene. Among bats, the late Oligocene to middle Miocene is dominated by rhinolophoids, many of which have European, Asian and African affinities. Mystacinids, megadermatids, hipposiderids and molossids are well-represented in the Oligocene to Miocene deposits. Vespertilionids are uncommon in the Oligocene to Miocene but become more diverse in the Pliocene to Holocene. Emballonurids and rhinolophids appear for the first time in the Plio-Pleistocene. Pteropodids are unknown prior to the Holocene. Murids span the early Pliocene to Holocene. In the oldest assemblage at Riversleigh, one undescribed lineage resembles archaic forms otherwise only known from the fossil records of Africa and Eurasia.

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MODERN understanding about the evolutionary history of Australia's mammals has derived from four main arenas of research: palaeontology, comparative anatomy, cytology, and molecular biology. While palaeontological and anatomical studies have been pursued since the early part of the 19th Century, neither cytology nor molecular biology made major contributions to understanding about the relationships of Australian mammals until the late 1970s (e.g., Kirsch 1977). Since then, molecular systematic studies in particular have played an increasingly significant role in testing and refining understanding about relationships at all levels from intraspecific to interordinal (e.g., Richardson *et al.* 1986; Westerman *et al.* 1990; Springer *et al.* 1994; Messer *et al.* 1998). In a burst of activity starting in 1983, fossil representatives of most families of living Australian terrestrial, arboreal and volant mammals have now been found, thereby providing minimal ages of family-level differentiation and much new information about the interrelationships of otherwise disparate groups.

It is hoped that what follows is a brief but succinct overview of current understanding about the fossil record and relationships of all families of Australian terrestrial, arboreal and volant mammals. As would be expected in an increasingly active field of research, much of this understanding is in the process of being tested and some has yet to be published. For this reason and because of page-length restrictions, the monophyly of most taxa in the cladograms has not been able to be rationalised here. Published and/or ongoing studies that do rationalise these hypotheses are indicated in the individually authored subsections that follow.

Higher-level systematic nomenclature used here, unless otherwise indicated, follows Aplin and Archer (1987). Concepts of biocorrelation and gaps in the record of Australian Tertiary mammal-bearing sediments follow Archer *et al.* (1997c). Abbreviations used here are as follows: my, million years; myo, million years old; mya or Ma, million years ago; Ka, thousand years ago; LF, Local Fauna (= a contemporaneous assemblage of creatures recovered from a single or closely associated series of fossil localities); lfs, local faunas; Fm, Formation (= a body of rock strata, commonly of similar rock type). Dental homology in marsupials follows Luckett (1993) for P3-M4 and Flower (1867) for I1-P2.

In the palaeodiversity figures below, we have amalgamated all taxa known from particular intervals of time as follows: early Cretaceous (taxa spanning only the late early Cretaceous from 115 to 100 my); early Paleocene (only the interval 63 to 61 my and only in Argentina); early Eocene (only one interval at approximately 55 my); latest Oligocene (only the latest late Oligocene from 26 to 23.3 my); early Miocene (all of it from 23.3 to 16.3 my); middle Miocene (all of it from 16.3 to 10.4 my); late Miocene (all of it from 10.4 to 5 my); early Pliocene (all of it from 5 to 3.3 my); late Pliocene (all of it from 3.3 to 2 my); Pleistocene (all of it from 2 my to 10,000 yrs); Holocene (all of the last 10,000 yrs). Allocation of particular faunal assemblages from Riversleigh to these time periods follows Archer *et al.* (1997c) and Creaser (1997). Hence, seven morphologically distinct dasyuromorphians indicated by Wroe and Muirhead (this work) for the early Miocene represents minimum species diversity for this group spanning this total interval of time. In these figures, taxa known from one or more of these intervals are shown as occurring throughout these intervals, despite the fact that in some cases they may only be known from a single fossil locality. This has been adopted because of current uncertainty about the *precise* ages (rather than 'early Miocene' etc.) of each of the hundreds of assemblages known. However, because mammal species commonly last 3 to 8 million years, these generalisations are probably not unreasonable.

SYNOPSIS AND LIMITATIONS OF THE FOSSIL RECORD OF AUSTRALIAN MAMMALS

In 1983, in a 432 page treatise over-viewing mammalian palaeofaunas of the world, Don Savage and Don Russell fairly summarised the highlights of the Australian Cainozoic record in five pages (accompanied by an upside down map of Australia!). At that time there were about 75 Tertiary species described. Subsequent growth in Australian palaeomammalogy led to many new discoveries which have more than trebled that level of understanding. Key events in the history of Australian mammals are summarised in Table 1. Correlation and age of significant Tertiary fossil mammal assemblages in Australia are summarised in Figure 1.

ark age 1' for Australian mammals between 220 to 115 mya; none are known despite being present in other areas of the world as early as 220 mya.

sktribosphenos nyktos, ~115 mya (e. Cret.), ?monotreme, peramurid or an unknown group (but almost certainly not a placental), Flat Rocks, Vic.

eropodon galmani , *Kollikodon ritchiei*, ~110 to 100 mya (e. Cret.), monotypic members of the monotreme families Steropodontidae and Kollikodontidae, Lightning Ridge, NSW.

)ark age 2' for Australian mammals from 100 to 55 mya.

onotrematum sudamericanum, 63 to 61 mya (e. Paleoc.), ornithorhynchid monotreme, Argentina (Patagonia), SAm (with oldest undoubted SAm marsupials and placentals).

larsupials probably reached Australia from SA, via Ant., sometime between 65 and 55 mya.

hylacotinga bartholomaii, microbiotheriids, other marsupials with SAm affinities, a ?dasyuromorphian, a perameloid, *Tingamarra porterorum* (possible placental) and *Australonycteris clarkeae* (archaeonycteridid bat), ~55 mya (e. Eoc.), Murgon, SE Qld.

Dark age 3' for Australian mammals extends from 55 to 26 mya.

after final separation from Ant. between 45 and 38 mya, apart from a 'spotty' archipelago linking SE Asia to Australia throughout Australia's northward drift, Australia's terrestrial mammals (but not bats) were isolated for 30 my resulting in a high level of endemism.

Most living families of Australian bats arrived (or evolved here) by 25 mya (l. Olig.); curiously, there is no pre-Holocene Australian record for pteropodids (fruit bats).

3etween 24 and 15 mya, much if not all of central and northern Australia supported rainforest.

3etween 26 and 23 mya (l. Olig. to e. Mioc.), some family-level groups went extinct (e.g., ilariids).

Mammal diversity in forest communities of e. Mioc. age (e.g., at Riversleigh, northwestern Qld) was very high, comparable to that found today in Borneo or Brazil and 44% greater in family-level diversity than the contemporary Wet Tropics rainforests of northeastern Queensland.

Endemic Australian bats (mystacinids) colonised New Zealand; others (a new Riversleigh group) may have colonised South America to become noctilionoids.

Australia crashed into SE Asia about 15 mya (m. Mioc.) after which time the New Guinea Highlands rapidly rose creating a rainshadow over northern Australia.

From 16 to 15 mya (m. Mioc.), Australia's forest mammals began a decline in diversity and distribution; family-level extinctions occurred between e. and m. Mioc. time (e.g., miralinids and wynyardiids).

Between 15 and 5 mya (m. to l. Mioc.), most of Australia began to dry and the central Australian forests declined.

'Dim age' for Australian mammals (very few sites known) from 12 to 5 mya.

New Guinea was probably colonised by dasyurids, bandicoots, zygomaturine diprotodontids and macropodine macropodids between 10 and 8 mya (l. Mioc.); however, phalangerids, dactylopsiline petaurids and acrobatids *could* have colonised New Guinea by 23 mya.

Murid rodents entered Australia from SE Asia via relatively dry corridors into northern Australia sometime between 8 and 5 mya (l. Mioc.).

By 5 mya (e. Plio.), many modern non-forest genera of marsupials had arisen and grass-eating marsupials (species of *Macropus* and modern types of vombatids) had appeared.

No plant assemblage in Australia can be described as arid, nor do grasslands develop, until sometime between 4 and 2 mya (e. Plio. to e. Pleist.).

Sometime between 4 and 1 mya (e. Plio. to Pleist.) Cuscuses probably became extinct in Australia and then later reinvaded from New Guinea.

By 2 mya (e. Pleist.), the first 'arid'-adapted marsupials appear (e.g., *Macropus (Megaleia)* sp.).

Sometime between 120,000 and 50,000 ya, Humans arrived in Australia; two or more types *may* have overlapped until 10,000 ya.

Probably by 50,000-40,000 ya, extinctions of most of Australia's 'megafaunal' mammals occurred resulting in the complete loss of diprotodontids, thylacoleonids and palorchestids as well as many genera and species in other families; the cause is controversial.

Approximately 4,000 ya, Dingoes were introduced to Australia possibly resulting in the extinction of mainland Thylacines (*Thylacinus cynocephalus*).

Contact with and colonisation by Europeans initiated the second major, ongoing extinction phase of Australian mammals.

Table 1. Summary of key events relating to the prehistory of Australian mammals. Abbreviations: mya, million years ago; e., early; m., middle; l., late; Cret., Cretaceous; Paleoc., Paleocene; Eoc., Eocene; Olig., Oligocene; Mioc., Miocene; Plio., Pliocene; Pleist., Pleistocene; NSW, New South Wales; Qld, Queensland; Vic., Victoria; SA, South Australia; Ant., Antarctica; WA, Western Australia; NT, Northern Territory; Tas., Tasmania; SAm, South America; N, northern; NE, northeastern; E, eastern; SE, southeastern; S, southern; SW, southwestern; W, western; NW, northwestern; PNG, Papua New Guinea.

Although it is likely that monotremes have a history in Australia that will eventually prove to be Jurassic in age, the base of the known Australian fossil mammal record starts in the late early Cretaceous (about 115 mya). Thus Australia's first profound 'Dark Age' extends from 220 (age of the oldest known mammals on other continents) to 115 mya; no Australian mammals from this interval are known. Early Cretaceous mammals in Australia come from two regions: Lightning Ridge, New South Wales (~110 to 100 myo, from the Griman Creek Fm); and Flat Rocks, Victoria (~115 myo, from the Wonthaggi Fm). Mammals recovered from Lightning Ridge represent two distinct families of monotremes (Musser 1998). The only mammal described from Flat Rocks is *Ausktribosphenos nyktos*, a creature of uncertain relationships although originally described as a placental (Rich *et al.* 1997; Archer *et al.* below). Although the late Cretaceous to middle Eocene rocks of most other continents have produced mammals in abundance, in Australia the relatively sparse rocks of this age have so far produced only dinosaurs and other non-synapsid vertebrates. Australia's second profound 'Dark Age' of mammalian evolution extends from 100 to 55 mya with no species known from this interval.

Illites in soft sediments exposed at Tingamarra, on the outskirts of the town of Murgon, southeastern Queensland, have been dated as >55.6 (earliest Eocene in age) on the basis of potassium/argon ratios (Godthelp *et al.* 1992). This age has been challenged by Woodburne and Case (1996) who suggest that the Tingamarra assemblage may be as young as late Oligocene in age (i.e., 25 myo). From these sediments have come many different kinds of mammals as well as osteichthyan fish, myobatrachid frogs (Tyler and Godthelp 1993), madtsoiid snakes (Scanlon 1993), trionychid turtles (Gaffney and Bartholomai 1979), mekosuchine crocodiles (Salisbury and Willis 1996) and passerine (Boles *et al.* 1994) as well as more archaic groups of birds including graculavids which are otherwise known only from late Cretaceous and Paleocene deposits in North America and probably Asia (Boles 1999). Where it has been possible to assess the biocorrelative significance of these non-mammalian vertebrates, they are broadly supportive of an early Eocene (or marginally older) age. Although the Tingamarra passerine is, by 20 million years, the oldest in the world, a significant pre-Oligocene Southern Hemispheric record was predicted by some palaeornithologists

(Boles 1995). Biocorrelative studies of the Murgon mammals, which include a ?placental (Godthelp *et al.* 1992), archaeonycteridid bat (Hand *et al.* 1994) and many marsupials including several with affinities to Casamayoran (early Eocene) as well as Tiupampian (Paleocene) South American groups (e.g., Archer *et al.* 1993; Godthelp *et al.* 1999), provide additional support for the early Eocene illite date. The archaeonycteridid bat in particular is closely related to earliest Eocene bats from North America and Europe. This interval in Australia was characterised by relatively warm, humid 'greenhouse' climatic conditions (McGowran and Li 1997).

The complete lack of knowledge about Australian terrestrial mammals from middle Eocene to middle Oligocene time, an interval of about 30 million years, is maddening. During this third profoundly 'dark age', Australia severed its last tenuous connections to the rest of Gondwana (Antarctica plus South America), sometime between about 46 and 35 mya, as it accelerated its northward drift towards the equator. From middle Eocene to late Oligocene time, Australia was characterised by relatively cool, dry 'icehouse' climatic conditions.

The latest Oligocene (about 25 to 23.3 mya) marks the beginning of a *relatively* well-documented phase in Australian mammal evolution. Fossil assemblages from two regions in particular, northeastern South Australia (the Tirari Desert in the Lake Eyre Basin, and the Lake Frome area in the Lake Frome Embayment) and Riversleigh (northwestern Queensland; described by Archer *et al.* 1997c as 'System A' local faunas) have provided an increasingly rich late Oligocene record. The Geilston Bay LF of Tasmania is probably early Miocene in age but the faunal assemblage is small and the taxa relatively poorly preserved. Eyre Basin Tertiary sediments have been dated with reasonable confidence using palaeomagnetostratigraphy (Woodburne *et al.* 1994). Riversleigh Tertiary sediments, previously dated by biocorrelations involving central Australian (marsupial) and European (bat) taxa, are now the subject of a uranium/lead dating program.

The early Miocene (about 23.3 to 16.3 mya) record documents Australia's most diverse mammalian faunas. These are best-known from Riversleigh (the 'System B' local faunas of Archer *et al.* 1997c) and the Tirari Desert (the Kutjamarpu LF). Less well-known assemblages occur in the Northern Territory (Kangaroo Well LF) and

Tasmania (Wynyard LF). As a measure of early Miocene diversity, a single assemblage at Riversleigh (Upper Site), interpreted to represent a closed forest community (Archer *et al.* 1997b), contains 64 species of mammal and 44% more family-level diversity than occurs today in the whole of the Wet Tropics rainforests of northeastern Queensland. The Leaf Locality may represent a riparian closed-forest community but the Riversleigh deposits of this age appear to indicate regional widespread, complex rainforest. If relatively drier communities bounded these forests, they left no trace in the known fossil record. Further, Martin (1998) has argued on the basis of palaeobotanical data that there is no evidence for arid conditions in Australia prior to the end of the Tertiary, in late Pliocene times.

Although early and middle Miocene mammal diversity was relatively high compared to diversity in Australia's contemporary forests, because of the geographically restricted nature of the palaeontological sampling areas, actual continental diversity at these times was almost certainly much higher than currently documented.

The middle to late Miocene (about 16.3 to 10 mya) marks the start of significant declines in rainfall following a pronounced climatic oscillation between 16 and 15 mya (McGowran and Li 1994). Middle Miocene mammal communities are only known from Riversleigh (those described as 'System C' assemblages (Archer *et al.* 1997c) and Bullock Creek in the Northern Territory (Murray and Megirian 1992). These are commonly characterised by less family, generic and species-level diversity than those of the early Miocene. What is known about mammals in most lineages demonstrates a rapid increase in average size over those of the early and middle Miocene.

The late Miocene is represented by very few Australian assemblages. Of these, the best-known are the Alcoota and Ongeva Local Faunas of the Northern Territory (Murray and Megirian 1992). These contain many medium to larger-size mammals but very few of the smaller kinds, leaving a gap in understanding about the evolutionary transition of smaller mammals from middle Miocene to Pliocene time. A single assemblage at Riversleigh, the Encore LF, may represent the early late Miocene with taxa that appear to be antecedent to Alcoota forms. This Riversleigh assemblage is also the oldest-known to include a wombat with ever-growing teeth (a species of *Warendja*-like vombatid), a suggestion of the presence of terrestrial plants with relatively

abrasive cell walls. The Beaumaris LF from Victoria is another late Miocene site but one with very few taxa represented. Drying conditions throughout much of the continent may account in part for the relatively poor late Miocene fossil record. This also appears to be the time during which many of the modern groups of marsupials (e.g., dasyuroids, peramelids, peroryctids and macropodids), bats (vespertilionids) and perhaps rodents (murids) underwent explosive radiations to produce the high diversity of species lineages present today.

Pliocene assemblages are widespread and known from all states except Tasmania and the Northern Territory. By this time, Australian mammal communities had significantly changed with representatives of many modern genera appearing for the first time including the first-known Australian rodents. Size increases continued in most lineages, most noticeably among herbivorous marsupials such as several diprotodontids which had become the size of cattle. The first, albeit rare occurrences in inland communities of grazing mammals in the early Pliocene suggests that grasses were increasing in abundance. Other early Pliocene communities, however, indicate the persistence of refugial rainforest in continentally peripheral areas such as Hamilton, Victoria. There are indications, mainly from palaeobotany, that the early Pliocene was a time of brief amelioration of a general drying and cooling trend with brief expansions of rainforest into mesic regions.

Pleistocene diversity has been under continuous investigation since fossil mammals were first found in Australia. At least 26 of the living genera are represented by Pleistocene species, although some of these may represent anagenetic lineages (e.g., *Macropus titan* to *M. giganteus*, and *Sarcophilus laniarius* to *S. harrisii*). Because of human impact and/or climatic change, most of the Pleistocene megafauna (Murray 1991), about 50 species, had vanished by about 40,000 years ago. A few megafaunal species underwent post-Pleistocene dwarfing in proportion to their absolute size such that some of the largest living kangaroos (e.g., species of *Macropus*) are 30% smaller than their Pleistocene ancestors. Dating of some Pleistocene megafaunal assemblages is controversial (Baynes 1997 and A. Baynes, pers. comm., 1997).

Holocene increases in species-level diversity for groups such as phalangerids, pseudocheirids, dasyurids, peroryctids, peramelids, potoroids, murids, vespertilionids and probably pteropodids

AUSTRALIAN MAMMALOGY

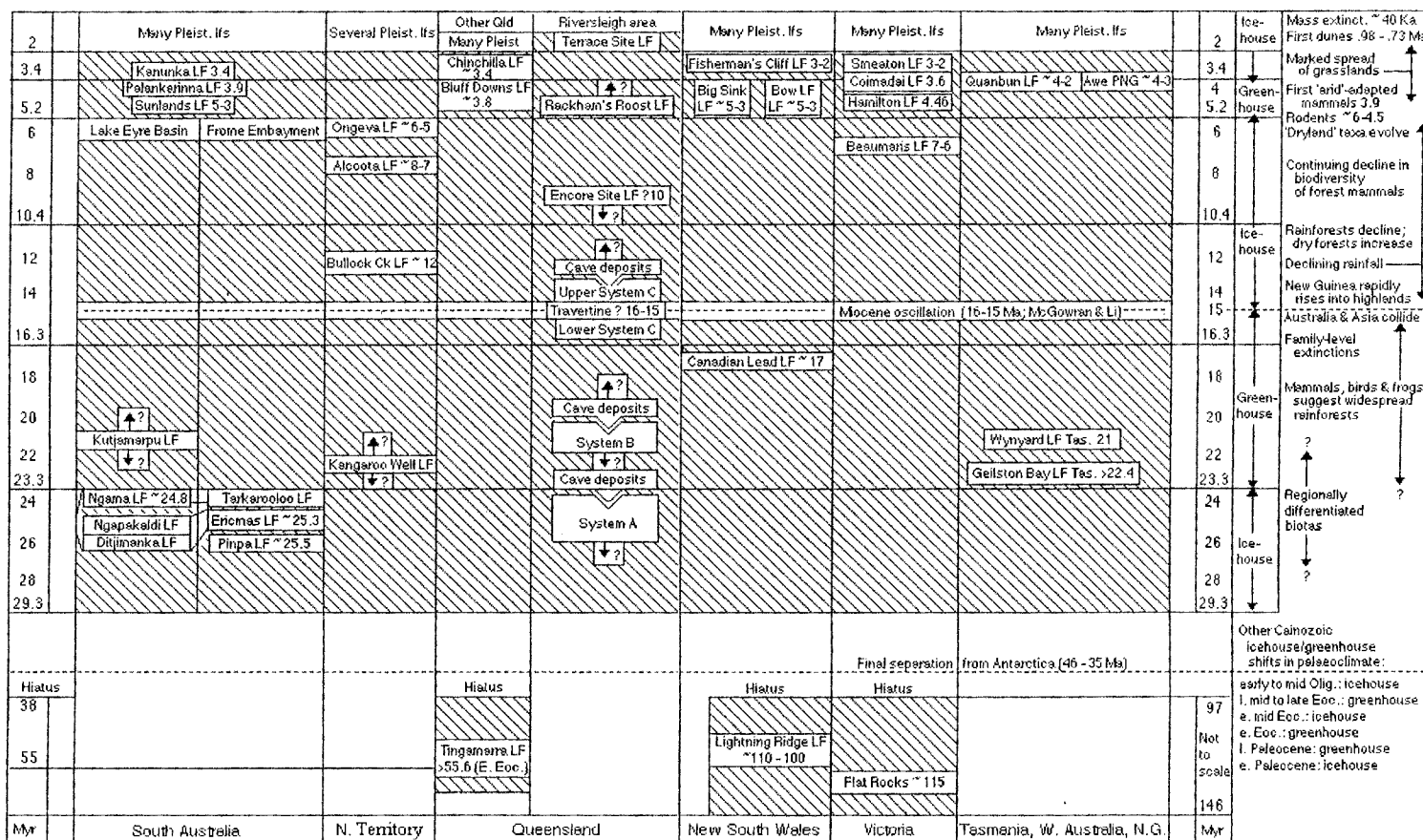| 2	Many Pleist. lfs	Several Pleist. lfs	Other Qld — Many Pleist	Riversleigh area — Terrace Site LF	Many Pleist. lfs	Many Pleist. lfs	Many Pleist. lfs	2	Ice-house	Mass extinct. ~40 Ka / First dunes .98 - .73 Ma
3.4	Kanunka LF 3.4		Chinchilla LF ~3.4		Fisherman's Cliff LF 3-2	Smeaton LF 3-2		3.4		Marked spread of grasslands
5.2	Palankarinna LF 3.9 / Sunlands LF 5-3		Bluff Downs LF ~3.8	Rackham's Roost LF	Big Sink LF ~5-3 / Bow LF ~5-3	Coimadai LF 3.6 / Hamilton LF 4.46	Quanbun LF ~4-2 / Awe PNG ~4-3	4 / 5.2	Green-house	First 'arid'-adapted mammals 3.9 / Rodents ~6-4.5
6	Lake Eyre Basin / Frome Embayment — Ongeva LF ~6-5					Beaumaris LF 7-6		6		'Dryland' taxa evolve
8		Alcoota LF ~8-7						8		Continuing decline in biodiversity of forest mammals
10.4				Encore Site LF ?10				10.4	Ice-house	Rainforests decline; dry forests increase
12		Bullock Ck LF ~12		Cave deposits				12		Declining rainfall
14				Upper System C				14		New Guinea rapidly rises into highlands
15				Travertine ? 16-15		Miocene oscillation (16-15 Ma; McGowran & Li)		15		Australia & Asia collide
16.3				Lower System C				16.3		Family-level extinctions
18					Canadian Lead LF ~17			18	Green-house	Mammals, birds & frogs suggest widespread rainforests
20	Kutjamarpu LF			Cave deposits				20		?
22		Kangaroo Well LF		System B			Wynyard LF Tas. 21	22		
23.3				Cave deposits			Geilston Bay LF Tas. >22.4	23.3		
24	Ngama LF ~24.8 / Tarkarooloo LF			System A				24		Regionally differentiated biotas
26	Ngapakaldi LF / Ditjimanka LF — Ericmas LF ~25.3 / Pinpa LF ~25.5							26	Ice-house	?
28								28		
29.3								29.3		
						Final separation from Antarctica (46 - 35 Ma)				Other Cainozoic icehouse/greenhouse shifts in palaeoclimate:
Hiatus / 38	Hiatus		Hiatus		Hiatus	Hiatus		97		e.arly to mid Olig.: icehouse / l. mid to late Eoc.: greenhouse / e. mid Eoc.: icehouse / e. Eoc.: greenhouse
55			Tingamarra LF >55.6 (E. Eoc.)		Lightning Ridge LF ~110 - 100			Not to scale		l. Paleocene: greenhouse / e. Paleocene: icehouse
						Flat Rocks ~115		146		
Myr	South Australia	N. Territory	Queensland		New South Wales	Victoria	Tasmania, W. Australia, N.G.	Myr		

Fig. 1. Correlation chart for Australian fossil mammal communities (local faunas) noted and/or contributing to understanding summarised in this paper.

6

indicated in the palaeodiversity figures below is almost certainly a reflection of the limitations of the Plio-Pleistocene fossil record. This is particularly the case for smaller mammals which are less likely to be collected.

RELATIONSHIPS OF AUSTRALIAN MAMMALS

The phylogenetic relationships of Australian mammals have been extensively examined at three levels: infrafamilial, interfamilial and interordinal. Three factors restrict ability to interpret their interordinal relationships with confidence. First, yalkaparidontians, yingabalanarids and the possible placental condylarth *Tingamarra porterorum* are only known from an inadequate fossil record. As a result, there are disagreements about their ordinal and interordinal relationships (see Archer *et al.* this work). Second, two of the orders (Chiroptera and Rodentia) have more extensive non-Australian representation and almost certainly arrived in Australia as diversified groups with closer phylogenetic relationships to non-Australian mammals. Third, character systems examined for representatives of many of the other orders have in some cases produced widely differing indications of phylogenetic relationship. For example, while most mammalogists regard monotremes to not only be outside of the clade containing marsupials and placentals but even outside of therian mammals, DNA-hybridisation suggests that monotremes may be the sister group of marsupials (e.g., Janke *et al.* 1997, Kirsch and Mayer 1998). Similarly, there is considerable disagreement about the interordinal relationships of peramelemorphians, dasyuromorphians, notoryctemorphians and diprotodontians based on divergent indications of albumin serology (e.g., V. Sarich, pers. comm. in Archer 1982a), whole serum serology (Kirsch 1977), 12S ribosomal RNA (Springer *et al.* 1994), protamines (Retief *et al.* 1995), DNA-hybridisation (Kirsch *et*

al. 1997), and morphology (Szalay 1982, 1994). Although there is general consensus, following studies of tarsal anatomy by Szalay (1982), that microbiotherians share a special relationship with Australian marsupials, there are arguments about the precise nature of their placement within Australidelphia, some concluding a special relationship with dasyuromorphians and peramelemorphians (albumin serology; V. Sarich, pers. comm. in Archer 1982a), others a sister taxon relationship with dasyuromorphians (Szalay 1994), dasyuromorphians and notoryctids (Retief *et al.* 1995), diprotodontians (Kirsch *et al.* 1997), and still others with the whole of the Australian marsupial radiation (e.g., Szalay 1982), or the Australian radiation plus the early Tertiary South American genus *Andinodelphys* (Marshall *et al.* 1990). Resolution of the interordinal relationships of Australian marsupials has been further complicated following the suggestion that peramelemorphians may lie outside of a clade inclusive of all other Australian marsupials and *Dromiciops*, or even outside of all extant marsupials (Springer *et al.* 1994; Retief *et al.* 1995).

Intraordinal and intrafamilial relationships are briefly explored in the individual contributions that follow. For some of these groups such as dasyuroids, perameloids and macropodoids, interfamilial phylogenetic relationships remain uncertain. In part this reflects the fact that although many modern families are present and distinct in 26 to 23 million-year-old sediments, the fossil record between 55 and 26 million years of age, the interval when most of these families probably differentiated from each other, is so far utterly silent. Further, confident resolution of many higher-level systematic problems may be beyond the current capacity of molecular systematic techniques. With continued research, both of these limitations must be overcome.

DIVERSITY AND RELATIONSHIPS OF LIVING AND EXTINCT MONOTREMES

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TWO early Cretaceous monotremes have been described from the Griman Creek Formation, Lightning Ridge, New South Wales. The platypus-like *Steropodon galmani* (family Steropodontidae) was Australia's first known Mesozoic mammal (Archer *et al.* 1985). A second taxon, *Kollikodon ritchiei* (family Kolliko-dontidae), characterised by unique bunodont teeth, may have specialised in eating crustaceans (Flannery *et al.* 1995). An edentulous maxillary fragment from Lightning Ridge has been described as possibly that of a monotreme (Rich *et al.* 1989). Edentulous lower jaw fragments of a monotreme-like mammal from Lightning Ridge have also been recovered.

The oldest undoubted ornithorhynchid is *Monotrematum sudamericanum,* from late early Paleocene sediments in Patagonia, Argentina (Pascual *et al.*1992). This species demonstrates that at least ornithorhynchids had a Gondwanan distribution (Pascual *et al.* 1992). Two species referable to the genus *Obdurodon* have been recovered from the late Oligocene central Australian Etadunna and Namba Formations: *Obdurodon insignis* (Woodburne and Tedford 1975; Archer *et al.* 1978) and the undescribed *Ob.* sp. A. *Ob. dicksoni,* a third *Obdurodon* species, has been recovered from the Riversleigh World Heritage fossil deposits in northwestern Queensland (Archer *et al.* 1992, 1993; Musser and Archer 1998). The only known Pliocene ornithorhynchid material consists of a limb fragment from the Bow Local Fauna, near Merriwa, NSW referred to the genus *Ornithorhynchus* (Rich *et al.* 1991b). Pleistocene ornithorhynchid material appears to represent the living *Ornithorhynchus anatinus* (e.g., Archer *et al.* 1978; Marshall 1992).

Echidnas of the genus *Megalibgwilia,* characterised by a beak shape intermediate between that of the living *Tachyglossus* and *Zaglossus,* are known from Pleistocene swamp and cave deposits from Tasmania, New South Wales and South Australia. This recently erected genus supersedes the assignment of several long-beaked types (e.g., *ramsayi*) to the genus *Zaglossus* (Griffiths *et al.* 1991). A middle Miocene echidna, *Echidna (Proechidna) robusta* Dun, 1895 from Gulgong, New South Wales, is probably a species of *Megalibgwilia* (Griffiths *et al.* 1991). A humerus found with the partial cranium of this specimen, originally described as ornithorhynchid (*Ornithorhynchus maximus* Dun, 1895), is tachyglossid and probably belongs to the individual represented by the cranium (Mahoney and Ride 1975). The huge '*Zaglossus*' *hacketti* from Western Australia may represent a distinct genus (J. Mahoney cited in Griffiths *et al.* 1991). *Zaglossus* material from the Pleistocene of New Guinea probably represents the living *Z. bruijnii* (Murray 1991). The living Short-beaked Echidna (*Tachyglossus aculeatus*) is known from many Pleistocene to Holocene deposits in southern Australia (Murray 1978, 1991).

The cladogram (Fig. 1) reflects the uncertain phylogenetic relationships of tachyglossids as well as the unresolved position of the very derived *K. ritchiei*. Some genetic studies infer that tachyglossids separated from ornithorhynchids near the end of the Cretaceous or early in the Tertiary (e.g., Westerman and Edwards 1992; Messer *et al.* 1998 but see Retief *et al.* 1993). Given the early Cretaceous age of the platypus-like *S. galmani,* such findings suggest that tachyglossids may have been derived from a platypus-like ancestor thus making the platypus lineage paraphyletic. However, Messer *et al.* (1998) suggest that these dates may be underestimates of divergence times because evolution of at least the milk protein α-lactalbumin appears to be slower in monotremes than in living therians.

Much of the monotreme fossil material is fragmentary and vast temporal gaps separate taxa. However, some tentative conclusions about historical diversity can be drawn. The presence of *S. galmani* in the early Cretaceous is testimony to the antiquity of platypus-like monotremes (Archer *et al.* 1985), while the presence of the contemporaneous, specialised *K. ritchiei* argues for far greater intraordinal diversity than previously anticipated (Flannery *et al.* 1995).

However, from the early Tertiary to the present, only ornithorhynchids and tachyglossids are represented. Ornithorhynchids may have been more diverse during the early to middle Tertiary (four species are known) while tachyglossids appear to have radiated during the Plio-Pleistocene, with at least five Pleistocene species recognised (Murray 1978; Griffiths *et al.* 1991).
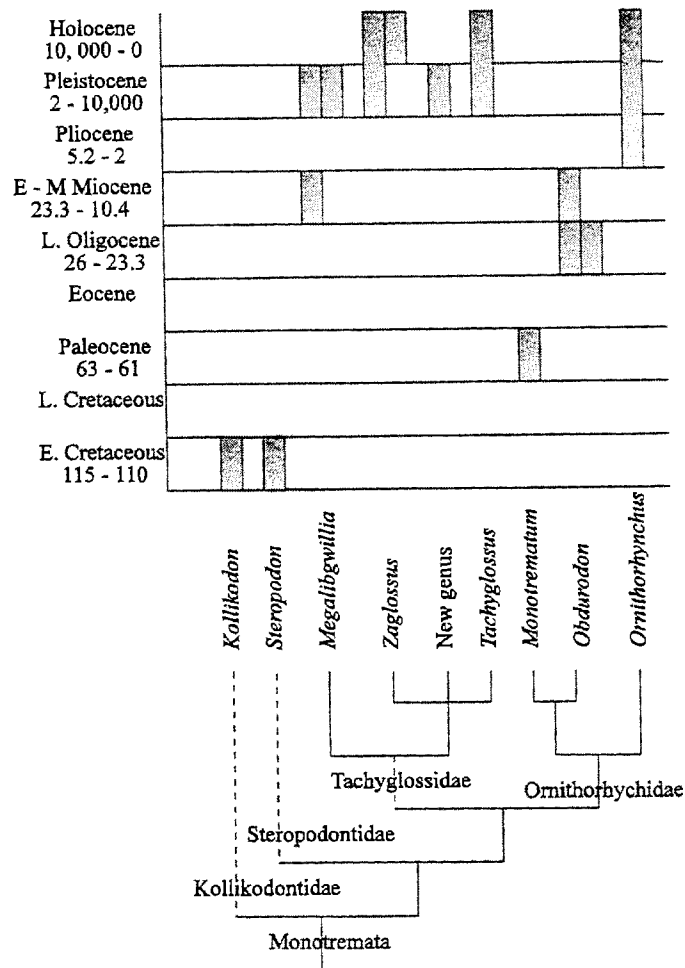
Fig. 1. Monotreme diversity through time: a cladogram of probable relationships (see text) within Monotremata. Uncertain relationships are indicated by dashed lines. Each block represents a distinct species. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.

Phylogenetic affinities of monotremes to other groups remain contentious. Dental structure, diagnosed as therian based on the triangular molar blades of *S. galmani* (Archer *et al.* 1985; Kielan-Jaworowska *et al.* 1987), may be autapomorphic with independent acquisition of therian-like triangular blade systems (Archer *et al.* 1992, 1993). Basicranial anatomy appears to link monotremes most closely with multituberculates (e.g., Wible and Hopson 1993; Meng and Wyss 1995). Several key Mesozoic taxa known from postcranial material exhibit advanced shoulder girdle morphology (e.g., Hu *et al.* 1997), placing the plesiomorphic shoulder girdle of monotremes between archaic morganucodontids or tricono-

dontids and the more derived multituberculates (Hu *et al.* 1997), and suggesting an early to late Jurassic origin for the monotreme shoulder girdle (Musser 1998). Genetic evidence is equivocal: Messer *et al.* (1998) support a middle Jurassic divergence of monotremes from therian mammals, although Westerman and Edwards (1992) place this split at the earliest Cretaceous. A close relationship between monotremes and marsupials to the exclusion of placental mammals has recently been suggested (Janke *et al.* 1997; Kirsch and Mayer 1998 in revisions of Gregory's [1947] Marsupionta hypothesis), although results from other molecular techniques argue against this

EVOLUTION OF AUSTRALIA'S MARSUPICARNIVORES: DASYURIDAE, THYLACINIDAE, MYRMECOBIIDAE, DASYUROMORPHIA *INCERTAE SEDIS* AND MARSUPIALIA *INCERTAE SEDIS*

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RECENT fossil discoveries have shed new light on the subject of Australian marsupicarnivore evolution (Fig. 1). The new material includes the first of Palaeogene age, as well as the first pre-Pliocene crania referable to the Dasyuridae and Thylacinidae. A new species (Godthelp *et al.* 1999), from the early Eocene Tingamarra Local Fauna, southeastern Queensland, is the oldest potential ancestor for the families of Dasyuromorphia. However, this species could be either an ameridelphian or australidelphian marsupial, and its position relative to dasyuromorphians is unclear. At the other end of the time scale, Recent, Pleistocene and Pliocene faunas are dominated by dasyurids (with at least 63 extant species), while Thylacinidae is represented by a single species (*Thylacinus cynocephalus*). The family Myrmecobiidae has no fossil record.

Fossil evidence suggests that the high diversity of dasyurids is a late middle Miocene to Pliocene phenomenon. Since the last substantial revision (Archer 1982b), seven new species of thylacinid have been described, all from late Oligocene to late Miocene deposits (Wroe 1996; Muirhead 1997; Murray 1997; Muirhead and Wroe 1998). Descriptions of four more new taxa are in progress. The rapidly expanding tally of Miocene marsupial carnivore taxa challenges the hypothesis of Flannery (1997), that Australia has not supported a diverse large mammalian carnivore fauna over the last 20 my (Wroe 1996, 1999a). In several highly localised local faunas of Miocene age from Riversleigh the number of large marsupial carnivores (*Dasyurus maculatus* size or greater) equals or exceeds that known for the vast majority of South American localities from the same epoch (Wroe and Myers 1998). Only two new late Oligocene to late Miocene dasyurid species are known. Wroe (1996, 1997) reassigned a number of pre-Pliocene 'dasyurid' taxa (e.g., *Ankotarinja*, *Keeuna*, *Wakamatha*) to Dasyuromorphia *incertae sedis* on the grounds that their placement within Dasyuridae was based on symplesiomorphies. A new Riversleigh species (Wroe 1999b), of early to middle Miocene age, is the oldest taxon confidently placed within Dasyuridae. It is basal to a monophyletic clade inclusive of the three extant dasyurid subfamilies (Sminthopsinae, Phascogalinae, Dasyurinae), none of which includes fossil taxa older than earliest Pliocene. Wroe (1998, 1999b) considers the possibility that the common origin of extant dasyurid subfamilies may have been as recent as the late Miocene. Alternatively, on the basis of molecular data, Krajewski *et al.* (1997b) postulate that the basal polytomy within Dasyurinae occurred about 15 million years ago. If this is correct then the common ancestor of modern dasyurids is more likely early Miocene in age. Many aspects of the most recent morphology-based review of dasyurid phylogeny (Archer 1982a) have been supported by subsequent molecule-based studies, but significant amendments have also been suggested (Krajewski *et al.* 1997a, 1997b). Notable among these has been the subsumption of Archer's Phascolosoricinae within Dasyurinae (Krajewski *et al.* 1994). A fundamental question that remains unanswered, using either morphological or molecular techniques, is the phylogenetic position of Myrmecobiidae.
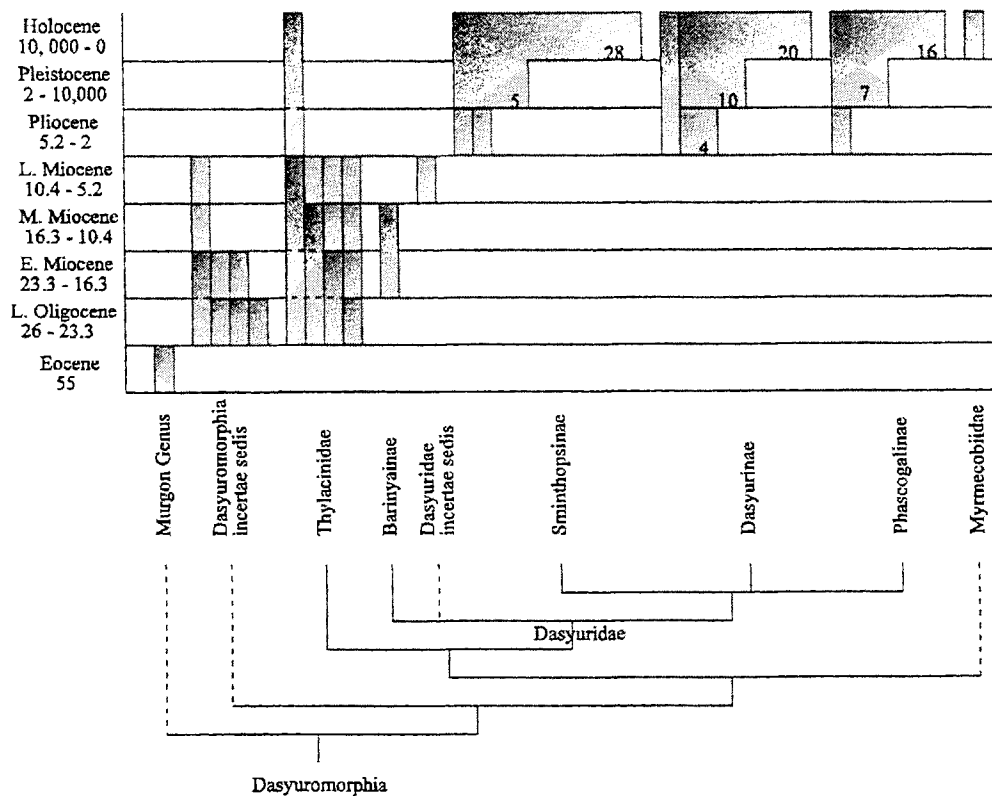
Fig. 1. Australian marsupicarnivore diversity through time and a cladogram of probable relationships within the group. Uncertain relationships are indicated by dashed lines. Although the Murgon taxon is presented in this context, its ordinal relationships are not necessarily with Dasyuromorphia. Each block represents a distinct species, species diversity is indicated by a number. Blocks that extend without breaks through more than one time period indicate evidently long-surviving species.

BANDICOOT DIVERSITY AND EVOLUTION (PERAMELEMORPHIA, MARSUPIALIA): THE FOSSIL EVIDENCE

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MODERN bandicoots (Order Peramelemorphia) comprise three families: Peramelidae, Peroryctidae and Thylacomyidae. Living peramelids (ordinary bandicoots) include eight species in three genera. Living peroryctids (forest bandicoots) include ten species in four genera. Living thylacomyids (bilbies) include two species (one recently extinct) in one genus. Only four fossil bandicoots have been described to date: the early Pliocene *Ischnodon australis* (Stirton 1955), the early Pliocene *Perameles allinghamensis* (Archer 1976) and *Perameles bowensis* (Muirhead *et al.* 1997), and the early to middle Miocene *Yarala burchfieldi* (Muirhead and Filan 1995). While *Ischnodon australis*, *P. allinghamensis* and *P. bowensis* have all been placed in

peramelemorphian families dominated by Recent taxa (i.e., Thylacomyidae for *I. australis* and Peramelidae for *P. allinghamensis* and *P. bowensis*), the older *Y. burchfieldi* cannot be placed within any currently recognised peramelemorphian family (Muirhead and Filan 1995). This Tertiary taxon is regarded as representing a new family that is the plesiomorphic sister group of a peramelid/peroryctid/thylacomyid clade Muirhead 1993, 1994; Fig. 1). No pre-Pleistocene peroryctids are known. Many other fossil peramelemorphians are known but undescribed including taxa from the early Eocene Tingamarra Local Fauna, late Oligocene and early Miocene
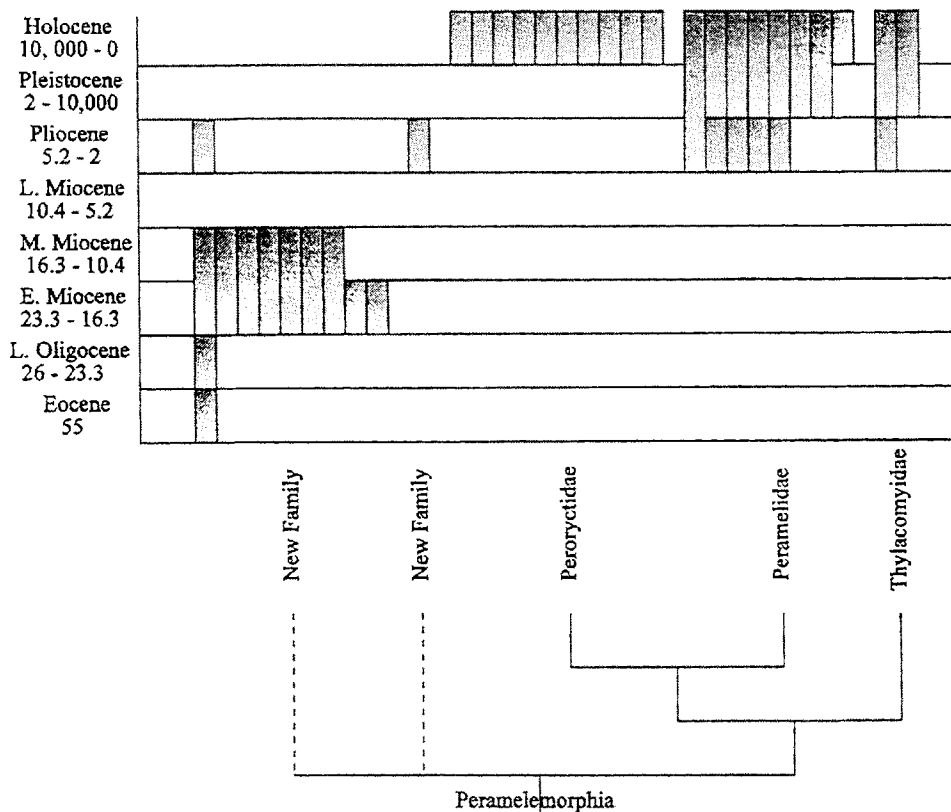
Fig. 1. Bandicoot diversity through time and a cladogram of probable relationships within the group. Uncertain relationships are indicated by dashed lines. Although the Eocene (Murgon) taxon is placed here among the most diverse of the two new families, its familial affinities are uncertain. Each block represents a distinct species. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.

assemblages of central Australia and late Oligocene to early Pliocene assemblages from Riversleigh in northwestern Queensland and early Pliocene taxa from Bluff Downs in northeastern Queensland (Rich *et al.* 1991b; Archer *et al.* 1993; Mackness *et al.* 1993; Muirhead 1994; Woodburne and Case 1996). Like *Y. burchfieldi*, none of the Oligo-Miocene Riversleigh taxa can be placed within the peroryctid/peramelid/thylacomyid clade (Muirhead 1994). Woodburne and Case (1996) similarly support a relatively late radiation of living peramelemorphians based on undescribed taxa from late Oligocene and early Miocene deposits of central Australia. In deposits younger than middle Miocene, there is no evidence of the archaic taxa typical of Oligo-Miocene deposits, with the possible exception of one species of an otherwise Miocene genus in the early Pliocene Hamilton Local Fauna

(Muirhead 1994; Dawson *et al.* 1999). All other Pliocene to Recent taxa fall within the peroryctid/peramelid/thylacomyid clade. This distribution suggests a post middle Miocene-pre Pliocene bottleneck for peramelemorphians, followed by a massive radiation of the 'modern' peramelid/peroryctid/thylacomyid clade – a scenario consistent with late Miocene vicariance events between New Guinea and the Australian mainland (Aplin *et al.* 1993). The fossil evidence, however, is in stark contrast to the Oligocene divergence of the living taxa proposed by biochemical analyses (e.g., 32 myo, Baverstock *et al.* 1990a; 24 myo, Baverstock *et al.* 1990b; 25 myo, Kirsch *et al.* 1997). The wide diversity of the Tertiary taxa and the presence of peramelemorphians in early Eocene deposits from Murgon (Archer *et al.* 1993; Godthelp *et al.* 1992) supports a considerably older derivation for the Peramelemorphia, evidence that provides support for the hypothesis of Kirsch *et al.* (1997) which suggests

on the basis of DNA-DNA hybridisation studies that peramelemorphians are distinct from all other Australian marsupials.

THE EVOLUTIONARY HISTORY OF NOTORYCTIDS, YINGABALANARIDS, YALKAPARIDONTIDS AND OTHER ENIGMATIC GROUPS OF AUSTRALIAN MAMMALS

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THERE are several highly autapomorphic Australian mammals whose relationships to other groups remain unclear. These include: notoryctids, yingabalanarids, yalkaparidontids, *Tingamarra porterorum*, *Thylacotinga bartholomaii*, microbiotheriids, *Ausktribosphenos nyktos* and other inadequately represented or unassessed taxa (Fig. 1).

Living notoryctids, or marsupial moles, include one or two species (depending on authority) in the genus *Notoryctes*. Aplin and Archer (1987), recognising the distinction of notoryctids as well as long-standing disagreements about their phylogenetic relationships, elevated them to ordinal status as notoryctemorphians, a view generally accepted. For example, Westerman (1991), on the basis of DNA-DNA hybridisation studies, supports the view that they should be a distinct order. At least one distinct genus of notoryctids is present in the early Miocene sediments of Riversleigh (Gott 1988; Archer *et al.* 1994, 1997). In terms of postcranial and dental remains, it is unmistakably notoryctid but it is much more plesiomorphic than the living taxa with a pre-zalambdodont molar morphology that clarifies the otherwise enigmatic structure of the upper molars of species of *Notoryctes*. There is no reason known to us why the Miocene taxon could not be ancestral to the species of *Notoryctes*.

Yingabalanara richardsoni (Archer *et al.* 1990), known so far from two isolated lower molars found in early Miocene sediments of the Riversleigh World Heritage area, was conservatively placed in its own family, Yingabalanaridae. The bizarre molar morphology of this animal has made it impossible to determine with confidence its inter-ordinal affinities. Discovery of the second molar (currently under study by one us, Y.W.) may help to narrow the range of possibilities considered by Archer *et al.* (1990) which included marsupials, noctilionoid bats, primates, symmetrodonts, zalambdodonts and tribotheres.

Yalkaparidon coheni and *Y. jonesi* (Archer *et al.* 1988), from the late Oligocene to middle Miocene sediments of the Riversleigh World Heritage area, are among the most specialised of any known Australian mammals. They combine unique and completely zalambdodont molars with an enormous, curved, hyselodont first incisor which extends below the whole of the cheektooth row. A skull of the former suggests marsupial affinities but beyond this nothing is certain. Szalay (1994) regards them to be aberrant diprotodontians presumably on the basis of the incisor formula which is I1-3/1. Archer *et al.* (1988) referred this genus to its own order, the Yalkaparidontia, based on its suite of very distinctive autapomorphic features and lack of undoubted synapomorphies with other orders of marsupials.

Tingamarra porterorum (Godthelp *et al.* 1992) was originally described, on the basis of a single lower molar, as a possible condylarth placental from the early Eocene Tingamarra Local Fauna from Murgon, southeastern Queensland. While a second, larger but otherwise similar taxon has since been recovered from the same deposit, it does not clarify the relationships of this puzzling mammal. It remains a less parsimonious possibility that this is a very distinctive group of marsupials that has converged on placental tooth morphology.
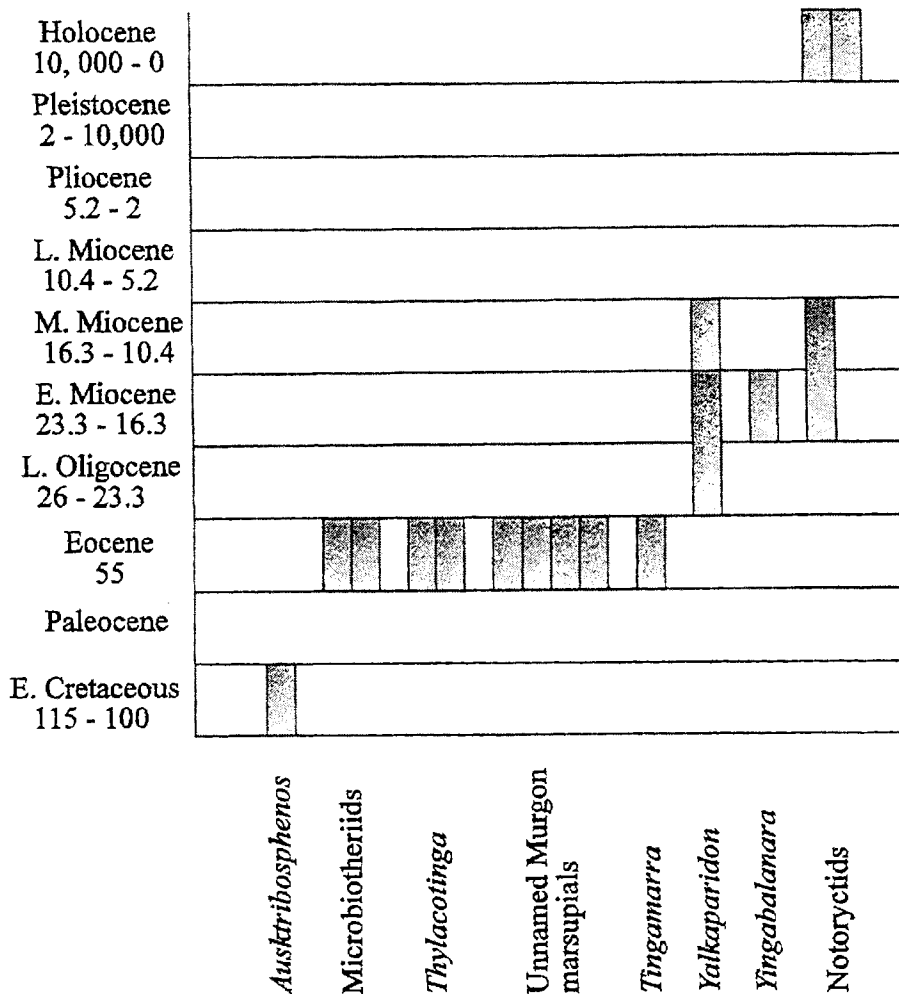
Fig. 1. Diversity through time of notoryctids, yingabalanarids, yalkaparidontids and other enigmatic groups of Australian mammals. Most of these are distinct from each other at the ordinal level. The interordinal relationships of all except (arguably) the microbiotheriids and notoryctids are unclear. Each block represents a distinct species. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.

Thylacotinga bartholomaii (Archer *et al.* 1993) was described, on the basis of isolated teeth from the early Eocene Tingamarra Local Fauna, as a semi-bunodont marsupial with uncertain ordinal affinities. Although the morphology of this animal is distinctive, bunodont molar morphology in general has been developed independently in several families of didelphimorphian, polydolopimorphian and diprotodontian marsupials. Similarities to possibly early Paleocene marsupials from Peru are most striking and the subject of ongoing research.

Since microbiotheriids were first hypothesised by Szalay (1982), on the basis of tarsal bone morphology, to have been the sister group (or ancestral) to Australian marsupials,

many other soft-tissue studies have corroborated this broad hypothesis. The details of the relationship are, however, controversial with other authors alternatively suggesting that microbiotheriids are the sister group to a combined dasyuroid/perameloid clade or the sister group of a combined dasyuroid/diprotodontian clade. Discovery of at least two microbiotheriid-like marsupials in the early Eocene Tingamarra Local Fauna may be seen as further support for this intercontinental connection.

Other enigmatic early Eocene taxa in the Tingamarra Local Fauna are less well represented. These range from bunodont to dilambdodont marsupials, most of which are known only from isolated teeth. Some resemble early Eocene groups known from Argentina such as caroloameghiniids. Continuing work on this deposit will almost certainly enable their relationships to be better assessed and these assessments published.

Ausktribosphenos nyktos (Rich *et al.* 1997) was described, on the basis of a dentary with four teeth, from early Cretaceous (~115 million-year-old) sediments at Flat Rocks, Victoria. Its authors suggest that it is most parsimoniously interpreted as a placental mammal. If so, it would be as old as any previously known in the world (e.g., *Prokennalestes* from Mongolia) and would challenge conventional understanding about the time of arrival of placentals into Australia. This interpretation has prompted spirited debate. Examination of the specimen by one of us (M.A.) suggests that *A. nyktos* may represent either an archaic monotreme, autapomorphic peramurid or a unique ordinal-level group that has converged on therian mammals. Some features of *A. nyktos* cited by Rich *et al.* (1997) as indicative of placental affinities (e.g., molar number, decrease in size posteriorly of molars, possession of wide talonids and possibly the presence of a submolariform last premolar) are also characteristic of monotremes. Peramurid affinities are suggested by the trigonid-like nature of the posterior premolar as in other peramurids including *Peramus* and the putative peramurid *Vincelestes*. Kielan-Jaworowska *et al.* (1998) have suggested that *A. nyktos* may have been derived from early symmetrodont stock based on certain primitive features of the mandible (including the probable presence of attached postdentary bones), the dentition being convergent on a tribosphenic pattern (as may be the case in monotremes: Archer *et al.* 1992). Discovery of additional materials will help to clarify the relationships of this very curious and oldest-known Australian mammal.

A somewhat mammal-like taxon from Lightning Ridge, New South Wales was described, on the basis of an edentulous maxillary fragment, by Rich *et al.* (1989). Alveoli indicate that the teeth were multi-rooted. Although this may well represent a mammal if not a monotreme (Musser, above), it might also represent a derived but non-mammalian synapsid. Until better material is found, this specimen will remain a tantalising mystery.

Several mammalian taxa described as fossils from Australia are even more problematical. Undoubted elephants were described by Richard Owen as *Mastodon australis* (Owen 1844) and *Notelephas australis* (Owen 1882). While it is possible (perhaps even probable) that these fossils were not collected in Australia, collection data indicate otherwise which leaves these records as provocative mysteries.

Other enigmatic mammal fossils include: *Cuscus procuscus* DeVis, 1889 probably from the early Pliocene Chinchilla Local Fauna; *Archizonurus securus* DeVis, 1889 probably from the Chinchilla LF; and *Chronozoon australe* DeVis, 1883 from the Chinchilla LF. It is possible that *C. australe* represents a sirenian but the relationships of the other two DeVis taxa which are each represented by a single incomplete postcranial element, are unclear. Details of these descriptions are compiled in Mahoney and Ride (1975).

DIVERSITY AND RELATIONSHIPS OF LIVING AND EXTINCT KOALAS (PHASCOLARCTIDAE, MARSUPIALIA)

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PHASCOLARCTIDAE is an ancient, once diverse marsupial family represented by a single extant species, the Koala *Phascolarctos cinereus*. The family is believed to occupy a key position near the base of the diprotodontian ordinal tree (Archer 1976; Archer and Hand 1987; Myers *et al.* this work). Recent classifications have separated phascolarctids from all other vombatomorphians (Myers *et al.* this work, fig. 1). Woodburne (1984) erected the superfamily Phascolarctoidea and Aplin and Archer (1987) the infraorder Phascolarctomorphia, each containing the single family Phascolarctidae. Of living groups, koalas are undoubtedly most closely related to vombatids, a relationship supported by both molecular and morphological data.

Six genera and at least 18 species of koalas are currently recognised (Fig. 1). Superficially there appears to have been an alarming decline in koala diversity. However, at any one time since the late Oligocene koala diversity has normally been low with a maximum of only two species contemporaneous in any given faunal assemblage. In terms of abundance, evidence from the fossil record suggests that koala populations are larger now than at any point in their history, a fact which has been linked to the spread of open sclerophyll forest during the mid-late Miocene. Archer and Hand (1987) hypothesised that a co-evolutionary relationship developed between koalas and eucalypts during the early Miocene, the age of the oldest known association between phascolarctids (e.g. *Litokoala kutjamarpensis*) and eucalypts (Stirton *et al.* 1967). Low-diversity rainforest populations of koalas in Australia's mid- to late Tertiary deposits may have resulted from competition with rapidly diversifying pseudocheirids and phalangerids.

Dental morphology within the family has remained relatively conservative over the last 25 million years, but large size differences between fossil koalas are apparent. During the Oligo-Miocene, species of *Madakoala* and *Perikoala* and the plesiomorphic Riversleigh koala were similar in size to the modern species, whereas species of *Nimiokoala* and *Litokoala* were half to two-thirds the size of *P. cinereus*. Conversely, in response to Australia's changing climate and vegetation, Plio-Pleistocene koalas increased markedly in size, culminating in the giant Pleistocene *Cundokoala yorkensis* Pledge, 1992 which was twice the size of the modern species. The establishment of *Cundokoala* as a genus distinct from *Phascolarctos* has been questioned (Black and Archer 1997a) and may not be justified on the basis of morphological differences. Consequently, *C. yorkensis* has been regarded here (Fig. 1) as a giant species of *Phascolarctos*. Similarly, features used to distinguish *Phascolarctos maris* Pledge, 1987b from *P. stirtoni* Bartholomai, 1968 may prove to fall within the boundaries of expected intraspecific variation of the latter. However, until this issue is resolved (Black, in prep.), they are treated as distinct species.

Current understanding of phascolarctid relationships based on dental morphology (Black and Archer 1997a) are presented in Figure 1. Species of *Phascolarctos* are the most derived phascolarctids and are most closely related to species of *Litokoala*. A new genus and species of koala from Riversleigh, northwestern Queensland (Black, unpubl.) is the most plesiomorphic koala. Previous analyses (Woodburne *et al.* 1987a; Black and Archer 1997a) tentatively include species of *Koobor* as plesiomorphic phascolarctids yet raise doubts about their position within the family. Pledge (1987a) suggested *Koobor* is more closely aligned with ilariids than phascolarctids but Myers and Archer (1997) found little support for this inclusion. Clarification of *Koobor*'s position within Phascolarctomorphia requires discovery of more complete material.
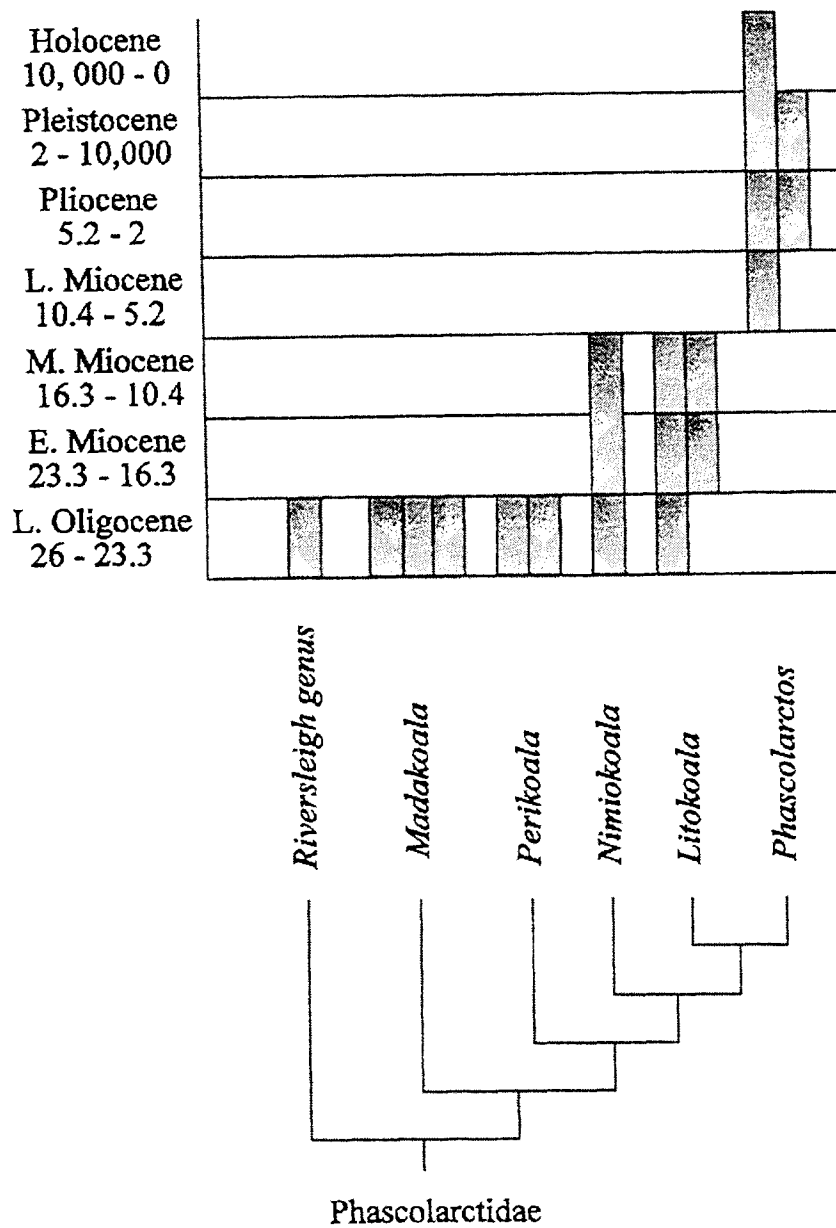
Fig. 1. Koala diversity through time and a cladogram of relationships within the group. Each block represents a distinct species. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.

DIVERSITY AND EVOLUTIONARY RELATIONSHIPS OF ILARIIDS, WYNYARDIIDS, VOMBATIDS AND RELATED GROUPS OF MARSUPIALS

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PRIOR to their discovery at Riversleigh, ilariids, with koala-like selenodont molar morphology, were known only from late Oligocene (25.5 mya) central Australian deposits: *Ilaria illumidens*, from the Pinpa Local Fauna, Lake Pinpa; and *I. lawsoni*, from the Ditjimanka Local Fauna, Lake Palankarinna (Tedford and Woodburne 1987; Woodburne *et al.* 1994). *Kuterintja ngama* (Pledge 1987), represented by one upper molar from the Ngama Local Fauna. Mammalon Hill, Lake Palankarinna, was slightly younger at approximately 24.8 mya. The geographic range of the latter species was significantly extended with discovery of indistinguishable cranio-dental material from White Hunter Site at Riversleigh, enabling tentative correlation of the central and northern Australian sites (Myers and Archer 1997).

No early to late Miocene sites at Riversleigh (Systems B and C; Creaser 1997) have produced ilariids, despite extensive investigation of sediments this age. While ilariid diversity may have been higher during the early stages of the late Oligocene, it apparently declined towards the latter stages resulting in family-level extinction by the beginning of the Miocene.

Ilariids are considered to be the primitive sister group of the Wynyardiidae and Diprotodontoidea (e.g., Munson 1992). Pledge (1987) considered *K. ngama* to be ancestral to the Pliocene species *Koobor jimbarratti* which would then be regarded as an ilariid rather than a phascolarctid. Myers and Archer (1997) considered the shared dental features of *Koobor* spp. and *Kuterintja ngama* to be symplesiomorphic. *Koobor* was found to be a primitive sister group of wynyardiids plus ilariids. Discovery of lower cheekteeth should resolve *Koobor's* position within Vombatiformes. In the meantime, we have left the position of *Koobor* as part of an unresolved polychotomy involving phascolarctids and vombatomorphians (Fig. 1).

The genotypic wynyardiid is a unique specimen, *Wynyardia bassiana*, comprising part of the skeleton and skull but lacking any teeth. Consequently, other species are only referred to this family on the basis, initially, of similar postcranial morphology, and subsequently dental similarity. There are thus at least six species in three genera, found in one or more of four localities: Tasmania (*Wynyardia*, Spencer 1901), early Miocene, about 20-21 my); Frome Basin, South Australia (*Muramura* sp. nov., Pinpa LF; *Namilamadeta snideri* (Rich and Archer 1979), Tarkarooloo LF); Lake Palankarinna, South Australia (*Muramura williamsi* (Pledge 1987), zone A Minkina LF; *Namilamadeta* sp. indet., zone D Ngama LF), and Riversleigh (2-3 *Namilamadeta* spp. nov., Systems A and B), and ranging in age from late Oligocene to early Miocene.

The skeletons of *Muramura* spp. allowed comparison with *Wynyardia* (Tedford *et al.* 1977), and their teeth with *Namilamadeta* (Rich and Archer 1979; Pledge 1987). Skulls are known for all three genera, but basicranial evidence for interrelationships is still to be assessed. Dentally, *Muramura* appears to be more plesiomorphic than *Namilamadeta*, and the skull, too, is more primitive. The considerably smaller skull of *Wynyardia* shows more resemblance to *Namilamadeta* from some Riversleigh sites, but still differs from all species. In general terms, the skulls of wynyardiids show remarkable gross similarities to those of the plesiomorphic wombat *Warendja wakefieldi* (Pledge 1992). Postcranially, *Wynyardia* and *Muramura* species are similar where they can be compared, and show notable similarities with wombats, although they are more plesiomorphic.
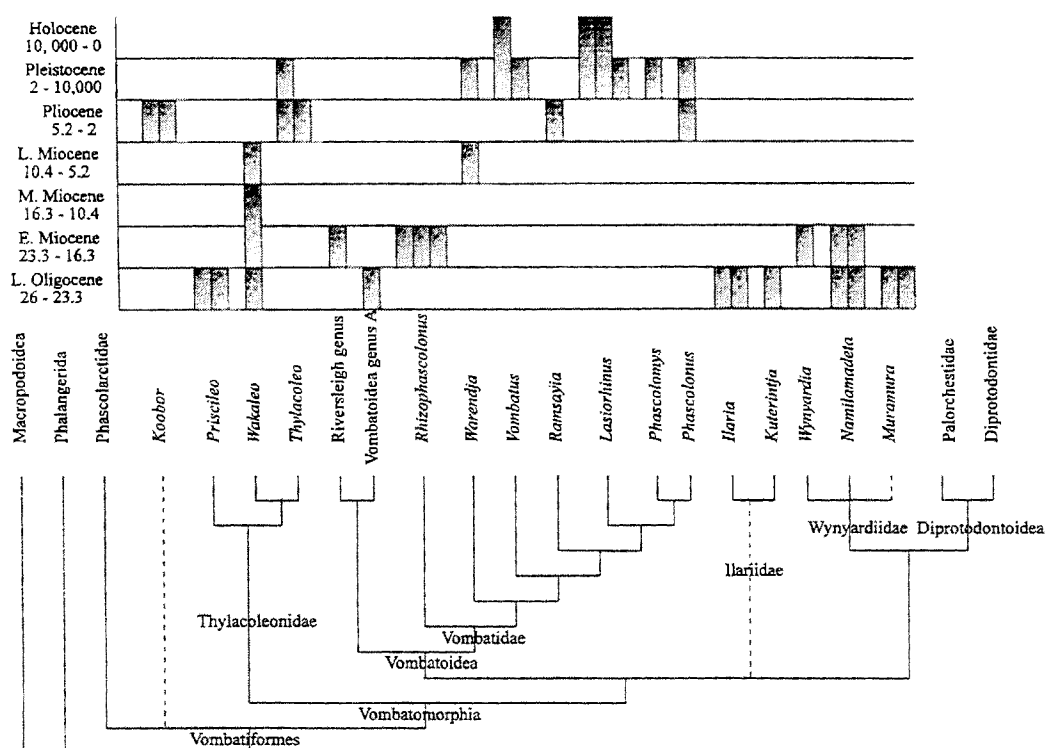
Fig. 1. Diversity through time and a cladogram of probable interfamilial and intergeneric relationships of ilariids, wynyardiids, vombatids, thylacoleonids and related groups of marsupials. Uncertain relationships are indicated by dashed lines. Each block represents a distinct species. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.

Phylogenetic relationships among vombatoids remain unresolved. Work in progress (Krikmann 1993; M. Archer and A. Krikmann) suggests there were three families. The first, from early Miocene Riversleigh deposits and the late Oligocene Pinpa Local Fauna (Tedford *et al.* 1977, as 'Vombatoidea Genus A'), is represented by primitive, low-crowned, browsing wombats with complex molar morphology and rooted teeth. The second includes *Rhizophascolonus crowcrofti* and at least two other wombat species with rooted but high-crowned teeth from the early to middle Miocene of Riversleigh and the central Australian Kutjamarpu Local Fauna. The third, Vombatidae, includes a

number of grazing wombat species with unrooted teeth, the earliest of which is a new species of *Warendja* from the late Miocene Encore Local Fauna of Riversleigh. However, the greatest diversity of vombatids did not occur until the early Pliocene (*Phascolonus* and *Ramsayia*) and Pleistocene (*Warendja, Phascolomys, Vombatus, Lasiorhinus*), with the increase paralleling the drying out and opening up of the continent and consequent proliferation of grasslands. There are three extant vombatids, species of *Vombatus* and *Lasiorhinus*, one of which (*Lasiorhinus krefftii*) is seriously endangered.

DIVERSITY AND RELATIONSHIPS OF DIPROTODONTOID MARSUPIALS

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TWO families of diprotodontoids are currently recognised: Palorchestidae (2 genera, 7 species); and Diprotodontidae containing Zygomaturinae (13 genera, 25 species) and Diprotodontinae (8 genera, 12 species). A third diprotodontid subfamily, the Nototheriinae (Stirton *et al*. 1967), is no longer considered valid (Archer 1977). A yet-to-be-described Pleistocene genus with two species that have both zygomaturine and diprotodontine features may constitute a third diprotodontid subfamily. The time at which Palorchestidae and Diprotodontidae diverged from a common ancestor is currently not known, but both families were distinct by the late Oligocene (Fig. 1).
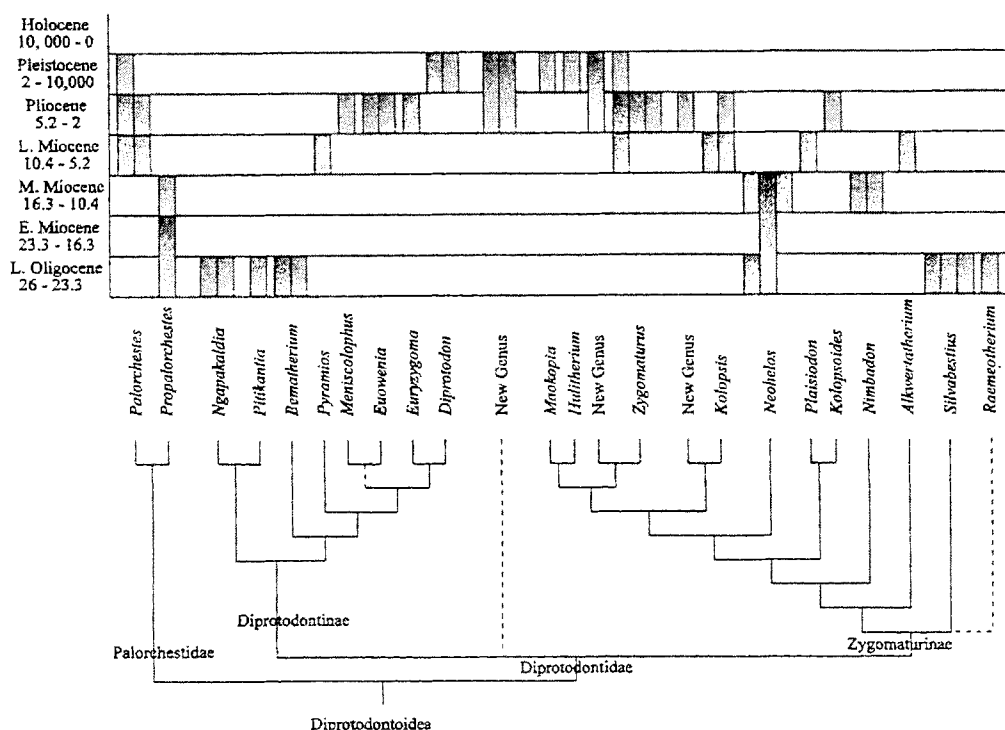
Fig. 1. Diprotodontoid diversity through time and a cladogram of probable interfamilial and intergeneric relationships. Uncertain relationships are indicated by dashed lines. Each block represents a distinct species. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.

Zygomaturine diprotodontids exhibit a higher diversity in Tertiary fossil assemblages than either diprotodontines or palorchestids possibly indicating an ability to exploit a greater range of environments (Black 1997b). Palorchestids are rare components of fossil assemblages which may indicate a solitary habit. Normally, no more than one species is present in faunal assemblages spanning the last 25 million years. Similarly, diprotodontines, although prolific in the late Oligocene and early Miocene, are rare throughout the rest of the Miocene but then diversify again in the Plio-Pleistocene. Drying of the Australian continent resulted in development of gigantic, highly specialised forms characterised by features useful for processing coarser food (e.g. diastemal crests and elaboration of blades in the dentition). In contrast, the New Guinea diprotodontoid

radiation consists of 'dwarf' zygomaturine species variously interpreted as either relict populations from Miocene Australia (Flannery 1988) or a mid-to-late Pliocene colonisation by a few derived Australian genera (Murray 1992). The reasons for the eventual extinction of the entire diprotodontoid radiation by the end of the Pleistocene has yet to be determined but it was probably a combination of factors including interaction with early humans, modification of the Australian environment by fire (which favoured the development of grasslands) and natural cycles of climatic change.

Interpretation of the phylogenetic relationships of diprotodontoids is hampered by the fact that many taxa are known only from isolated elements and there is a general paucity of late Miocene and early Pliocene material. Analysis of variation in several groups has revealed sexual dimorphism and ontogenetic variation which has not been taken into account in some taxonomic assignments. There has also been an underestimation of diversity in the late Tertiary with assignment often made to taxonomic 'waste bins' like 'notothere'. The current understanding of phylogenetic relationships is shown in Figure 1. Monophyly of the group has been questioned

(Archer 1984; Aplin and Archer 1987; Murray 1990a), there being few synapomorphies recognised. Within Diprotodontidae, zygomaturines appear to have been derived from a primitive diprotodontine-like form in which the parastyle on P3 was reduced, a theory first proposed by Stirton *et al.* (1967) and later confirmed by the discovery and analysis of dentitions of *Silvabestius michaelbirti* from Riversleigh (Black and Archer 1997b). This species is believed to be antecedent to the entire zygomaturine radiation (Black and Archer 1997b). Previous authors (e.g. Aplin and Archer 1987; Marshall *et al.* 1990) include *Ngapakaldia* and *Pitikantia* within Palorchestidae on the basis of similarities in the basicranium, features since recognised (e.g. Archer 1984; Murray 1986,1990a) as plesiomorphic for Vombatomorphia. Murray's (1990b) description of *Propalorchestes* dentitions demonstrates that it is the plesiomorphic sister group of *Palorchestes*, exhibiting subselenodont molars transitional between selenodont wynyardiids and the fully bilophodont molars of *Palorchestes*. Consequently, *Ngapakaldia* and *Pitikantia* are currently recognised as primitive diprotodontines (Murray 1990; Black 1997).

DIVERSITY AND EVOLUTIONARY RELATIONSHIPS OF MARSUPIAL LIONS

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THE marsupial lion family Thylacoleonidae has a fossil history that spans the late Oligocene through to late Pleistocene. There are three genera and a total of nine species (Myers *et al.* this work, fig. 1). The oldest member of the family is the late Oligocene cat-sized *Priscileo pitikantensis* from central Australia (Rauscher 1987). A second, smaller species, *P. roskellyae*, has been described on the basis of the dentition and a nearly complete skull from early Miocene sediments of the Riversleigh World Heritage area (Gillespie 1997). The dog- to leopard-sized species of *Wakaleo* include *W. oldfieldi* from the early Miocene Kutjamarpu Local Fauna of South Australia and faunal assemblages at Riversleigh, *W. vanderleuri* (also known from a complete skull) from the middle Miocene Bullock Creek Local Fauna of the Northern Territory, and *W. alcootaensis* from the late Miocene Alcoota Local Fauna of the Northern Territory (Clemens and Plane 1974; Archer and Rich 1982; Murray *et al.* 1987). A fourth species

representing a smaller, more plesiomorphic form is currently being described (Gillespie in press) from late Oligocene sediments at Riversleigh (Archer *et al.* 1997c). The dog- to lion-sized species of *Thylacoleo* (Wroe *et al.* submitted) include *T. crassidentatus* and *T. hilli*, both from widespread early Pliocene deposits, and *T. carnifex* which is very widespread in Pleistocene deposits (Archer and Dawson 1982).

Lineages of both *Wakaleo* and *Thylacoleo* demonstrate morphoclinal changes through time that link otherwise distinct species. These changes generally include an increase in size, an increase in the proportional length of P3/3, and loss or reduction of the posterior molars (Murray and Megirian 1990; Archer and Dawson 1982). Although Tertiary marsupial lions are not common as fossils (a fact presumably reflecting their ecological role as carnivores), what is known suggests that up to two different-sized species

coexisted in single ecosystems. For example, in the late Oligocene to early Miocene deposits of Riversleigh, a small species of *Priscileo* coexisted with a much larger species of *Wakaleo*. Similarly, in the Bow Local Fauna of New South Wales, the small *Thylacoleo hilli* coexisted with the much larger *T. crassidentatus* (Archer and Dawson 1982).

Hypothetical intrafamilial relationships for thylacoleonids are shown as part of Figure 1 in Myers *et al.* (this work). Understanding of these relationships has changed with discovery of new Riversleigh taxa. Previously the structural differences between species of *Wakaleo* and *Thylacoleo*, especially loss of P[1] and P[2] in *Wakaleo*, did not support an ancestor/descendant relationship between the two genera (Clemens and Plane 1976). However, the presence of these teeth in a new species of *Wakaleo* from Riversleigh makes it possible to argue that this lineage was ancestral to the species of *Thylacoleo*. In addition, species of *Priscileo* exhibit no features that prevent them from being ancestral to species of *Wakaleo* and *Thylacoleo*.

DIVERSITY AND EVOLUTION OF PHALANGERID, EKTOPODONTID, MIRALINID AND PILKIPILDRID MARSUPIALS

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THE superfamily Phalangeroidea contains at least three families: Phalangeridae, the extinct Miralinidae and Ektopodontidae. Pilkipildridae may also belong here, but there is significant doubt about its relationships (e.g., Archer *et al.* 1987; Brammall and Archer this work).

Phalangerids are found throughout much of Meganesia. There are six genera: the bear cuscus *Ailurops*; cuscuses *Phalanger, Strigocuscus* and *Spilocuscus*; brush-tailed possums *Trichosurus*; and scaly-tailed possums *Wyulda*. Four phalangerid species have been described from the fossil record: *Trichosurus dicksoni* and *Strigocuscus reidi* from Miocene assemblages in the Riversleigh World Heritage area of northwestern Queensland (Flannery and Archer 1987) and *Trichosurus hamiltonensis* and *Strigocuscus notialis* from the early Pliocene Hamilton Local Fauna of Victoria (Flannery *et al.* 1987b). A species of *Wyulda* has also been reported but not named from the Miocene sediments of Riversleigh (Archer *et al.* 1994).

Miralinids include species of *Miralina* from Oligo-Miocene sediments in central Australia (Woodburne *et al.* 1987b) and an undescribed genus and species from the early Miocene of Riversleigh.

Four genera of ektopodontids have been described: *Ektopodon* and *Chunia* from Oligo-Miocene assemblages in central Australia (Woodburne and Clemens 1986a; Woodburne *et al.* 1994); and *Darcius* from the early Pliocene Hamilton Local Fauna of Victoria (Rich 1986).

Another undescribed genus is known from Riversleigh. An unnamed and as yet generically unassessed ektopodontid is present in the early Pleistocene Portland Local Fauna of Victoria.

Two genera of pilkipildrids have been described: *Djilgaringa* from Riversleigh and central Australia; and *Pilkipildra* from central Australia (Archer *et al.* 1987). Additional potentially distinct pilkipildrid material from Riversleigh is currently under study by M.O. Woodburne.

Relationships between phalangerids, miralinids, ektopodontids and pilkipildrids are unclear (Fig. 1). Historically, the very strange teeth of ektopodontids made it difficult to place them phylogenetically. With discovery of the more 'conventional' molars of species of *Chunia* and the less specialised dentitions of miralinids, it became apparent that ektopodontids were at least distantly related to phalangerids (Tedford *et al.* 1977; Woodburne and Clemens 1986a; Woodburne *et al.* 1987b). Miralinids and ektopodontids are now thought to be sister groups, and together form the sister group of phalangerids (Aplin and Archer 1987; Woodburne *et al.* 1987b). Pilkipildrids are considered *incertae sedis* by Archer *et al.* (1987). They suggested that this family is either the sister group of petauroids, the sister group of phalangeroids or part of an unresolved trichotomy.

Relationships within Ektopodontidae and Phalangeridae are still contentious. *Chunia* is

considered to be the most plesiomorphic ektopodontid, and *Ektopodon* and *Darcius* are derived sister groups (Woodburne and Clemens 1986b). The new genus from Riversleigh may put these relationships in doubt. Phalangerids were originally separated into four genera: *Ailurops*, *Phalanger*, *Trichosurus* and *Wyulda*. *Phalanger* has since been considered paraphyletic and split into three genera: *Phalanger*, *Strigocuscus* and

Spilocuscus (Flannery *et al.* 1987a). *Strigocuscus* was placed as the sister genus of *Trichosurus* plus *Wyulda* based on morphological characters (ibid). Molecular studies, however, placed some members of *Strigocuscus* back within *Phalanger* (Colgan *et al.* 1993). The uncertain position of *Strigocuscus gymnotis* within Phalangeridae could affect generic allocation of fossil species originally placed in this genus (*viz.*, *S. reidi* and *S. notialis*).
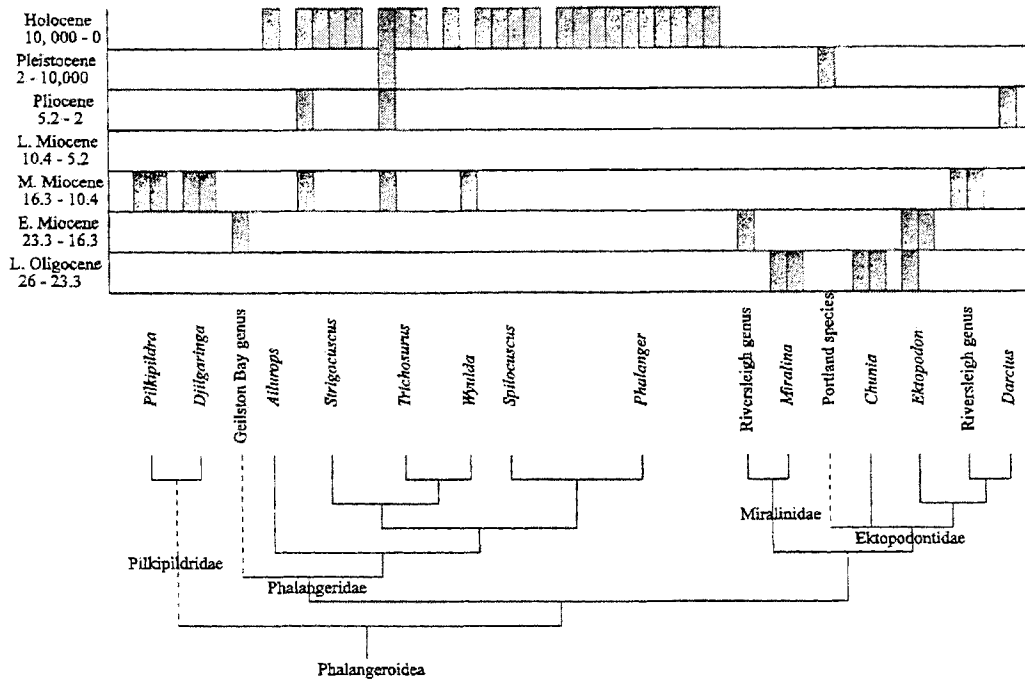

Fig. 1. Diversity through time and a cladogram of probable interfamilial and intergeneric relationships of phalangerid, ektopodontid, miralinid and pilkipildrid marsupials. Uncertain relationships are indicated by dashed lines. Each block represents a distinct species. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.

LIVING AND EXTINCT PETAURIDS, ACROBATIDS, TARSIPEDIDS AND BURRAMYIDS (MARSUPIALIA): RELATIONSHIPS AND DIVERSITY THROUGH TIME

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THE smallest contemporary possums of Australia and New Guinea are placed in four families: the Petauridae (*Petaurus*, *Gymnobelideus*, *Dactylopsila*); Acrobatidae (*Acrobates*, *Distoechurus*); Tarsipedidae (*Tarsipes*); and Burramyidae (*Cercartetus*, *Burramys*) (Aplin and Archer 1987; Strahan 1995). All living representatives (except *Burramys parvus*) are arboreal although some live in heath (tarsipedids and some species of *Cercartetus*). All are scansorial. The species of two genera (*Petaurus*, *Acrobates*) are also gliders. All of these families have a Tertiary as well as Quaternary record except tarsipedids which as yet have no pre-Pleistocene record (Fig. 1).
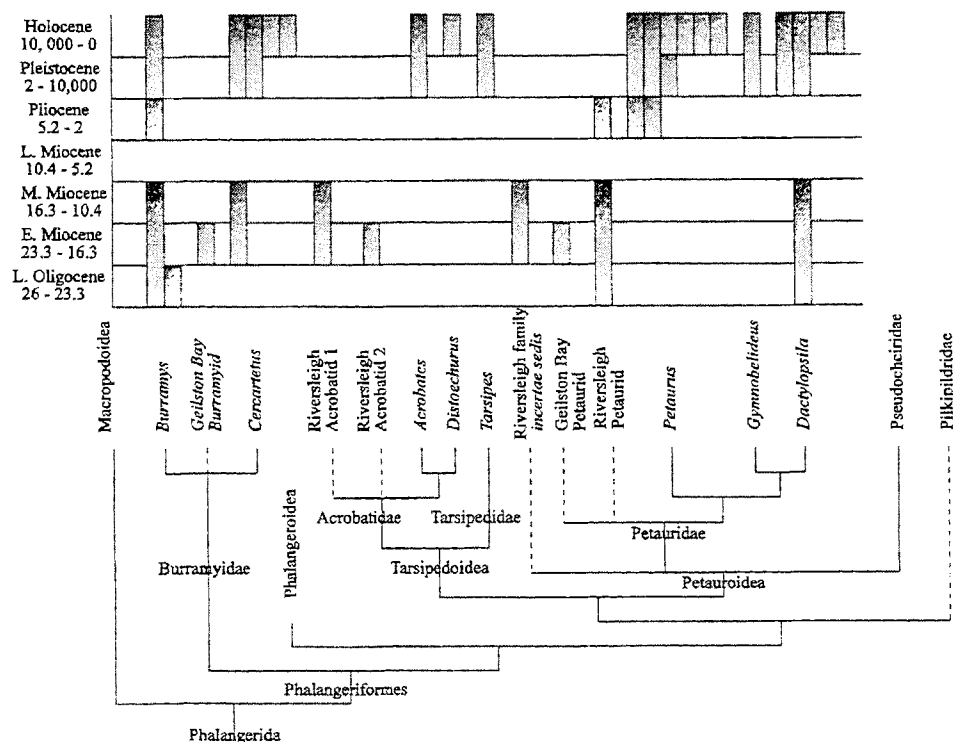
Fig. 1. Diversity through time and a cladogram of probable interfamilial and intergeneric relationships of acrobatids, tarsipedids and burramyids. Uncertain relationships are indicated by dashed lines. Each block represents a distinct species. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species

Fossil burramyids ('pygmy possums') include a plethora of relatively specialised species of *Burramys* with plagiaulacoid premolars, all so far only known from lowland rainforest assemblages of late Oligocene (taxa in the Ngama and diverse Riversleigh assemblages; Pledge 1987c; Brammall and Archer 1997) to early Pliocene age (Turnbull *et al.* 1987b) in

northwestern Queensland, the Tirari Desert and western Victoria. An unnamed burramyid was reported from the early Miocene Geilston Bay Local Fauna (Tedford *et al.* 1975). At least one (unnamed) Tertiary fossil species of *Cercartetus* is known from Miocene sediments at Riversleigh. Records of large species '...similar in some ways to the living *Cercartetus...*' (e.g., Woodburne *et al.* 1985, p355) from late Oligocene deposits of the Tirari Desert and Frome Embayment actually refer to pilkipildrid possums (Crosby *et al.* this work).

There are at least two undescribed acrobatids ('feather-tail possums') from early and middle Miocene deposits of Riversleigh that represent this highly specialised group. The living arboreal *Distoechurus pennatus* is a rainforest inhabitant in contrast to the glider *Acrobates pygmaeus* which inhabits wet and dry sclerophyl forests.

The fossil record of petaurids is more diverse.

Dactylopsila ('striped possums'), modern species of which are strictly rainforest inhabitants, have been found in late Oligocene to middle Miocene deposits at Riversleigh. The oldest representatives of the genus *Petaurus* are from the early Pliocene Hamilton Local Fauna in Victoria. Although the postcranial anatomy of the Pliocene taxa is unknown, all modern species of this genus are gliders. Another generically distinctive group of petaurids, from late Oligocene to middle Miocene deposits at Riversleigh, appears to be closely related to an early Pliocene taxon from the Rackham's Roost Local Fauna of Riversleigh. At least one petauroid is interpreted to be among the unnamed taxa from the early Miocene Geilston Bay Local Fauna of Tasmania (Tedford and Kemp 1998). A highly distinctive petaurid-like group, known from the early to middle Miocene of Riversleigh, appears to represent a plesiomorphic sister group to Petauridae.

LIVING AND EXTINCT PSEUDOCHEIRIDS (MARSUPIALIA, PSEUDOCHEIRIDAE): PHYLOGENETIC RELATIONSHIPS AND CHANGES IN DIVERSITY THROUGH TIME

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THE family Pseudocheiridae is comprised of ten genera of ringtail possums and greater gliders. Six genera (*Hemibelideus, Petauroides, Pseudochirops, Petropseudes, Pseudocheirus* and *Pseudochirulus*) contain extant as well as extinct species; four genera (*Paljara, Pildra, Marlu* and *Pseudokoala*) contain only extinct species. The highest species-level diversity for this family occurs today in rainforest environments of northern Australia and New Guinea. The only living species found in relatively drier areas of Australia, such as open forests and woodlands, are the Common Ringtail (*Pseudocheirus peregrinus*), Greater Glider (*Petauroides volans*) and Rock Ringtail (*Petropseudes dahli*).

Pseudocheirid species diversity was greater in the late Oligocene to early Miocene than at present (Fig. 1) with, for example, up to nine species

present in a single local fauna at Riversleigh (Archer 1992; Archer *et al.* 1994).

The oldest-known pseudocheirids are late Oligocene in age from the Tirari Desert and Frome Basin of South Australia and the Riversleigh World Heritage area of northwestern Queensland. These are referable to the genera *Pildra, Marlu* and *Paljara* (Woodburne *et al.* 1987c; Archer 1992; Archer *et al.* 1997a). The species of *Paljara* include the most plesiomorphic known pseudocheirids which appear to retain, for example, well-developed paraconids on the first lower molar. Current research on undescribed Riversleigh specimens referable to *Paljara* indicates that more than one species and possibly up to three species are represented by the material. The species of *Pildra* are the next most plesiomorphic and are highly diverse in the
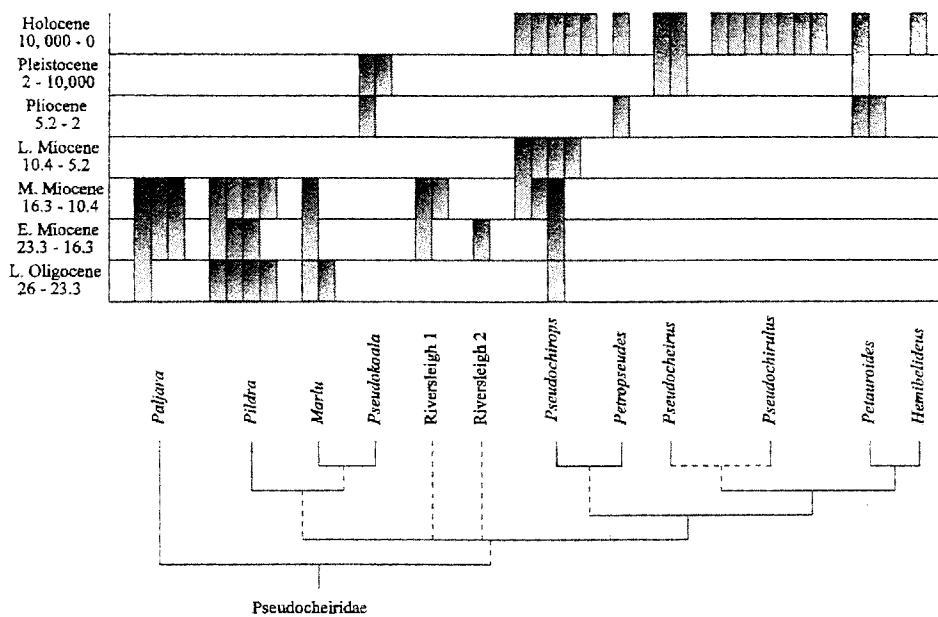
Fig. 1. Pseudocheirid diversity through time and a cladogram of probable intergeneric relationships. Uncertain relationships are indicated by dashed lines. Each block represents a distinct species. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.

Oligocene to Miocene sediments of South Australia and Queensland. Species of *Marlu* are less diverse being known from possibly only two species in the Tirari Desert deposits, one of which may also be represented at Riversleigh.

Species of *Pseudokoala* are known from the early Pliocene Hamilton LF and from various Pleistocene deposits in South Australia and New South Wales. Archer *et al.* (1997a) suggest that the Miocene or early Pliocene genus *Corracheirus* Pledge, 1992 is a junior synonym of *Pseudokoala* and that all species of this genus occupied rainforest. *Pseudokoala cathysantamaria* from the early Pleistocene Portland Local Fauna of Victoria was a giant megafaunal ringtail that weighed possibly ten kilograms.

Of the extant ringtail genera, *Pseudochirops* has the oldest record with a minimum of three as yet unnamed species occurring in Oligo-Miocene deposits at Riversleigh. Another as yet unnamed extinct species possibly referable to *Pseudochirops* occurs in the late Miocene Alcoota LF (Archer and Bartholomai 1978). *Petropseudes*, which some authors regard to be a junior synonym of *Pseudochirops*, has a fossil record that extends

back to the early Pliocene at Riversleigh. From the same early Pliocene Riversleigh deposit also comes the oldest record of the living species, *P. dahli*. *Petauroides* may be represented by the early Pliocene species *P. stirtoni* and *marshalli* (Turnbull and Lundelius 1970; Turnbull *et al.* 1987a; Archer 1984). There are no pre-Pleistocene records for *Pseudocheirus*, *Pseudochirulus* or *Hemibelideus*.

Considered overall, a massive radiation of archaic ringtails clearly characterised the late Oligocene to middle Miocene. The only 'modern' group represented among these is *Pseudochirops*. We suspect that our sustained failure to find Tertiary records for *Pseudochirulus* and *Pseudocheirus* indicate that they were a late Miocene to Pliocene and perhaps Pleistocene radiation in New Guinea and Australia respectively.

Intergeneric phylogenetic relationships of pseudocheirids are either unresolved or controversial (Fig. 1). Woodburne *et al.* (1987c) have proposed that *Pildra* and the common ancestor of *Marlu* and *Pseudokoala* are sister taxa. However, Springer (1993), on the basis of dental synapomorphies, suggests in contrast that species of *Marlu*, *Pseudokoala* and extant pseudocheirids may form a clade to the exclusion of species of *Pildra* and *Paljara*. Relationships of extinct to extant ringtails

have not been clarified, in part because of the incomplete fossil record. Many different fields of research (molecular and morphological) provide evidence to suggest that, among extant genera, *Hemibelideus* and *Petauroides* are sister taxa, *Pseudochirops* and *Petropseudes* are sister taxa (Archer 1984; Baverstock 1984; Baverstock *et al.* 1987, 1990c; Kirsch *et al.* 1997; McKay 1984; McQuade 1984; Springer 1993; Springer *et al.* 1992), and *Pseudochirulus* forms a monophyletic group (Archer 1984; Baverstock *et al.* 1990; Flannery 1994; Springer 1993; Springer *et al.* 1992). The phylogenetic position of *Pseudocheirus* and the trichotomy between *Hemibelideus-Petauroides*, *Pseudochirops-Petropseudes* and *Pseudochirulus* remain unresolved because of disagreements about the most appropriate methods of phylogenetic analysis.

Petauroids (pseudocheirids plus petaurids) appear to be most closely related to tarsipedoids (acrobatids and tarsipedids) (Aplin and Archer 1987; Baverstock 1984; Baverstock *et al.* 1987; Kirsch *et al.* 1997).

The relationships of petauroids to burramyoids and phalangeroids have not been clarified; see Springer and Kirsch (1991) and Springer and Woodburne (1989) for conflicting phylogenetic conclusions.

Archer (1984) and Woodburne *et al.* (1987c) have suggested the possibility that pseudocheirids are the outgroup to all other phalangeridans because of their retention of many plesiomorphic dental features (e.g., complete diprotodontian dental formula, paraconid on the first lower molar and a well-developed stylar shelf on the upper molars).

EVOLUTION AND DIVERSITY OF KANGAROOS (MACROPODOIDEA, MARSUPIALIA)

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NUMEROUS attempts have been made to unravel the complexities of kangaroo phylogeny. Character systems utilised in such analyses include: morphological (e.g., Bensley 1903; Raven and Gregory 1946; Tate 1948; Archer 1984; Flannery 1989); cytological (e.g., Sharman 1989); immunological (e.g., Kirsch 1977; Baverstock *et al.* 1989, 1990b); and molecular biology (e.g., Westerman *et al.* 1990; Kirsch and Foeste 1995). Earlier attempts, particularly those reliant on morphological characters, were hampered by the lack of an adequate fossil record extending much further back than the Pliocene. That situation has improved with discovery of older Tertiary kangaroos in a variety of deposits in the Northern Territory (late Miocene deposits at Alcoota and Bullock Creek), South Australia (deposits in the Lake Eyre and Frome Basins) and Queensland (Riversleigh). Riversleigh is particularly important because it includes sites ranging from late Oligocene to Holocene in age, and which yield very well preserved kangaroo fossil remains, including complete skulls and some articulated skeletons for many taxa.

Flannery's (1989) analysis of macropodoid phylogeny is the first comprehensive attempt to incorporate data obtained from Oligo-Miocene taxa. Notable among these are lophodont representatives of two previously unknown groups: Balbarinae and Bulungamayinae, both described by Flannery *et al.* (1983). They assigned Balbarinae to Macropodidae and Bulungamayinae to Potoroidae. Case (1984) disagrees with placement of Bulungamayinae within Potoroidae, maintaining that lophodonty represents a macropodid synapomorphy. Flannery's (1989) phylogenetic analysis supports placement of Bulungamayinae as a monophyletic group within Potoroidae, but indicates Balbarinae as a likely paraphyletic macropodid group, directly ancestral to both Macropodinae and Sthenurinae.

Cooke (1997a) indicates that lophodonty has arisen independently in these two subfamilies, representing another example of the rampant evolutionary convergence that plagues kangaroo phylogenetics. Cooke (1997a, in press) argues that characters such as a laterally broad M_1 trigonid, absence of ornamentation of the posterior face of the hypolophid of lower molars, elongate permanent premolars and parietal-alisphenoid contact on the lateral wall of the cranium, represent synapomorphies uniting bulungamayines and macropodids. A phylogenetic analysis by Cooke (1997b) incorporates cranial and dental characters present

in remains discovered at Riversleigh subsequent to Flannery's (1989) analysis. It indicates that Balbarinae represent a monophyletic group, basal to all other macropodoids (and therefore should be elevated to familial status as Balbaridae). This analysis supports the monophyly of Hypsiprymnodontidae (Ride 1993) but indicates that bulungamayines are members of a large, pectinately branching clade that includes as bulungamayines some taxa previously regarded to be potoroines (*Bettongia moyesi*, *Wakiewakie*

lawsoni and *Purtia mosaicus*), sthenurines and macropodines. Bulungamayines appear in this analysis to be a paraphyletic stem group, occupying much the same position as Flannery (1989) argued for balbarines.

Recent studies of cranial remains of the propleopine *Ekaltadeta ima* by Wroe *et al.* (1998) indicate potential synapomorphies uniting Balbarinae and Propleopinae which casts some doubt on the monophyly of Hypsiprymnodontidae (*sensu* Ride 1993; see Fig. 1).
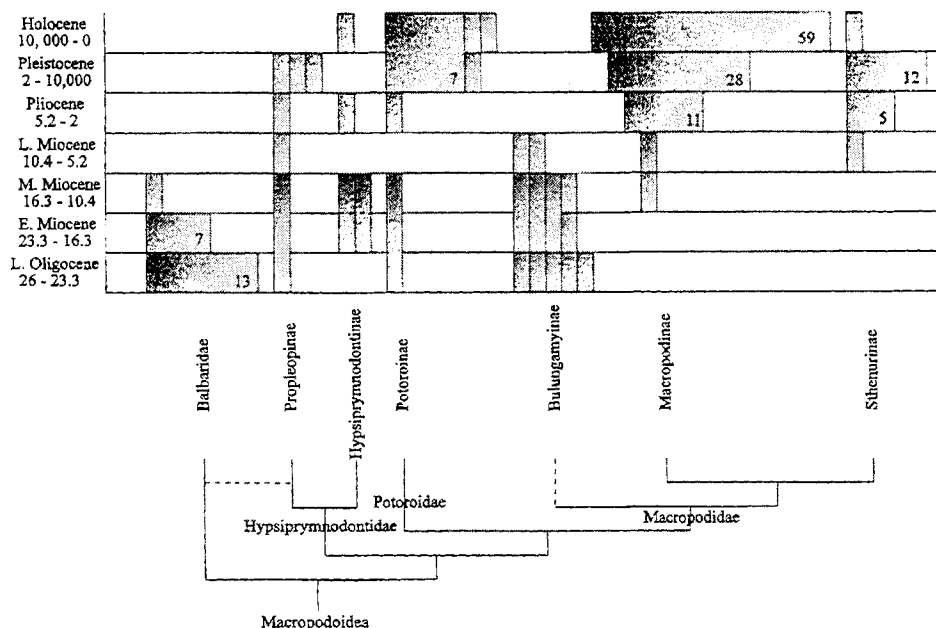

Fig. 1. Kangaroo diversity through time and a cladogram of probable interfamilial and subfamilial relationships. Uncertain relationships are indicated by dashed lines. Particularly uncertain is the position of Propleopinae. Each block represents a distinct species unless species diversity is indicated by a number. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species. Unindicated are many Pleistocene occurrences of living macropodids among the undifferentiated Pleistocene cohort.

More recent phylogenetic analysis of macropodoids by Kear (1998), utilising postcranial morphology, supports the monophyly of balbarines and their status as a basal macropodoid group. However, it also suggests that Bulungamayinae may be polyphyletic.

Uncertainties indicated in Figure 1 are a measure of the lack of resolution about key aspects of macropodoid phylogeny. However, continuing discovery of new fossil material from Riversleigh and elsewhere supplies new data which, together with that contributed from other fields, enable existing hypotheses to be continuously tested. Evidence from postcranial

fossil remains of the kind routinely found at Riversleigh will be of particular importance in this regard.

Current research by Kear (1998) on postcranial morphology of Riversleigh macropodoids suggests that the transition from more quadrupedal gaits to bipedal hopping occurred during the late Oligocene to early Miocene. Assessment of postcranial remains of a late Oligocene Riversleigh balbarine (*Nambaroo*) indicates that the forelimb to hindlimb ratio was comparable to that of *Hypsiprymnodon moschatus* (a habitual quadruped; Johnson and Strahan 1982). Other features also suggest that this animal

did not hop. These include reduced quadratus femoris and adductor magnus muscle scars on the femur, shortened tibia/fibula contact and a short, broad foot. Morphology of the forelimb also hints at quadupedalism and, combined with a high degree of lateral flexibility in the pedal digits and a well developed first toe, may be indicative of albeit limited climbing ability.

Middle to late Miocene macropodoids such as the Riversleigh bulungamayines *Ganguroo bilamina* Cooke, 1997a, and a species of *Wanburoo* sp. (Cooke 1999) suggest a more bipedally adapted morphology, particularly in the pes, with a shift of digits II and III ventromedially below digit IV (accompanied by a loss of digit I), and shortening of the navicular facet on the astragalus. Pedal development in *Wanburoo* sp. also suggests limited capacity of the upper ankle joint for fore-aft motion (possibly in response to a transfer of support of the body weight to digit IV), thus making the pes functionally monodactyl.

The origin of kangaroos remains a vexed question. Most recent authors (Aplin and Archer 1987; Flannery 1987; Springer and Woodburne 1989; Marshall *et al.* 1990; Ride 1993) have favoured a sister-group relationship between macropodoids and phalangeroids. Recent cladistic analyses of kangaroos (e.g., Flannery 1987, 1989; Cooke 1997b) have used phalangerids as an outgroup, although Wroe *et al.* (1998) suggest that Burramyidae is possibly more appropriate for this role, thereby renewing interest in a potential relationship first suggested by Broom (1896).

What is clear is that the origin of kangaroos must be sought further back in time than the late Oligocene. The oldest known kangaroos, from Oligo-Miocene deposits at Riversleigh and central Australia, demonstrate an already considerable degree of diversity, particularly within Balbarinae and Bulungamayinae. The record indicates a marked and steady decline in diversity of some macropodoids (notably balbarines) during the Oligocene and Miocene. In contrast, there was clearly an explosive radiation in macropodines and sthenurines from late Miocene to Quaternary time, probably a measure of the late Cainozoic development and spread of grasslands.

AUSTRALIAN FOSSIL BAT DIVERSITY AND EVOLUTION

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THE Australian fossil bat record is one of the world's oldest and best. *Australonycteris clarkae*, recovered from 55 million-year-old sediments near Murgon, southeastern Queensland, is one of the world's oldest bats (Hand *et al.* 1994). Since its description, additional fossil material from Murgon (including postcranial remains) clearly indicates *Australonycteris* is a member of the family Archaeonycterididae, an archaic bat group otherwise known only from early to middle Eocene sediments in Europe and North America. How bats first reached Australia is not yet known; dispersal could have been through either South America or southeastern Asia.

There is a gap in the Australian fossil record for bats (as for all non-marine mammals) between 55 and 26 million years ago. By the early to middle Tertiary all modern bat families had evolved, with the weight of evidence now suggesting that many modern bat families evolved in the Southern Hemisphere in the early Eocene (Sigé 1991; Simmons 1996). The next oldest Australian bat record is a single tooth from the 26 million-year-old Ditjimanka LF of the Lake Eyre Basin which was described by Archer (1978) as a possible rhinolophid but which is now understood to be a mystacinid (see below).

Hipposiderids and megadermatids dominate the 25 to 4 million-year-old Riversleigh freshwater limestone deposits, representing more than half of Australia's Tertiary bats, with emballonurids, molossids, vespertilionids and mystacinids comprising the rest (Fig. 1).

In general, Australian Oligo-Miocene bats include ancestors or close relatives of extant Australian taxa (e.g., *Macroderma* and *Brachipposideros* spp.), relatives of extinct and extant non-Australian taxa (e.g., *Xenorhinos* and *Riversleigha* spp.), and taxa representing archaic cosmopolitan groups with no living descendants (e.g., *Petramops* and *Hydromops* spp.). Australian Pliocene bats are typically closely related to, or represent early populations of, extant Australian bats (e.g., *Taphozous* spp., *Macroderma gigas*, *Micronomus* sp.).

A minimum of 22 hipposiderid species occur in Riversleigh's Oligo-Miocene deposits, with some taxa represented by many hundreds of individuals. Hipposiderids have not yet been

recorded from Australian Tertiary deposits outside the Riversleigh region. In some Riversleigh deposits (e.g. Upper and Bitesantennary Sites), as many as eight hipposiderid species (representing four genera) appear to be syntopic. The predominance of hipposiderids (in both diversity and abundance) in Riversleigh's limestone deposits is perhaps not surprising since almost all living hipposiderids are cave-dwellers and most extinct taxa have been recovered from cave or karstic deposits.
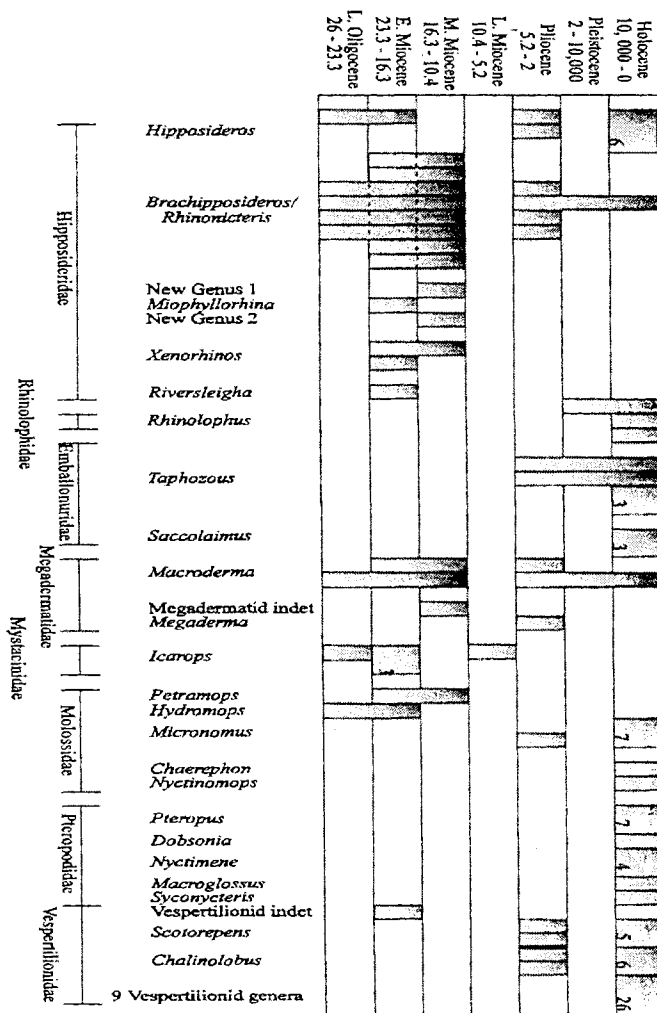

Fig. 1. Australian bat diversity through time. Each block represents a distinct species unless species diversity is indicated by a number. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.
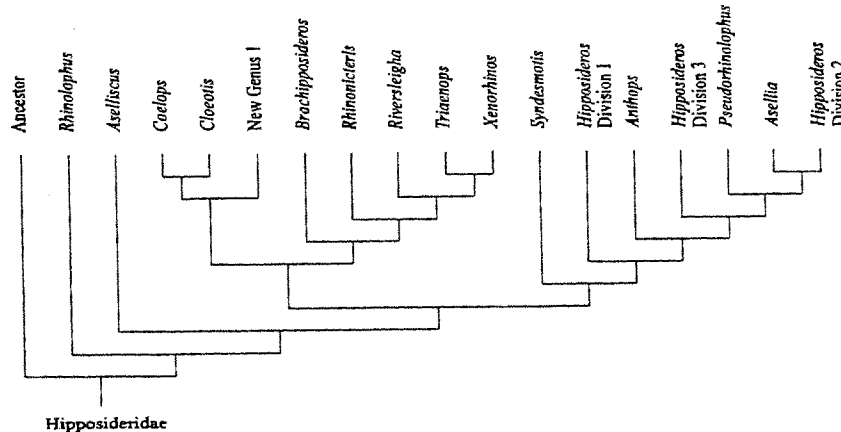
Fig. 2. Cladogram of possible relationships among hipposiderids (after Hand and Kirsch 1998).

However, high diversity also appears to have occurred in European middle Tertiary karstic and lacustrine deposits (commonly five species, Remy *et al.* 1987), suggesting a once more diverse hipposiderid radiation worldwide. Six genera of hipposiderids are now described from Riversleigh (*Brachipposideros, Hipposideros, Rhinonicteris, Riversleigha, Xenorhinos* and *Miophyllorhina*; Sigé *et al.* 1982; Hand 1993, 1997a,b,c, 1998a,b). The latter four genera are known only from Australia. *Brachipposideros* and *Hipposideros* have much broader distributions: the former in Oligo-Miocene sediments of western Europe and northern Africa (Sigé *et al.* 1994), and the latter represented by at least 55 modern species throughout the Old World tropics. Only three extinct species of *Hipposideros* have been described worldwide, two of these being from Riversleigh: the early Miocene *Hipposideros bernardsigei* (Hand 1997a) and the Pliocene *H. winsburyorum* (Hand and Godthelp 1999). Five species of the *Brachipposideros-Rhinonicteris* clade are represented in Riversleigh's Tertiary sediments and the oldest representatives of the living northern Australian *R. aurantius* (Sigé *et al.* 1982; Hand 1997b). Another three species of this clade are yet to be described from the Pliocene Rackham's Roost deposit, and at least six others from Oligo-Miocene sediments.

Skulls have been described for all hipposiderid genera represented at Riversleigh with the exception of *Miophyllorhina*. Additional, generically distinct hipposiderid taxa have yet to be described.

Although some Australian fossil hipposiderids are members of highly specialised, derived lineages (e.g., *H. bernardsigei*), many seem to belong to a group of relatively plesiomorphic lineages (e.g., *Rhinonicteris, Xenorhinos, Brachipposideros*) which represent early (though nonetheless specialised) offshoots of the hipposiderid radiation. Because of the diversity of plesiomorphic hipposiderids (fossil and living) in the Australian Region (Fig. 2), Hand and Kirsch (1998) speculate that the primary radiation of the family probably occurred here.

Eight Australian fossil megadermatids have been described: seven from Riversleigh Tertiary sediments and one from Wellington Caves, New South Wales (Hand 1985, 1995, 1996; Hand *et al.* 1988). Most appear related or referable to the endemic Australian genus *Macroderma* but several appear to represent quite different lineages. Of these, *Megaderma richardsi* (Hand 1995), from the Pliocene Rackham's Roost Site, is the first Australian record of this otherwise Afro-Eurasian genus which elsewhere has a record that extends from the late Oligocene to Holocene. The earliest fossil representatives of the living *Macroderma gigas* also occur in the Rackham's Roost deposit (Hand 1996). A second, large Pliocene species (*Macroderma koppa*) is known from Wellington Caves (Hand *et al.* 1988). The record for *Macroderma* extends from the late Oligocene to Recent with a maximum of two species occurring syntopically during that period.

Australian Tertiary molossids are known from Riversleigh and also from Bluff Downs, northeastern Queensland. These bats were present in Australia from at least the late Oligocene. Several species occur in Riversleigh's Oligo-Miocene deposits. Two species have been described: *Petramops creaseri*, a plesiomorphic taxon from the middle Miocene (Hand 1990), and a species of the otherwise Eurasian subgenus *Mormopterus* (*Hydromops*) from the late Oligocene and early Miocene (Hand *et al.* 1997). Riversleigh's *Petramops* and *Hydromops* species do not appear to be closely related to each other, nor do they appear to be ancestral to any living Australian molossid. They represent part of an older, archaic bat fauna that was widespread, and had close relatives in Eurasia and North America. The modern Australian subgenus *Mormopterus* (*Micronomus*) is represented in Riversleigh's Pliocene Rackham's Roost Site, and the Pliocene Bluff Downs deposit on Allingham Creek near Charters Towers (Hand *et al.* 1999).

The first pre-Pleistocene record for New Zealand's only endemic mammal family, the Mystacinidae, has been found in Australia. Several species of the new genus *Icarops* are known from early and middle Miocene Riversleigh deposits and another species from middle Miocene limestone sediments at Bullock Creek, Northern Territory (Hand *et al.* 1998). The presence of plesiomorphic mystacinids in the Australian Tertiary suggests an Australian origin for the family. Geographic and phylogenetic data suggest the most likely time of dispersal from Australia to New Zealand would have been the middle to late Oligocene. The Australian Miocene mystacinids provide the only Tertiary record of a very distinctive southern bat lineage of which a single, threatened species (*Mystacina tuberculata*) survives in New Zealand.

Other non-rhinolophoid bats are rare and fragmentary in Riversleigh's Oligo-Miocene

deposits. This rarity may relate to relative scarcity of non-rhinolophoids in the Riversleigh region, or northern Australia, during the Oligo-Miocene or, more likely, preservational biases due to the roost and habitat preferences of such taxa. To date, the only Oligo-Miocene vespertilionid known from Australia is a single tooth from an early Miocene Riversleigh site. By Pliocene time, vespertilionids had increased in number in the Riversleigh region with at least four vespertilionid species represented in the Rackham's Roost deposit; the fragmentary remains are possibly referable to the modern Australian genera *Chalinolobus* and *Scotorepens*, neither of which has an older record anywhere. The only Tertiary emballonurids known from Australia are two Pliocene species of *Taphozous* from Riversleigh's Rackham's Roost deposit, one species of which may represent the living Australian *T. hilli* from northwestern Australia. This Afro-Australasian genus has Miocene records in both Africa and Europe (Butler and Hopwood 1957; Butler 1969, 1978; Legendre 1980); the now cosmopolitan family Emballonuridae may date back to the earliest Eocene of England (Hooker 1996).

Rhinolophids have been recorded only from Pleistocene deposits in eastern Australia (Archer *et al.* 1984) and, incredibly, pteropodids have no fossil record in Australia. These groups appear to be fairly recent immigrants to our shores, although both have early to middle Tertiary records elsewhere. It is possible that in Australian tropical palaeofaunas, such as those of Riversleigh, hipposiderids filled the rhinolophid niche (Hand 1998b). In the case of pteropodids, competition with marsupials for food resources may have played a role in preventing their Tertiary colonisation of Australia, or perhaps suitable food resources may not have been readily available in Australia until the recent past.

DIVERSITY, RELATIONSHIPS AND ORIGINS OF THE TERTIARY AND QUATERNARY RODENTS OF AUSTRALIA

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ENDEMIC Australian rodents make up about 25% of the modern species-level diversity of terrestrial mammals of that continent. All living taxa, which comprise at least 70 species in 15 genera, are placed in the family Muridae. Despite relatively high modern diversity, the Australian fossil record of murids is very limited and only known to

extend with certainty back to the early Pliocene (Fig. 1). Even then, no Pliocene fossil assemblage in Australia, except that from the early Pliocene Rackham's Roost deposit of the Riversleigh World Heritage area of northwestern Queensland, has more than 2% of its species-level diversity represented by murids.
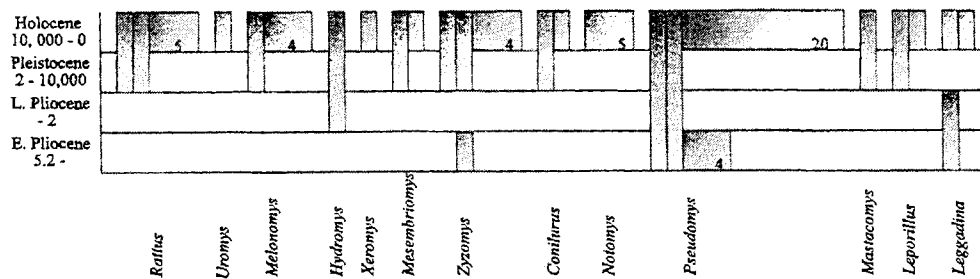
Fig. 1. Australian rodent diversity through time. Each block represents a distinct species unless species diversity is indicated by a number. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.

To date only two undoubtedly distinct, extinct fossil species have been named from Australia: *Pseudomys vandycki* Godthelp, 1989 from the early Pliocene Chinchilla LF of southeastern Queensland; and *Zyzomys rackhami* Godthelp, 1997 from Riversleigh's early Pliocene Rackham's Roost deposit. There are other undescribed Pliocene species in the genera *Leggadina, Pseudomys* and *Zyzomys* (part of the Rackham's Roost assemblage) and *Hydromys* (from the Floraville assemblage of northern Queensland), and other undescribed taxa from Pleistocene deposits around the continent. Several Australian living genera lack any fossil representation. Overall, this relatively poor fossil record for such a diverse modern group may reflect biases in collection strategies, which traditionally favoured discovery of larger mammals, and problems in taphonomy, with smaller, more fragile specimens being less likely to end up as fossils.

Among Pliocene rodents in Australia, the Rackham's Roost assemblage appears to be the oldest. All of its rodent taxa except one represent murines. The exception is a dendromurine-like animal, a group still living in Africa but once widespread across Eurasia including Thailand. This unexpected discovery indicates that the initial wave of immigrants into Australia was more complex than previously assumed.

The diversity of endemic murine genera in the Rackham's Roost assemblage suggests one of two things. Murids invaded Australia much earlier than Rackham's Roost time to enable evolution of these distinctive groups on this continent. Alternatively, murids may have entered Australia already differentiated (somewhere in southeastern Asia) into at least this many groups. Considering

the first hypothesis, the potential for a much earlier origin is limited by the total absence of rodents in the late Miocene Alcoota and Ongeva Local Faunas of the Northern Territory (8 and 7 my respectively; e.g. Murray and Megirian 1992), despite years of collecting at those sites. This does not rule out a time of origin between latest late Miocene and early Pliocene (7 to 5 million years ago), a time of climatic crisis in Australia and elsewhere (Archer *et al.* 1995). At present, however, there is no way to test these alternative scenarios.

What little is known about the generic representation and probable habitat requirements of the Rackham's Roost murids suggests that murids first invaded Australia from southeastern Asia via the Indonesian Archipelago. The earliest invaders probably utilised expanding corridors of relatively dry habitat developing at the time across northwestern Australia.

The apparent absence of murids from Pliocene sites in southern Australia may be attributed to two factors. In the case of the Bow LF of New South Wales, it is likely to be due to taphonomic bias against preservation of small mammals. In the case of the Hamilton LF in Victoria, it is more likely to be related to palaeohabitat. It is generally accepted that the Hamilton LF represents a rainforest assemblage (Archer *et al.* 1995), a contemporary habitat from which 'Old Endemics' are absent.

Relationships of the dendromurine-like rodent have yet to be determined but almost certainly these lie outside Australia. Nothing can be said either, with certainty, about the broader relationships of Australia's endemic murine genera. Molecular and genetic data suggest they

are each other's closest relatives thereby forming a distinct 'Australian clade' (Watts and Baverstock 1995).

Species of *Rattus* in the Plio-Pleistocene deposits at Floraville, northern Queensland, are the earliest record of the genus in Australia. This record postdates an explosion in diversity in southeastern Asia (Chaimanee and Jaeger 1999). It seems probable that the Floraville *Rattus* lineage is part of this southeastern Asian adaptive radiation. Other endemic Australian species of *Rattus* appear, in contrast, to be descendants of a second wave of immigrants that arrived from New Guinea. No representatives of this group are known from pre-Pleistocene deposits anywhere in Australia.

ACKNOWLEDGEMENTS

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