

Fossil Mammals of Riversleigh, Northwestern Queensland: Preliminary Overview of Biostratigraphy, Correlation and Environmental Change

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Abstract

Aspects of the results of studies of the fossil-rich Cainozoic deposits of Riversleigh, northwestern Queensland, are reviewed. A summary of five selected Riversleigh faunas representing the primary periods of the region's Cainozoic history is provided. Faunal and environmental changes over the last 25 000 000 years in the Riversleigh region are identified and changes in Australia's rainforest mammal communities over the same period are discussed. Evidence for the origin of Australia's modern mammal groups from ancestors now known to have lived in the Tertiary rainforests of northern Australia is reviewed. The geological record for Riversleigh's more than 100 local faunas is considered. At least three primary intervals of Oligo-Miocene deposition, one of Pliocene and many of Pleistocene and Holocene deposition are identified. An appendix is provided in which the principal faunal assemblages from Riversleigh are allocated to these depositional intervals. The evidence for correlating Riversleigh local faunas with faunal assemblages in the rest of Australia and the world is reviewed. Oligo-Miocene, Pliocene and Pleistocene marsupial and monotreme fossils correlate Riversleigh's local faunas with others from central and eastern Australia; bats correlate them with faunal assemblages in Europe; rodents correlate them with Pliocene assemblages in eastern Australia.

Key words: Monotremata, Marsupialia, Chiroptera, Muridae, Pisces, Amphibia, Reptilia, Aves, Mammalia, Evolution, Extinction, Rainforest, Freshwater Limestone, Tertiary, Oligocene, Miocene, Pliocene, Pleistocene, Holocene, Correlation, Stratigraphy, Palaeoecology.

INTRODUCTION

Despite long-term interest in the distinctive mammals of modern Australia, understanding about their origin and diversification has lagged far behind that of all other continents except Antarctica (Archer and Bartholomai 1978, Archer 1984, Hand 1984, Woodburne *et al.* 1985). The reasons for this are manifold but primary among them has been the apparent scarcity of rich Cainozoic fossil deposits. Until 1983 most investigations into the early diversification of Australia's terrestrial mammals focussed on the Oligo-Miocene deposits of the Lake Eyre Basin and Frome Embayment of South Australia and isolated early Miocene faunal assemblages from Tasmania. In that year the extent of richly fossiliferous Tertiary deposits at Riversleigh (Fig. 1), some of which had been systematically studied as early as 1967 (Tedford 1967), began to become apparent (Archer, Hand and Godthelp 1986).

Examination of these Riversleigh deposits, which appear to span the last 25 000 000 years, has led to many publications (e.g., Archer, Hand and Godthelp 1988b, Anon. 1989a,b) and on-going research focussed on individual taxonomic groups. Here we present a broad

summary of the current biostratigraphic data with a focus on Riversleigh's mammal record and its interpretation in a local as well as general context. Many students and colleagues involved in analyses of Riversleigh materials have contributed to the ideas presented here and to the growing awareness of the significance of the Riversleigh discoveries.

Although Riversleigh's fossil mammal deposits were originally thought to represent one distinct assemblage of medial Miocene animals (the Riversleigh Local Fauna of Tedford 1967, from his Sites A-D), we now recognise about 100 local faunas from this area representing: 1, at least three periods of Oligo-Miocene time (about 25 to 15 million years BP) which we define as Systems A-C with System A being between late Oligocene to early Miocene in age, System B possibly early to middle Miocene and System C possibly middle Miocene to early late Miocene; 2, at least one Pliocene assemblage (about 3-5 million years BP), Rackham's Roost Local Fauna; 3, many Pleistocene assemblages (between 2 million and 10 000 years BP) from cave and ancient riverine deposits such as Terrace Site; and 4, many Holocene (i.e., Recent) assemblages (less than 10 000 years BP) some of which appear to span the arrival of introduced mammals and Europeans.

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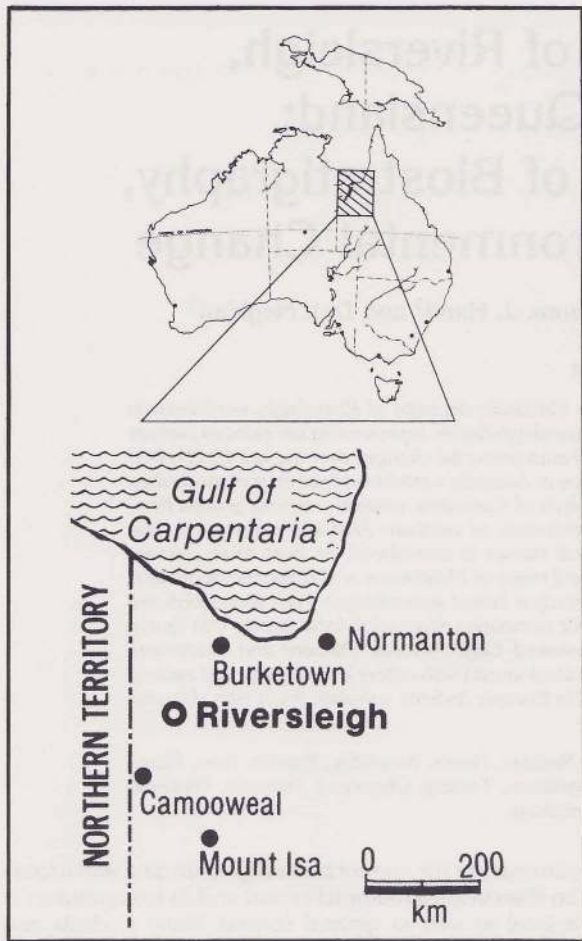


Fig. 1. The location of Riversleigh within the Gulf country of northwestern Queensland. (After Archer, Hand and Godthelp 1986).

Considering the vast expanse and complexity of the Riversleigh sediments, the large number of local faunas, the early state of analyses of both the geology and the faunas and the fact that this summary does not include the preliminary results of the non-mammal data under study, the diagrams and summaries presented here *must* be treated as preliminary assessments. It would be naive of us to presume that after a combined total of only 12 months spent in the field at Riversleigh, we would be aware of all major features of the area. With each successive expedition, more is learned about the inter-relationships of the various sediments within the region and about the faunal assemblages they contain. As more of the various sediments are processed, the diversity, relationships and non-Riversleigh occurrences of some of the Riversleigh animals necessitate a continual revising or refining of the 'big' picture.

This overview includes: 1, a faunal list from Riversleigh's Upper Site Local Fauna to introduce the biostratigraphic issues involved; 2, a summary of species-level diversity (for mammals) in six representative, different-aged local faunas (Riversleigh LF from 'Site D'; Upper Site LF; Bitesantennary LF; Dwornamor LF from Gag Site; Rackham's Roost LF; and the modern (still-living) fauna of Riversleigh Station); 3, a consideration of apparent trends in Australia's rainforest mammal communities through time; 4, a summary of what we at present interpret to be the stratigraphic relationships of representative Riversleigh local faunas; 5, some of the bases for approximating the ages of Riversleigh's local faunas; and 6, an appendix listing the principal local faunas under study with a tentative assessment of their relative ages.

Systematic nomenclature used for marsupial groups follows Aplin and Archer (1987); that for bats follows Hand (1984); that for non-Riversleigh faunal assemblages and stratigraphy follows Archer (1984) and Woodburne *et al.* (1985). In the species list, the authorship of a taxonomic name is followed by the author's last name, a comma and the date of publication. If no comma separates an author from the date of publication (the format also used here for a conventional text reference), the reference is to a work in which the taxon is discussed or perhaps re-defined.

The term rainforest covers a multitude of vegetation types (e.g., Webb, Tracey and Williams 1984; Webb, Tracey and Jessup 1986). Our interpretation of the Oligo-Miocene rainforests of Riversleigh, based on the faunas they contained, are that they were dense, species-rich gallery rainforests probably similar to those that persist today in mid-montane New Guinea.

Fossil collecting localities in Riversleigh are called 'sites' (e.g., Upper Site, Gag Site, Outasite). Regionally clustered sites that appear to be superpositionally-related (differing in age but not significantly in position) and/or space-related (spatially isolated but approximately contemporaneous) comprise what we have come to call 'Systems'. Our aim in using these concepts is to draw attention to the apparent age-related (sequential or comparable) nature of sites that occur as geographically defined clusters (the Systems) in the Riversleigh region. Our restricted use of the term 'System' should not be confused with the stratigraphic analogue of the chronologic term 'period' (e.g., the Tertiary System and Tertiary Period; Raup and Stanley 1971). Nor should our Systems be interpreted as regional faunas or assemblages of contemporaneous faunas because Systems B and C (at least) are clearly time-transgressive.

We regard each site in a Riversleigh System to be *potentially* unique in time as well as space. In contrast, each Riversleigh System is interpreted to have accumulated over a fixed *interval* of time within a specific area. For example, Gag Site (which may be middle Miocene in age) occurs as an isolated bone-rich deposit within

the Gag Plateau (a major topographic feature in the Riversleigh region) and is part of System C which as a whole appears to span middle Miocene to early late Miocene time. However, all of these preliminary stratigraphic concepts will require revision as understanding about the nature and relationships of the sediments develops.

An assemblage of animals from a single site is called a local fauna (often abbreviated LF; plural, lfs or LFs if specific sites are named; e.g., the Upper Site LF, the Outasite and Upper Site LFs). A few local faunal names differ from their corresponding site names (e.g., Dwornamor LF from Gag Site) but most are the same as the site name, commonly but not always less the word 'site' (e.g., Henk's Hollow Site, Henk's Hollow LF; but Upper Site, Upper Site LF). Each of the Riversleigh Systems contains many non-identical and different aged local faunas. A glossary of additional terminology is provided.

THE UPPER SITE LOCAL FAUNA: AN INTRODUCTION TO RIVERSLEIGH

Of the many faunal assemblages from Riversleigh, we chose the Upper Site Local Fauna to introduce this review of Riversleigh's biostratigraphic record. As will be discussed in more detail below, by any modern standards, this is a very diverse local fauna with almost twice the number of mammal families and twice the number of marsupial species of any surviving Australian or New Guinean ecosystem.

Upper Site was discovered on the inclined slope of Godthelp Hill by H. Godthelp in 1985. It stands proud of the surrounding slope as an erosional remnant of a slightly higher level thus earning its name. We quarried approximately 1 tonne of fossiliferous limestone from this site in 1985 and another 0.5 tonne in 1986, almost all of which is now processed. After dissolution of the limestone with dilute acetic acid and recovery of the small to large specimens, the acid-insoluble residues were sorted under a microscope to recover isolated teeth and other tiny items.

The animals recovered included a diverse assemblage of vertebrates as well as, perhaps most surprisingly, uncrushed arthropods. Wrinkled sheets of what we interpret to be algal mats were also recovered. Many of the invertebrate remains (in particular, dozens of coleopteran larvae; 'Genus and sp. 1' in the list below) occurred in vertical tube-like extensions of these mats which may have grown down into the bottom mud of the pond or hung below the algal mats if they floated. Although similarly preserved invertebrates are now known from other sites, the Upper Site invertebrate fauna is so far the most diverse.

Upper Site Local Fauna

Mollusca

Gastropoda (snails; pers. comm. Coleman, Australian Museum)

Family?

--Genus and sp.

Family?

--Genus and sp.

Family?

--Genus and sp.

Arthropoda (pers. comm. P. Jell, Queensland Museum)

Diplopoda

Family? (no. of genera undet.)

--Genus and sp. 1

--Genus and sp. 2

--Genus and sp. 3

--Genus and sp. 4

Insecta

Hymenoptera

Formicidae (ants; no. of genera undet.)

--Genus and sp. 1

--Genus and sp. 2

Hemiptera

Cicadidae (cicadas)

--Genus and sp. 1

Coleoptera

Curculionidae (weevils)

--Genus and sp. 1

Families? (no. of genera undet.)

--Genus and sp. 1

--Genus and sp. 2

Crustacea

Isopoda (slaters)

Family?

Genus and sp. 1

Pisces

Teleostii

Family?

--Genus and sp.

Amphibia

Anura (frogs; pers. comm. M. Tyler, University of Adelaide)

Leptodactylidae (leptodactylid frogs)

--*Crinia* sp.

--*Kyarranus* sp. 1

--*Kyarranus* sp. 2

--*Lechriodus intergerivus* Tyler, 1989

--*Limnodynastes* sp. 1

--*Limnodynastes* sp. 2

Hylidae (hylid frogs)

--*Litoria* sp. 1

--*Litoria* sp. 2

--*Litoria* sp. 3

--*Litoria* sp. 4

--*Litoria* sp. 5

--*Litoria* sp. 6

--*Litoria* sp. 7

--*Litoria* sp. 8

Reptilia

Squamata

Ophidia (snakes; pers. comm. J. Scanlon, University of New South Wales)

Pythonidae (pythons)

--cf. *Montypythonoides riversleighensis* Smith and Plane, 1985

Matsoiidae (large extinct snakes)

--Genus and sp. new

Typhlopidae (blind burrowing snakes)

--? *Ramphotyphlops* sp.

Elapidae (poisonous snakes)

--New genus? and sp.

Lacertilia

Agamidae (dragons; pers. comm.

J. Covacevich and P. Couper, Queensland Museum)

--*Physignathus* sp. cf. *P. leseurii* (Gray, 1831)

--*Physignathus* sp.

--Genus and sp. new

Gekkonidae (geckoes; pers. comm. M.

Hutchinson, La Trobe (University)

--[not yet determined]

Scincidae (skinks; pers. comm. M. Hutchinson)

--[many taxa but not yet determined]

Varanidae (monitor lizards; pers. comm. R.

Molnar, Queensland Museum)

--[not yet determined]

Crocodylia

Crocodylidae (crocodiles; pers. comm. P. Willis, University of New South Wales)

--Genus? and sp. new; cf. *Quinkana*

Aves (birds; pers. comm. W. Boles, Australian Museum)

Ratites

Dromornithidae (giant mihirung flightless birds)

--*Barawertornis tedfordi* Rich, 1979

--*Bullockornis* sp. cf. *B. planei* Rich, 1979

Casuariidae (emus and cassowaries)

--*Dromaius gidju* Patterson and Rich, 1987

Passeriformes (no. of genera not yet determined)

Menuridae (lyrebirds)

--Genus? and sp. new

Family(ies)?

--Genus and sp. new 1

--Genus and sp. new 2

--Genus and sp. new 3

Mammalia

Marsupialia

Dasyuromorphia

Dasyuridae (tiny to medium-sized carnivorous marsupials; pers. comm. J. Muirhead, University of New South Wales)

--Genus and sp. new 1

--Genus and sp. new 2

--Genus and sp. new 3

--Genus? and sp. new 4

?Dasyuridae

--Genus and sp. new

Thylacinidae (thylacines; pers. comm. J. Muirhead)

--*Nimbacinus dicksoni* Muirhead and Archer, 1989

Peramelemorphia (bandicoots; pers. comm. J. Muirhead)

New family 1 (extinct 'V.D.' bandicoots)

--Genus and sp. new 1

--Genus? and sp. new 2

?Peroryctidae (forest bandicoots)

--Genus and sp. new 1

--Genus? and sp. new 2

--Genus? and sp. new 3

--Genus? and sp. new 4

--Genus? and sp. new 5

--Genus? and sp. new 6

Notoryctemorphia

Notoryctidae (marsupial moles; pers. comm.

M. Gott, (University of New South Wales)

--Genus and sp. new

Yalkaparidontia

Yalkaparidontidae (extinct family)

--*Yalkaparidon coheni* Archer, Hand and Godthelp, 1988

Diprotodontia

Vombatiformes

Phascolarctomorphia

Phascolarctidae (koalas)

--*Litokoala* n. sp.

--Genus and sp. indet.

?New family 2

--Genus and sp. new

Vombatomorpha

Thylacoleonidae (extinct marsupial lions)

--*Wakaleo* sp. cf. *W. oldfieldi* Clemens and

Plane, 1974

--Genus and sp. new cf. *Priscileo*

Wynyardiidae (extinct sheep-sized browsers)

--? *Namilamadeta* n. sp.

Diprotodontidae (giant extinct browsers)

--*Neohelos tirarensis* Stirton, 1967

--Genus and sp. new

--Genus? and sp. new

New family 3

--Genus and sp. new

Phalangerida

Burramyidae (pygmy possums)

--*Burramys* n. sp.

--*Cercartetus* n. sp.

Phalangeroidea

Phalangeridae (brush-tail possums and cuscuses)

--*Trichosurus* sp. cf. *T. dicksoni* Flannery and Archer, 1987a

--? *Strigocuscus* sp.

Pilkipildridae (extinct small omnivorous possums)

--? *Djilgaranga* sp.

Petauroidea

Petauridae? (gliders and relatives)

--Genus and sp. new

New family 4

--Genus and sp. new 1

--Genus and sp. new 2

Pseudocheiridae (ringtail possums)

--*Paljara* n. sp.

--cf. *Pildra* sp.

--cf. *Pseudochirops* 1 (small)

--cf. *Pseudochirops* 2 (middle)

--cf. *Pseudochirops* 3 (large)

?New family 5

--Genus and sp. new

Acrobatidae (feather-tail possums)

--New gen.? cf. *Acrobates*

--Genus? and sp. new

Macropodoidea

Potoroidae (rat-kangaroos; pers. comm. B.

Cooke, Brisb. College of Adv. Ed. and U.N.S.W.)

Hypsiprymnodontinae

--*Hypsiprymnodon* sp. new

Propleopinae

--*Ekaltadeta* sp. cf. *E. ima* Archer and Flannery, 1985

Balungamayinae

--cf. *Wabularoo* n. sp.

--cf. *Gumardee* n. sp.

--Genus and sp. new 1

--Genus? and sp. new 2

--Genus? and sp. new 3

Potoroinae

--*Wakiewakie lawsoni* Woodburne, 1984a (Godthelp, Archer, Hand and Plane 1989)

Macropodidae ('ordinary' kangaroos; pers. comm. B. Cooke, Brisb. College of Adv. Ed. and U.N.S.W.)

Balbarinae

--?*Nambaroo* sp. new 1

--?*Nambaroo* sp. new 2

?Marsupialia

Yingabalanaridae (extinct family of probable marsupials)

--*Yingabalanara richardsoni* Archer *et al.*, 1989

Placentalia

Chiroptera

Microchiroptera

Rhinolophoidea

Megadermatidae (ghost bats)

--*Macroderma* sp.

Hipposideridae (leaf-nosed bats)

--*Brachipposideros* sp. 1

--*Brachipposideros* sp. 2

--*Brachipposideros* sp. 3

--*Brachipposideros* sp. 4

--*Brachipposideros* sp. 5

--Genus and sp. indet. 1

--Genus and sp. indet. 2

Vespertilionoidea

Molossidae (free-tail bats)

--Genus and sp. indet.

Family?

--Genus and sp. indet.

The questions we find ourselves asking about Riversleigh assemblages of this kind form the substance of the rest of this paper. Can we determine the nature of the palaeoenvironments that these assemblages represent (e.g., rainforest, open forest, woodlands etc.) and can we distinguish different microenvironments within these broader categories? How did faunal diversity vary with time in the Riversleigh region? What happened to the various groups present in the region during the time interval represented by the Riversleigh deposits? What subsequently happened throughout Australia to faunal diversity within the ecosystems represented by the older deposits of Riversleigh? How many different kinds and ages of fossil deposits are represented in the Riversleigh region? Can we correlate the kinds and ages of the various Riversleigh animals with those previously known from Australia and the rest of the world?

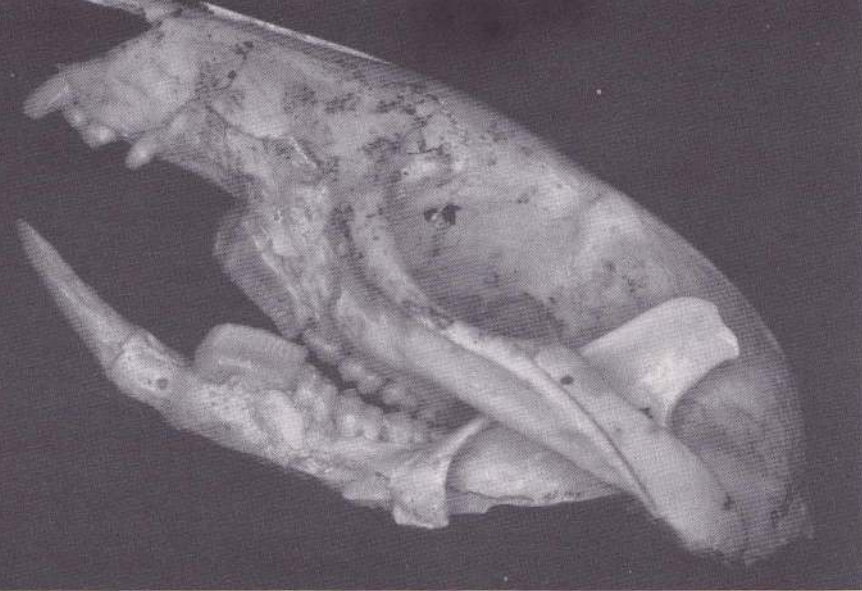
CAINOZOIC CHANGES IN MAMMALIAN DIVERSITY: THE EVIDENCE FROM RIVERSLEIGH

One of the most striking attributes of the Oligo-Miocene lfs of Riversleigh has been their high family-level and species-level diversity compared with previously known Australian fossil faunas. Here we will attempt to quantify and comment on this feature.

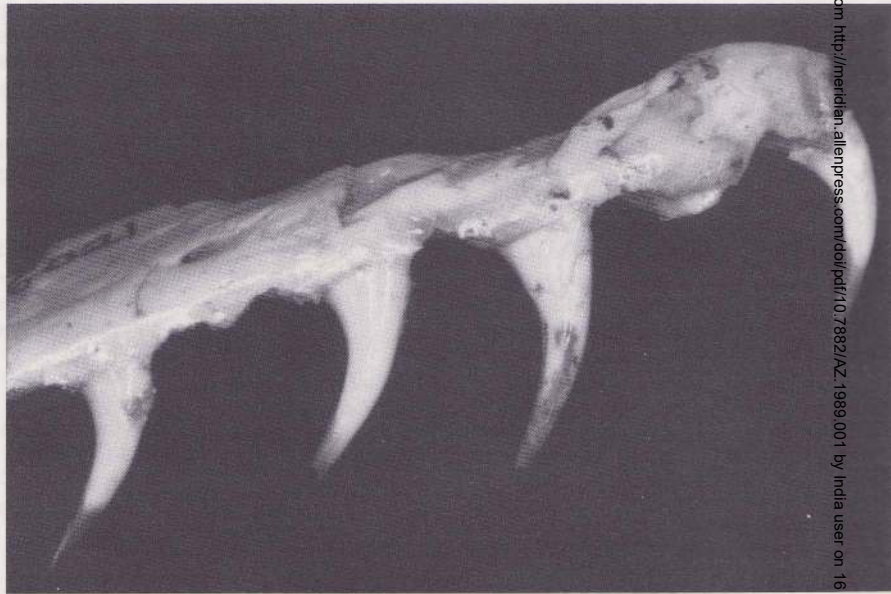
Table 1 presents a comparison of mammal species-level diversity in six of the Riversleigh local faunas, including the modern environment: Riversleigh LF (= 'Riv.' in Table 1); Upper Site LF (= 'U. '); Bitesantennary LF ('B. '); Dwornamor LF (= 'D. '); Rackham's Roost LF (= 'R.R. '); and the modern local fauna of the Riversleigh region (= 'Mod.').

Species-level diversity has been calculated for family-level units. However, a few taxa cannot be allocated to modern families and, as a result, they are listed at whatever level of relationship seems most appropriate (e.g., the 'vombatomorphic' taxon from the Upper Site LF is clearly not a vombatid but it appears to represent a taxon close to this group).

The numbers of taxa shown in all of the extinct lfs are also undoubtedly minimal estimates. In most cases these numbers will rise once the groups are systematically studied. Further, the data for the recently discovered Bitesantennary LF are very incomplete because to date we have only processed about 0.25 tonnes (i.e., about 3%) of the available material. We have added it in here because it represents undoubted Oligo-Miocene cave sediments, one of the major types of sediment represented in the Riversleigh region.



The fossilised skull and lower jaw of an extinct Riversleigh rat-kangaroo, Bettongia moyesi. This animal was a distant relative of living Bettongs.



The jaw and teeth of the giant Riversleigh python known as Montypythonoides riversleighensis. It may commonly have reached lengths of seven metres.



The skull and lower jaw of Yalkaparidon coheni, one of the unique Riversleigh species now placed in its own order of mammals, the Yalkaparidontia.

Table 1. Species diversity by family

Local Fauna (millions of years)	Riv. ?20-25	O. ?20	B. ?	D. ?15	R.R. 3-5	Mod. ¹ 0
Family²						
Thylacinidae ³	1	1	—	2	—	—
Dasyuridae ⁴	1	5	1	6	3	2
cf. Peroryctidae	—	6	?3	7	—	—
Peramelidae	—	—	—	—	2	—
Perameloidea ⁵	—	2	—	3	—	—
Notoryctidae ⁶	—	1	—	—	—	—
Phascolarctidae ⁷	—	2	—	2	—	—
?Phascolarctoidea ⁸	—	1	—	—	—	—
Diprotodontidae ⁹	4	3	—	2	—	—
Palorchestidae ¹⁰	2	—	—	?1	—	—
?Wynyardiidae ¹¹	1	1	—	—	—	—
Vombatomorpha ¹²	—	1	—	—	—	—
Thylacoleonidae ¹³	1	2	—	—	—	—
Burramyidae ¹⁴	—	2	—	2	—	—
Phalangeridae ¹⁵	—	2	—	3	—	—
Pilkipildridae ¹⁶	—	1	—	1	—	—
Pseudocheiridae ¹⁷	—	5	—	9	1	1
Petauridae ¹⁸	—	1	—	—	—	—
Petauroidea ¹⁹	—	1	—	1	—	—
Petauroidea ²⁰	1	2	—	1	—	—
Acrobatidae ²¹	—	?2	—	1	—	—
Potoroidae ²²	3	8	—	8	1	—
Macropodidae ²³	1	2	—	2	3	6
Yalkaparidontidae ²⁴	—	1	—	1	—	—
Yingabalanaridae ²⁵	—	1	—	—	—	—
Hipposideridae ²⁶	?1	7	6	4	3	3
Megadermatidae ²⁷	—	1	—	2	2	?1
Molossidae ²⁸	—	1	—	—	—	2
Emballonuridae	—	—	—	—	1	?2
Vespertilionidae	—	?1	—	—	4	8
Pteropodidae	—	—	—	—	—	?3
Muridae ²⁹	—	—	—	—	13	7
Canidae ³⁰	—	—	—	—	—	1
Hominidae	—	—	—	—	—	1
Tachyglossidae	—	—	—	—	—	1
Totals (min. numbers):	16	63	10	58	33	38

Additional families from other Riversleigh local faunas³¹

A. Cainozoic changes in diversity and habitats within the Riversleigh region

Allowing for the artificially low number of taxa so far recovered from the newly discovered Bitesantennary LF, the low number of mammals known from the deep-water facies represented by the Riversleigh LF and the probably low diversity of the largely megadermatid-collected assemblage from Rackham's Roost (see below), it is evident that species diversity in the region has dropped markedly from a high in the late Oligocene to early Miocene faunas to a low in the Pliocene/Quaternary. The drop in endemic family-level diversity over the same period is even more striking: from at least 34 (at least 7 in addition to those represented in the Upper Site LF; see Table 1 plus footnotes) in the Oligo-Miocene to no more than 14 in the modern community.

We interpret the older Riversleigh lfs (i.e., Systems A-C) to represent rainforest communities for five main reasons: 1, high species diversity in restricted local faunas (e.g., 63 mammal species in Upper Site LF) indicate a rich, finely-divided and stable (i.e., constant) resource base; 2, as a correlate, complex feeding guilds involving up to 6 species of small sympatric mammals are evident within particular morphologically similar groups (e.g., the peroryctid-like bandicoots; pers. comm. J. Muirhead), a situation most likely to reflect high resource diversity and environmental stability; 3, the high number of sympatric obligate leaf-eaters in single local faunas (e.g., 9 species of selenodont pseudocheirids and 3 selenodont phascolarctoids in the Dwornamor LF) indicates that many different species of trees occurred within relatively small areas, a common feature of rainforests but not sclerophyll forests; 4, the presence of many

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taxa otherwise only known from rainforest communities (e.g., *Strigocuscus* [Flannery and Archer 1987a], *Hypsiprymnodon* [Flannery and Archer 1987b], diverse *Pseudochirops*-type pseudocheirids, *Cercartetus caudatus*-like burramyids, diverse peroryctids and log-runner birds [*Orthonyx*; Boles 1988]); and 5, while there are vast numbers of browsing marsupials, there is a complete absence of grazers (i.e., no macropodine macropodids or vombatids) suggesting that the forest canopy was closed except over pools where aquatic grasses may have grown.

The last point deserves elaboration. High-crowned macropodids do not make their first appearance until the Bullock Creek LF (middle Miocene [central Northern Territory]; see below) and even there they are extremely rare (Cooke *et al.* in prep.). Undoubted grazers do not become a significant feature of Australia's mammal communities until the early Pliocene (the Bluff Downs [northeastern Queensland], Chinchilla [southeastern Queensland] and Bow [eastern New South Wales] LFs; Archer 1984, Woodburne *et al.* 1985). Early reports of grass pollens in the Oligo-Miocene Etadunna Formation in South Australia (e.g., Harris cited in Woodburne *et al.* 1985) may represent aquatic rather than emergent grasses (H. Martin, pers. comm.).

We are unclear about the precise nature of the Oligo-Miocene rainforests of Riversleigh because we have no direct record of the plant species themselves. However, the high mammal diversity in single locations (particularly for sympatric obligate folivores: at least 12 in the Dwornamor LF from System C) and the presence of a wide size range of herbivores (from mouse- to cow-size) suggests a comparably high diversity of plant species and multi-level distribution of these resources within the forest. This suggests a complex lowland gallery rainforest with a partially open understorey.

We interpret the marked drop in species-level and family-level diversity between the Oligo-Miocene and Pliocene/Quaternary local faunas of Riversleigh to mirror the regional collapse of the rainforest communities and their replacement with open forest/savannah habitats.

Looked at more carefully, it is evident that most of the losses in species-level diversity have been among the marsupials and most of the gains by addition of placental groups (e.g., murids, vespertilionids, emballonurids, rhinolophids and pteropodids).

Considering marsupials over this period, while many groups suffered extinction or severe reduction, the grazing macropodids markedly increased (see below). Conversely the generally browsing to omnivorous potoroid kangaroos markedly declined during the same period.

Within the placental groups over this same period, a change is evident in bat diversity. High diversity of

rhinolophoids (specifically hipposiderids and megadermatids) in the older deposits gives way to higher diversity of vespertilionids in the younger deposits (Hand 1987; see below). This inversion reflects a similar change over the same period in Europe (Hand 1984, 1987) and probably reflects a world-wide late Cainozoic change from more tropical conditions in the early to middle Tertiary to more xeric conditions in the late Tertiary to Quaternary.

The paucity of marsupials known from the Pliocene Rackham's Roost LF may be anomalous because it could be the result of limited prey selection by megadermatid bats. This fauna is dominated by small mammals of a size able to be carried by these carnivorous bats. However, when we compare species- and family-level diversity in this site with that from Gotham City Site, another megadermatid-accumulated assemblage but one from the Oligo-Miocene System C, the marked drop in diversity is still evident. For example, although acrobatids, burramyids, petauroids, small phalangerids, peroryctids and a new family of tiny perameloids (all small enough to be megadermatid prey) are present in the Gotham City LF, they are missing from the Rackham's Roost LF.

We consider that changes in Riversleigh's snake assemblages over this same time period are a significant part of the whole picture because they may provide information about when the ancestral Gregory River began to flow into the Gulf of Carpentaria. Scanlon (1988) notes that while pythonid, madtsoiid, typhlopoid and elapid snakes are well-documented from the Oligo-Miocene Riversleigh deposits, the aquatic acrochordids (file snakes) are not. File snakes are common in the modern Gregory River as they are in all of the river systems of northern Australia open to the sea, being aggressive colonisers of any accessible fish-rich freshwater bodies. They are also distributed widely around the northern areas of the Indian Ocean and almost certainly entered Australian freshwaters from the oceans to the north. The oldest file snakes (*Acrochordus dehmi*) from Siwalik sediments of medial Miocene age in southern Asia are clearly derived members of the group. Hence we suggest that the absence of file snakes from all of Riversleigh's more aquatic Oligo-Miocene units (e.g., Site D, D-Site equivalent units, Melody's Maze Site, Ringtail Site, Quentin's Quarry Site and Bob's Boulders Site), presuming they were present at the time in the waters to the north of the continent, indicates that the Riversleigh depositional basins were not at that time open to the sea. The ancestral northward flowing Gregory River probably did not establish itself until late Miocene or early Pliocene time.

B. Mid to late Cainozoic changes in Australian rainforest communities

Mid to late Cainozoic changes in habitats and diversity within the Riversleigh region appear to include loss of

rainforest probably by late Miocene to Pliocene time. What happened to Australia's rainforest mammals after this time? Some lineages became extinct; some persisted in rainforest remnants in eastern Australia; and some responded to the loss of rainforest by adaptation to more mesic habitats (see below).

We have compared (Fig. 2A-D) species diversity within mammal families for four Cainozoic rainforest mammal faunas: **Upper Site LF** (System B of Riversleigh's Oligo-Miocene sequence); **Hamilton LF** (an early Pliocene rainforest assemblage from western Victoria; Turnbull and Lundelius 1970 and various papers by Turnbull *et al.* in Archer 1987); the modern **Atherton** rainforest mammal assemblage of northeastern Queensland; and **mid-montane P.N.G.** (data provided by T. Flannery for living mammals in this habitat in Papua New Guinea).

We chose these four for the following reasons. The Upper Site LF is now one of the oldest-known undoubted rainforest mammal assemblages from Australia³². The Hamilton LF is the only known Pliocene rainforest mammal assemblage from this continent. Although Riversleigh's Rackham Roost is Pliocene, it appears to represent an open forest or woodland habitat. There are no known early or mid Pleistocene rainforest mammal assemblages. The Atherton rainforest is among the richest of Australia's tropical rainforest refugia. The P.N.G. mid-montane rainforest was chosen because it contains many taxa that are at least distant relatives of taxa known from Riversleigh's Oligo-Miocene rainforest assemblages and because it contains New Guinea's richest mammal assemblages.

Each of these assemblages has its limitations and/or biases, hence comparisons between them must be made with caution. Specifically, despite the Upper Site LF's relatively high diversity, a better indication of faunal diversity within the Riversleigh region at that time would require a compilation of contemporary lfs. For example, it is evident that many other families (e.g., ilariids, ektopodontids, miralinids) were probably represented in the Riversleigh region during Upper Site time because they are present in other adjacent System B local faunas. Further, there is no evidence for transportation of any of the Upper Site material to the restricted, irregularly shaped deposit (about 2 m²) from which the sample was obtained so we presume that the Upper Site LF contains taxa that were actually sympatric within the immediate area. Consequently, we caution that the number of species and families listed for Upper Site are almost certainly significant underestimations of biotic diversity in the region at that time.

The same is true for the Hamilton specimens (collected from exposures less than 10 m²) none of which shows signs of transportation from a wider source area. However, diversity for this assemblage is almost certainly under-represented by the local fauna because

many rainforest groups (e.g., dasyuroids, perameloids, hipposiderids and petauroids) are diverse on either side of the early Pliocene. Consequently, we presume that few of the processes responsible for collecting the substance of the Upper Site LF were operating in the Hamilton area. It is also possible that the lower diversity reflects a different kind of rainforest (i.e., probably cool temperate *Nothofagus* rainforest at Hamilton vs warm tropical gallery rainforest at Riversleigh). Unfortunately, because the Hamilton LF is Australia's only-known Pliocene rainforest mammal assemblage, we have no other link between the Oligo-Miocene lfs of Riversleigh and those of the present.

In contrast, mammal data for the mid-montane rainforests of Papua New Guinea and the rainforests of the Atherton Tableland have been obtained by comprehensive surveys of large tracts of forest and hence are more likely to approximate total regional diversity than the fossil local faunas.

Based on his experience with mid-montane rainforest faunas of P.N.G., Ken Aplin (pers. comm.) suggests that diversity in more restricted areas of this habitat (e.g., ranging altitudinally between 1 000-1 500 metres) would be significantly less than that given in Fig. 2D. Specifically, he would expect to find in a region of this more restricted size *no more than*: 25 murids; 7 vespertilionids; 7 pteropodids; 7 dasyurids; 6 hipposiderids; 5 phalangerids; 3 rhinolophids; 3 emballonurids; 4 peroryctids; 4 macropodids; 4 pseudocheirids; 2 petaurids; 2 molossids; 1 burramyid; 1 petaurid; 1 acrobatid; and 1 tachyglossid. However, it would still be unlikely that these 83 mammal species would occur close enough together to be found in a single fossil deposit like Upper Site. Hence we caution that the figures for diversity given in Fig. 2 are almost certainly higher than they would be if they had been determined by the same means that gathered the Upper Site LF.

If we consider the probable histories and similarities of the mammal communities of the four rainforest local faunas selected for comparison, the Upper Site LF (augmented as noted above) diversity, if not taxa, would probably have been typical for at least northern Australian lowland rainforest of the Oligo-Miocene. Following decline of this pan-continental rainforest, probably in the late Miocene, descendant ecosystems persisted as remnant rainforests in areas of eastern Australia.

The Hamilton LF community probably represents an early Pliocene rainforest refugium on the southeastern edge of the continent. The Upper Site and Hamilton LFs share several mammalian genera such as *Hypsiprymnon*, *Cercartetus*, *Burramys*, *Strigocuscus*, *Trichosurus* and possibly *Petaurus*.

The Atherton LF represents a similar although modern refugium for tropical rainforest in northeastern Australia. It shares several mammalian genera with the Upper Site

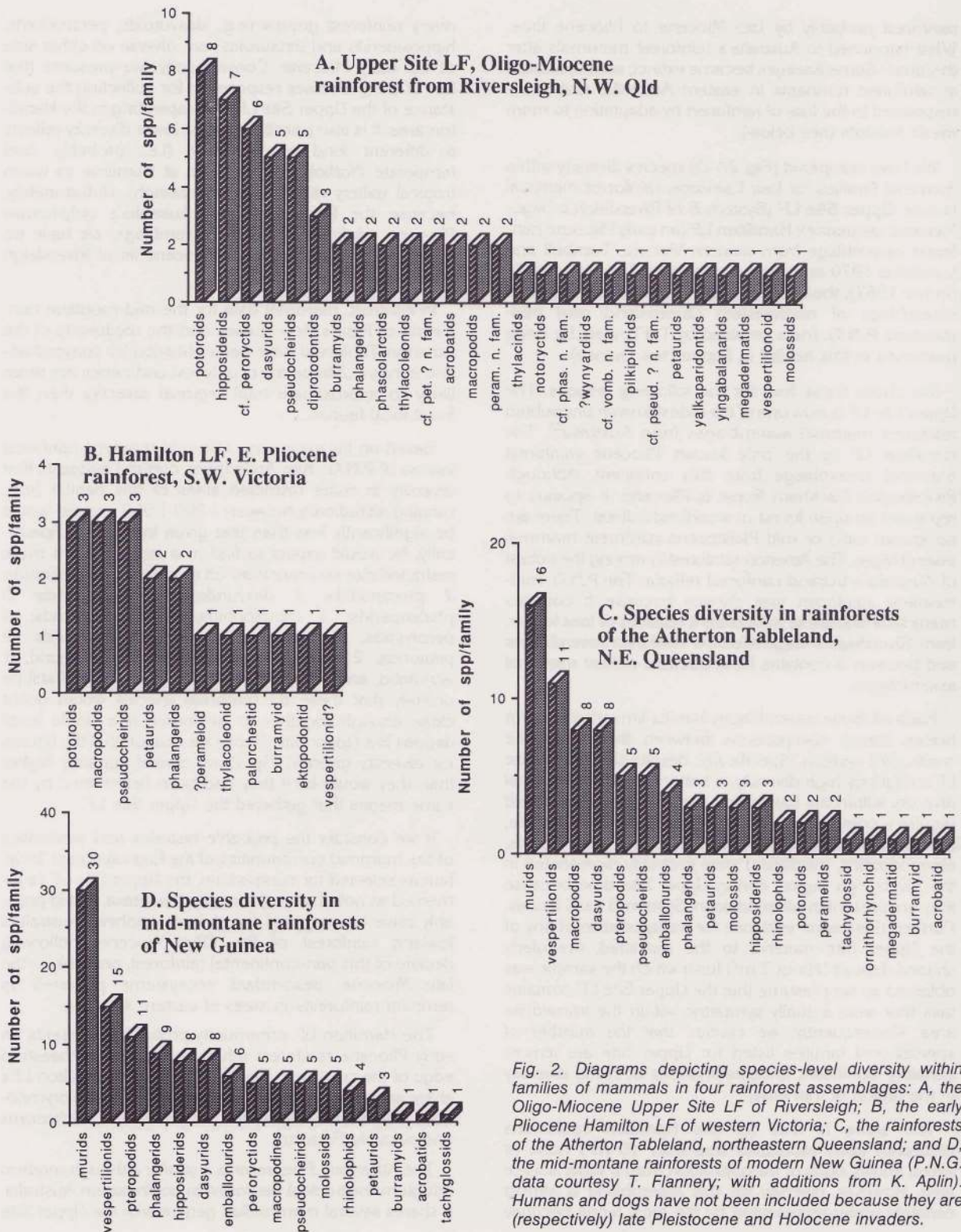


Fig. 2. Diagrams depicting species-level diversity within families of mammals in four rainforest assemblages: A, the Oligo-Miocene Upper Site LF of Riversleigh; B, the early Pliocene Hamilton LF of western Victoria; C, the rainforests of the Atherton Tableland, northeastern Queensland; and D, the mid-montane rainforests of modern New Guinea (P.N.G. data courtesy T. Flannery; with additions from K. Aplin). Humans and dogs have not been included because they are (respectively) late Pleistocene and Holocene invaders.

LF including *Macroderma*, *Hipposideros*, *Hypsiprymnodon*, *Cercartetus*, *Pseudocheirus* and *Trichosurus*. It shares *Hypsiprymnodon*, *Strigocuscus*, *Trichosurus* and possibly *Pseudocheirus* with the Hamilton LF. Palynological analyses from Lynch's Crater (Kershaw 1976) suggest that during the Pleistocene the Atherton rainforests underwent episodes of severe contraction, a stress that may have reduced mammal diversity in that region.

The P.N.G. mid-montane rainforest mammals may have been isolated from their Australian counterparts since the early Miocene (Flannery 1989; see below), although ephemeral Pliocene corridors or dispersal routes to and from Australia are indicated by shared genera of kangaroos (*Protemnodon*) and diprotodontids (*Nototherium*) in the ?early Pliocene Awe LF (Plane 1967, Woodburne *et al.* 1985) and murids and tree kangaroos (*Dendrolagus*) in Pliocene/Pleistocene lfs of eastern Australia and New Guinea but evidently not the Hamilton LF or the older Oligo-Miocene rainforest faunas of Riversleigh.

The apparent absence of potoroids, phascolarctids, notoryctids and megadermatids (conspicuous elements in the Upper Site LF) from the whole of the New Guinea's modern rainforests suggests that: 1, New Guinea may not have been available for colonisation in the Oligo-Miocene, although current views are that New Guinea and Australia were a continuous land mass from at least the Oligocene until the early Miocene from which time New Guinea was isolated from Australia by water possibly until the Pleistocene (Flannery 1989); and/or 2, there may have been filter barriers (geological, climatic or biological) isolating New Guinea (e.g., large murids in New Guinea may have presented a competitive barrier to the late Tertiary dispersal of potoroids from Australia); and/or 3, the presently 'missing' groups may have reached New Guinea but suffered pre-modern extinction. Submergence of much of lowland New Guinea in the late Miocene could have contributed to the extinction of any potoroids that had managed to colonise the area because most Australian potoroids live in lowland environments. It is of course also possible that some of these 'missing' groups (particularly the smaller ones like notoryctids and megadermatids) do occur in New Guinea but have not yet been detected.

Five apparent temporal changes evidenced by these four rainforest mammal communities invite comment: 1, the apparent progressive extinction of family-level groups; 2, the corresponding increase in intrafamilial diversity of particular groups (macropodids, murids, vespertilionids, emballonurids, rhinolophids and pteropodids); 3, the size, relationships and possible food plants of rainforest mammals that declined; 4, the rise of placental diversity and its possible correlates; 5, the first appearance in the Oligo-Miocene rainforest communities of groups that survived in mesic environments.

Extinction of family-level groups from rainforest communities

This progressive loss reflects the overall trend noted above for declining diversity within the Riversleigh region. The Upper Site LF has 27 families (with at least 63 species); the Hamilton LF 11 (with at least 19 species); the Atherton rainforest 18 (with 80 species); and the mid-montane P.N.G. rainforest 15 (with 117 species).

We interpret this decline in family-level diversity to reflect in part presumed changes in the plant communities since the Oligo-Miocene and reactions to the arrival of various placental groups including, in the late Pleistocene, humans. Changes in Tertiary rainforest plant communities may have resulted from increased seasonality and/or deterioration of Australia's rainfall regimes in the late Miocene. Reduction of the diversity of rainforested habitats across central and northern Australia is unlikely in itself to be the explanation for the decline in mammalian diversity within Australian rainforests because all of the extinct groups had sympatric representatives in the Oligo-Miocene communities of Riversleigh.

It is possible that the high diversity characteristic of the Oligo-Miocene lfs of Riversleigh reflects specific attribute(s) of that region that no longer exist in association with Australian rainforests. It is perhaps significant that the high hipposiderid diversity (5 spp) characteristic of the older Riversleigh lfs is best matched in restricted areas of southeastern Asia (e.g., Borneo with 8 spp) where lowland tropical rainforest carpets a limestone terrain riddled with caves, a palaeoenvironment we suggest may have been present in the Riversleigh region during the Oligo-Miocene.

If we look at the families that declined to extinction in Australia's rainforests, most were represented by only one or two species of small (notoryctids, yalkaparidontids, pilkipildrids etc.) to medium-sized (ilariids, miralinids, wynyardiids etc.) mammals. Losses of this kind may not have required very significant alterations to the rainforest habitats. Of these groups, only the notoryctids survive, as descendant populations in xeric environments (the Marsupial Mole of the central Australian deserts; see below).

Other losses from rainforest communities were more profound such as those of diprotodontids, palorchestids, thylacoleonids and phascolarctids all of which were middle-sized to large mammals. For losses of this kind, we presume that more profound changes occurred to the rainforests although they may be changes that occurred in the Quaternary rather than the Tertiary. All of these groups except phascolarctids vanished from mesic environments in the late Pleistocene, their disappearance possibly reflecting the arrival of Australia's first humans at least 50 000 years ago. The times of their disappearance from rainforests is not clear but zygomaticurine

diprotodontids, at least, persisted in upland rainforests of New Guinea until 20 000 years ago (*Hulitherium*; Flannery and Plane 1986).

Increase with time in intrafamilial diversity of macropodids, murids, vespertilionids, emballonurids and pteropodids

In general, the decline with time of rainforest marsupials and rise of placentals is apparent (Fig. 3). Placentals have come to represent more than 50% of the modern rainforest mammal faunas of both Australia and New Guinea in contrast to the 16% of the Oligo-Miocene Upper Site LF. However, the changes from what we interpret to be the 'archaic' kind of Australian rainforest assemblage (such as that of Upper Site) appear to be more profound in the New Guinean mid-montane communities than in the Atherton rainforests of Australia.

Relevant here are questions about the relationships of the drifting Australia to adjacent land masses as it moved into lower latitudes after breaking free from Antarctica. In contrast to previous widespread views which depict a vast, *vacant* ocean barrier between the drifting Australia and southeastern Asia, the northern edge of the Australian continental shelf has evidently been the end of an albeit ephemeral archipelago linking it to southeastern

Asia since at least the late Cretaceous (e.g., Audley-Charles 1987; Fig. 4). The northern portions of this archipelago (e.g., Sumatra, Java and western Sulawesi) are Asian in origin while the southern portions (e.g., Timor, Seram and eastern Sulawesi) are Gondwanan.

By 40 million years ago (Fig. 4A), in the late Eocene, perhaps only 5 million years after Australia finally separated from Antarctica, the submerged shelf of Australia included the Gondwanan relicts of Timor, Tanimbar, Seram, Banggai-Sula the eastern half of Sulawesi and the then small island of New Guinea. In turn, these were adjacent to a string of possibly emergent Asian islands including Java and Sumatra which indirectly 'linked' the Australian continent to mainland southeastern Asia.

By 30 million years ago (Fig. 4B), in the late Oligocene, New Guinea may have been a small area of lowland but the archipelago linking Australia to southeastern Asia was less strung out and beginning to deform as Australia ploughed northwards. At this time New Guinea was probably covered in tropical lowland rainforests which might have permitted colonists from comparable habitats in northern Australia. The rapid rise of New Guinea from 15 million years ago is evident from the fact that the central highlands consist of middle Miocene marine limestones. We have previously

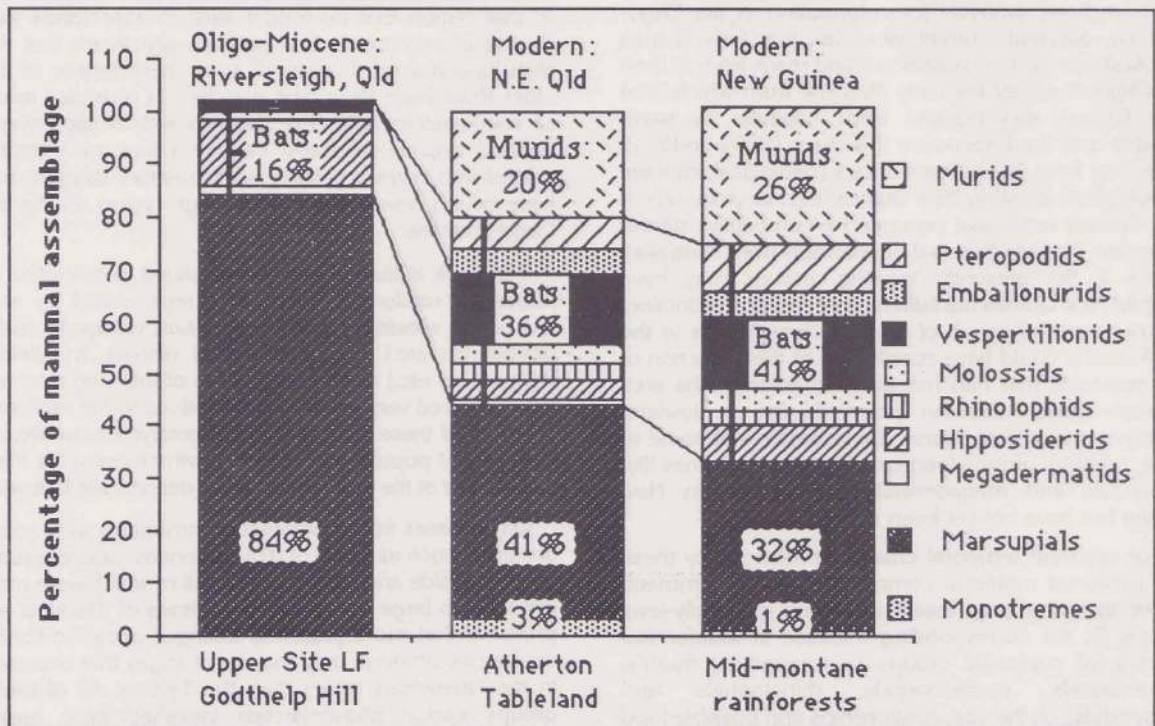


Fig. 3. Changes within rainforest communities in the relative abundance (species percentages) of monotremes, marsupials, bats and rodents from the Oligo-Miocene Upper Site LF to modern Australian (Atherton) and New Guinean (mid-montane) rainforests. The Hamilton LF is not included because, although it represents a Pliocene rainforest, it is evidently biased against volant and small terrestrial mammals and would misrepresent the transition between the Oligo-Miocene and recent communities.

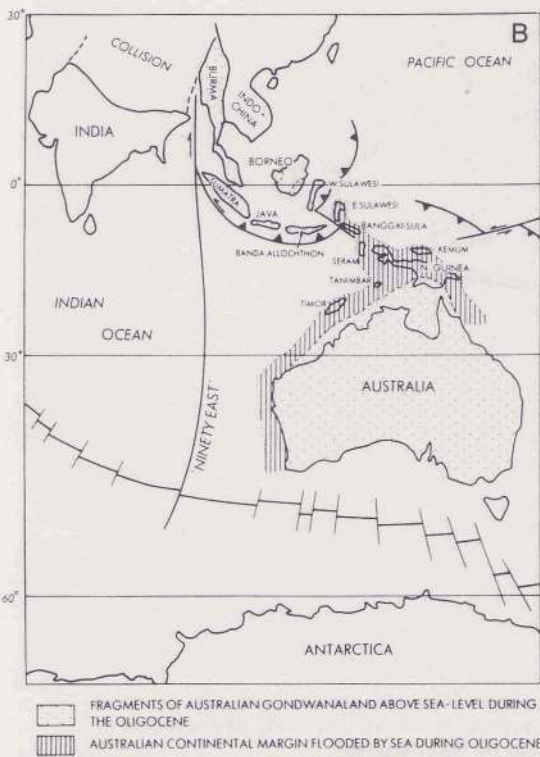
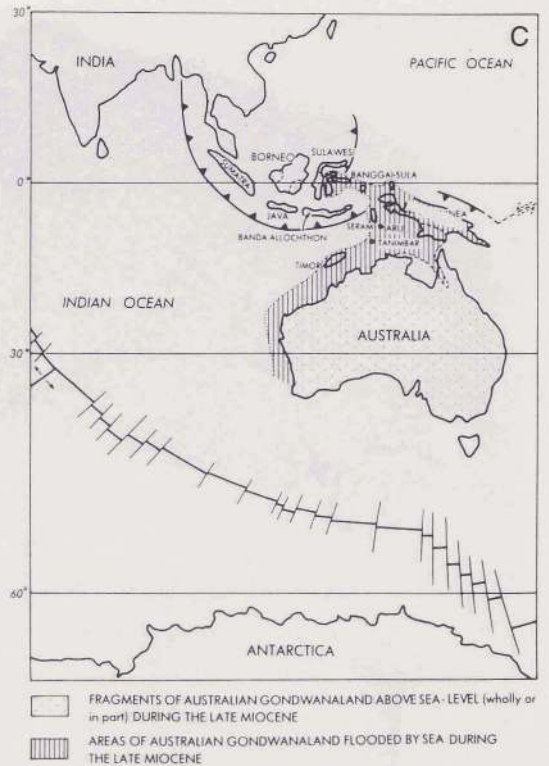
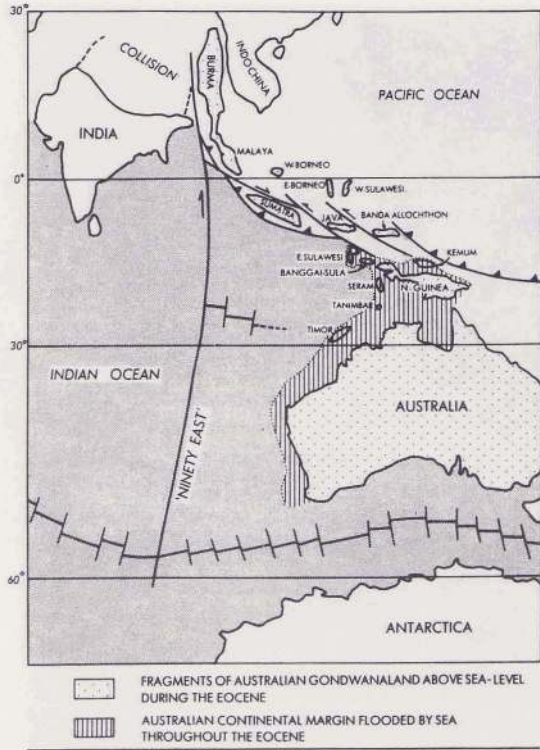
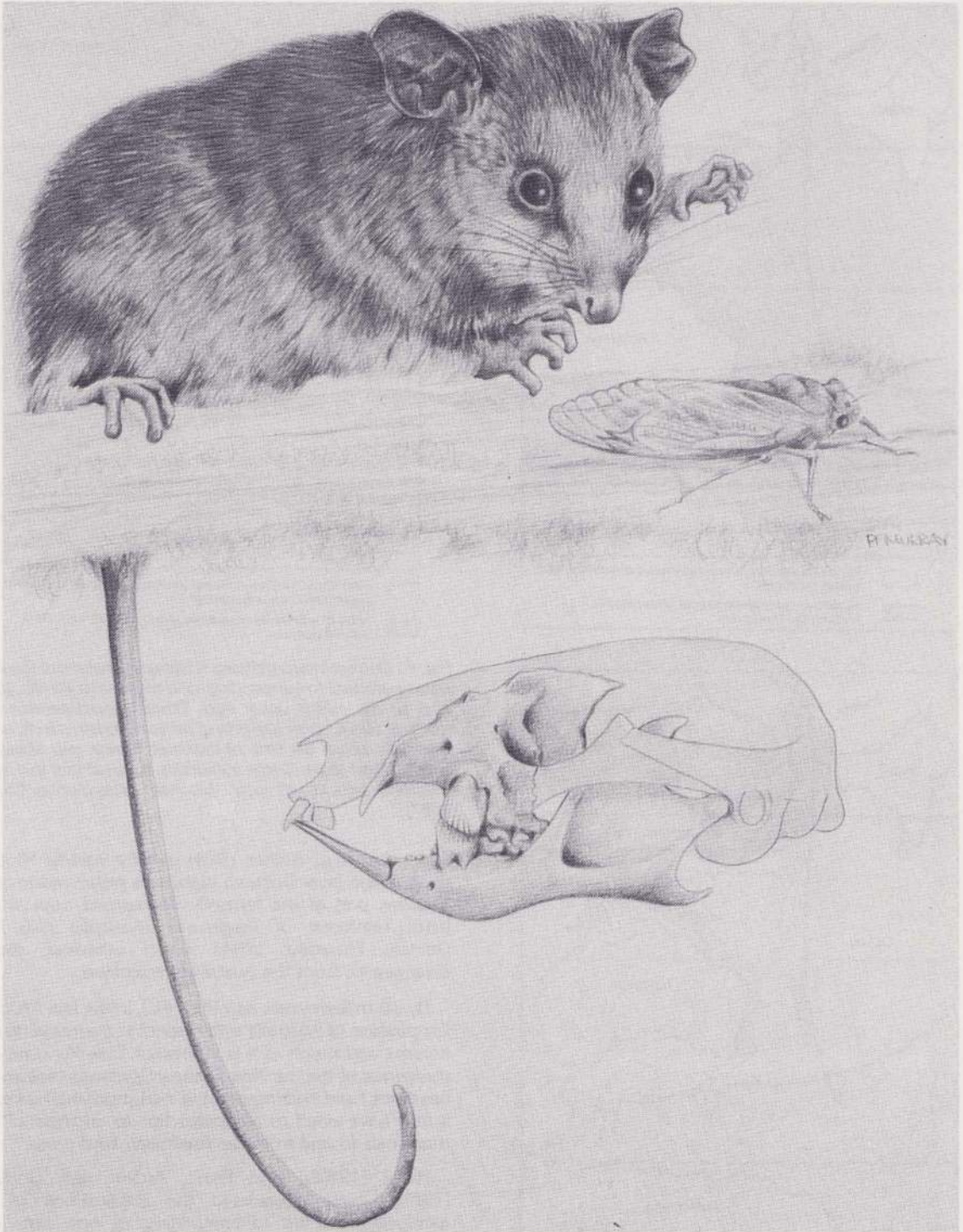


Fig. 4. Current interpretations of the relationships of the Australian continent to surrounding land masses at 40 (A), 30 (B) and 10 (C) million years ago. There is considerable controversy about some aspects of these reconstructions and in particular about the time of fusion of Burma and Malaya to southeastern Asia. Some authorities suggest that this fusion occurred prior to 40 mya. (Modified after Audley-Charles 1987)

suggested (e.g., Archer 1984) that the middle Miocene uplift of the New Guinean highlands preserved in rising altitudes part of the formerly widespread tropical lowlands rainforest of Meganesia (Australia plus New Guinea; Filewood 1984) which otherwise almost disappeared from the Australian mainland.

By 10 million years ago (Fig. 4C), in the late Miocene, the position of Australia with respect to surrounding land masses was much as it is at present. Late Miocene submergence of the New Guinean lowlands (see above) need not have endangered the mid-montane biotas but it may have acted as an obstruction to dispersal of land mammals to and from the Australian land mass.

Hand (1989b) and Hand, Archer and Godthelp (1989b) have considered the implications of this archipelago to an understanding of how bats may have dispersed to and from Australia in the early to middle Tertiary. Marsupials do not appear to have made effective use of this route to disperse from Australia to



A species of Burrmys unique to Riversleigh's older deposits. These tiny animals were quite common in the lowland rainforests of the day but their living descendants survive only in the alpine region of southeastern Australia. (Drawing by Peter Murray).

southeastern Asia but it is clear that it was used by the invading rodents in the middle to late Tertiary and by humans and dingoes in the Quaternary.

Perhaps the higher diversity of placental mammals in mid-montane New Guinea (Fig. 3) has resulted from that area's relatively longer period of exposure to placental invasions. However, considering the antiquity of the archipelago that links southeastern Asia to Australia as closely as it does to New Guinea, dispersing placentals may have been landing on the shores of Australia for at least as long as they have on those of New Guinea.

Conversely, perhaps many of the Oligo-Miocene marsupial groups originating in Australia were unable to disperse to New Guinea. Flannery (1989) argues that by early Miocene time, mammals in the Meganesian region had separated into two biogeographically isolated sub-regions: Australia (with a blend of 'archaic' and diverse relatively 'modern' marsupial groups) and New Guinea (with a subset of only the more 'modern' groups). Placental invaders into New Guinea may have simply insinuated into niches unoccupied by marsupials but found the same niches occupied in Australia. In this case, the 'modern New Guinean' mid-montane faunal balance summarised in Fig. 3 may fairly reflect that region's late Tertiary diversity.

The only known Tertiary mammal fauna from New Guinea is the Pliocene Awe LF of P.N.G. (Plane 1967). It contains only a subset of 'modern' groups such as macropodine macropodids (unknown in Australia prior to the late Miocene), diprotodontids (groups similar to late Miocene or even Pliocene taxa in Australia), one dasyurid (representing *Myoictis*, a derived dasyurine; Archer 1982) and an indeterminate number of murids.

In sum, in large part because of the depauperate late Tertiary and non-existent middle Tertiary lfs from New Guinea, we are uncertain about the significance of the differences between modern New Guinean and Australian mammal diversity in rainforests.

While most rainforest marsupial groups in Australia declined before the Pliocene, macropodids increased in diversity. By early Pliocene time there were many macropodid lineages in and outside of rainforests. Their increase appears to correspond with the decline in balungamayine potoroids, a diverse group of Oligo-Miocene 'rat-kangaroos' that had evolved lophodont teeth similar to those of macropodids (Flannery, Archer and Plane 1983).

The seemingly 'sudden' appearance in the Pliocene Rackham's Roost LF of 13 spp of murids (Godthelp in prep.) and the subsequently rapid rise in diversity of this group throughout the Australian region by late Quaternary time are striking features of the late Cainozoic record. It seems highly probable that rodents were in

Australia prior to Rackham's Roost time and possibly as early as the late Miocene although there are no rodents known from the late Miocene Alcoota (Northern Territory) or Beaumaris (Victoria) LFs. This absence from the Alcoota LF is probably significant and suggests that rodents entered Australia sometime between Alcoota and Rackham's Roost time. One of us (Godthelp), having studied modern murids and the diverse Rackham's Roost assemblage, is convinced that rodents first entered Australia through the drier, non-rainforest corridors of southern Indonesia (Timor, Sumba, Java etc.) rather than via New Guinea. It is not clear how soon after their first arrival that murids invaded Australia's rainforests.

The post-Oligo-Miocene decline in the diversity of peroryctids (only one of which, the Rufous Spiny Bandicoot *Echymipera rufescens*, survives in Australia's rainforests), 'V.D.' bandicoots (which vanished before the Pleistocene) and possibly the smaller omnivorous potoroids may be related to the late Tertiary murid radiation. All three groups overlapped in size and probably dietary preference. However, the fact that peroryctids are largely confined to rainforests while murids appear to have primarily radiated in drier habitats strains the argument for competitive exclusion. Certainly none of the old endemic murid genera (*Zyromys*, *Conilurus*, *Pseudomys*, etc.) occupy rainforest niches today. The only murid genera that are well-represented in Australian rainforests (e.g., species of *Melomys*, *Uromys*, *Rattus* etc.) have New Guinean affinities and, if the fossil record from eastern Australia is a reliable guide, did not appear in Australia before the Pleistocene.

The increase in vespertilionid bat diversity is almost as striking as that of murids. From 1 or 2 taxa in the Oligo-Miocene lfs of Riversleigh, to 4 in the Rackham's Roost LF, at least 8 in Riversleigh's modern fauna, 11 in the Atherton rainforest and 15 in the mid-montane rainforests of New Guinea, the increase in diversity in and outside of rainforests is clear.

Emballonurids show a similar if more recent increase in diversity. None is known from the Oligo-Miocene rainforest faunas of Riversleigh; 1 species is known from the Pliocene Rackham's Roost LF; 2 coexist in the Riversleigh region today; 4 occur today in the Atherton rainforests; and 6 live in the mid-montane rainforest of P.N.G. The higher diversity in modern rainforests suggests that during Rackham's Roost time they may have been present in higher numbers in east coastal rainforests and possibly entered Australia from the north, via rainforest corridors, sometime between the middle Miocene and early Pliocene.

This same scenario may apply to rhinolophids. This group of bats does not appear to be represented in any of the various aged Riversleigh fossil deposits; nor are they found in the area today. However, two species are

known from modern Australia and both are restricted to the east coast. Four species occur in the mid-montane rainforests of New Guinea and in any one habitat three may be sympatric. Their presence in the forests of eastern Australia evidently represents a relatively recent invasion from New Guinea probably via northeastern Queensland, perhaps in the Pliocene or Pleistocene.

Pteropodids appear in the Riversleigh record, suddenly, in the late Quaternary — there being not a single tooth to represent this distinctive group of herbivorous bats in the Oligo-Miocene, Pliocene or Pleistocene lfs. Considering modern diversity in Australia (e.g., 5 spp in the Atherton rainforest) and abundance, particularly of the species of *Pteropus*, the absence of this group from the Rackham's Roost LF puzzles us. This apparent absence could be an artifact of limited preparation of Rackham's Roost material. However, because New Guinea as a whole has 25 species of pteropodids as opposed to Australia's 8, it is possible that Australia was only relatively recently colonised by this group of bats.

Hand (1989b) suggests that pteropodids may have colonised New Guinea prior to the establishment of arboreal fruit-, blossom- and nectar-feeding possums; conversely, they may have had difficulty invading Australian ecosystems because of the abundance there of a wide variety of arboreal possums. The Quaternary establishment of pteropodids in Australia's northern rainforests may have followed late Tertiary declines of many of Australia's phalangeridans such as the smaller phalangeroids and a wide range of petauroids. But without a pre-Pleistocene record of pteropodids in New Guinea or Australia or of pre-Pleistocene possums from New Guinea, evidence for or against possible late Cainozoic competition between these groups does not exist.

Overall, the increases in diversity of murids, vesperilionids, pteropodids and macropodids more than accounts for the higher species diversities of the Atherton and mid-montane P.N.G. rainforest communities. In the Atherton rainforests, 50% of the mammal diversity is now made up by these four groups. In contrast, in the Oligo-Miocene Upper Site LF, these groups comprise no more than 5% of the mammal assemblage.

The size, relationships and food-plants of rainforest mammals that declined

One of the most striking contrasts between the older rainforest communities and those that survive today is the presence in the former of many medium-sized to large mammals. In particular, the diprotodontids, palorchestids, thylacinids, wynyardiids, ilariids and thylacoleonids were mostly dog- to cow-sized mammals. In contrast, in the modern P.N.G. and Atherton rainforests, although dingoes and/or thylacines were present, the rest of the endemic mammals are no larger than a tree-kangaroo.

What happened in these forests to cause the loss of these large animals? As noted above, at least for diprotodontids and probably palorchestids, thylacinids and thylacoleonids, the arrival of humans in Australia may well have been a significant factor. However, ilariids and wynyardiids did not survive beyond the middle Miocene so their declines require a different explanation.

Considering the phylogenetic relationships of the now extinct large rainforest herbivores from Riversleigh, most were vombatiform (*sens.* Woodburne 1984b, Aplin and Archer 1987) diprotodontian marsupials that were also present in the Ditjimanka and Pinpa LFs of South Australia. The early Pliocene Hamilton LF retains only a single vombatiform group, the palorchestids. The Oligo-Miocene decline from the rainforests of these vombatiform groups, most of which are only known from medium-sized to large species, coincides with the apparent rise in diversity of the rainforest phalangeridans (*sens.* Aplin and Archer 1987) which, although already diverse in the Upper Site LF, today are the only diprotodontian marsupials in rainforests. Phascolarctids, which were not uncommon in the Riversleigh rainforests, had evidently vanished from this habitat by the early Pliocene (Archer and Hand 1987). It would appear that the Oligo-Miocene rainforests of Riversleigh represent a turning point in rainforest mammal assemblages where the vestiges of an older vombatiform radiation overlapped with the rapidly diversifying phalangeridan marsupials.

It is relevant to point out here that although vombatiform marsupials declined in rainforests during the Tertiary, some vombatiform groups (e.g., diprotodontids, vombatids, palorchestids and thylacoleonids) underwent significant late Cainozoic adaptive radiations in the open forests and grasslands alongside similarly spectacular radiations of mesic and arid kangaroos. However, by the end of the Pleistocene, all of the vombatiform groups in these drier habitats except for vombatids and phascolarctids had vanished.

Among the smaller rainforest mammals that declined or were lost after the Oligo-Miocene are several enigmatic groups known only from the older Riversleigh local faunas including yalkaparidontids and yingabalanarids. Similarly, pilkipildrids, miralinids and several odd phalangeridan groups (e.g., an unnamed family of phalangeroids from the System B lfs) vanished after the Oligo-Miocene. Other small phalangeridan groups, such as burramyids, acrobatids, petauroids and ektopodontids persisted in Australian rainforests until at least the early Pliocene and then declined or went extinct (e.g., ektopodontids) in that habitat.

Most of Riversleigh's larger Oligo-Miocene rainforest mammals, apart from kangaroos, were quadrupedal, terrestrial browsers similar to the placental tapirs that survive today in the rainforests of Malesia. Consequently we presume that they fed on an understorey of relatively

soft-leaved plants within the forest. The same may have been the case for the gigantic (up to 500 kg) dromornithid birds that were abundant in the rainforests of Riversleigh. If the rainforest food resources of these giants vanished for whatever reason, it would explain their demise and that of the carnivores (e.g., thylacoleonids) that may have fed on them. However, other factors such as climatic changes may have caused their extinction without exterminating their food plants. The hypertrophied spines on many wattles (*Acacia* spp.), which seem unnecessarily large to deter living herbivorous marsupials (R. Wells, pers. comm.), may be persistent defence mechanisms against browsers that no longer exist. Large-spined acacias in Africa are eaten by elephants and giraffes.

The first appearances of many now mesic groups of mammals in the Oligo-Miocene rainforests of Riversleigh

The general hypothesis that Australia's Oligo-Miocene rainforests were the 'Green Cradle' for its xeric marsupials was advanced by Archer, Hand and Godthelp (1988b) and Archer and Hand (1987) so we will only summarise it here.

In essence, it appears that one of three things happened to each of the various groups of mammals present in the Oligo-Miocene lfs of Riversleigh: 1, extinction before the Pliocene (e.g., yalkaparodontids, ilariids, wynyardiids, yingabalanarids, pilkipildrids, balungamayine potoroids); 2, persistence in refuge rainforest environments (e.g., hypsiprymnodontine potoroids, peroryctid bandicoots, *Strigocuscus*, *Pseudochirops*); or 3, adaptation to the non-rainforest environments that began to dominate much of Australia by the Pliocene.

We have already considered examples of the first two fates. It is the third that deserves further consideration here. Among the mammal groups present in the Oligo-Miocene lfs of Riversleigh that subsequently adapted to non-rainforest environments, there are two primary categories: 1, those that persist(ed) in relict rainforests as well as the relatively new mesic and xeric habitats (e.g., ornithorhynchids, species of *Trichosurus*, *Cercartetus*, dasyurids, macropodids, potoroine potoroids, acrobatids, *Macroderma*, hipposiderids, vespertilionids, molossids; and among now extinct groups, diprotodontids, palorchestids, thylacoleonids, thylacinids); and 2, those that persist only in mesic and/or xeric habitats (e.g., notoryctids, phascolarctids, vombatids, petaurids, *Bettongia*, *Burramys*).

The same pattern we see for mammals has commonly appeared for other groups of vertebrates known from the older Riversleigh deposits. For example, Boles (1989) has identified among Riversleigh's rainforest birds (including logrunners, *Orthonyx* and possible lyrebirds, *Menura*), taxa related to 'drier' groups including emus (Casuariidae) and cockatoos (Cacatuidae), swifts (Apodidae), storks (Ciconiidae), hawks (Accipitridae) and

button-quails (Turnicidae). He interprets some of these (e.g., the casuariid) to represent possibly ancestral groups for more mesic descendants.

It is possible that many of the modern mesic groups became pre-adapted within the Oligo-Miocene rainforests for survival outside of that habitat. For example, Archer and Hand (1987) suggested that koalas may have specialised on ancestral eucalypts within rainforests which in turn specialised on nutrient deficient soils. Consequently, when the rainforest declined in central Australia leaving vast areas of nutrient-deficient soils, this pre-adapted, 'symbiotic' pair would have been able to thrive. In this instance, we are, however, puzzled as to why phascolarctids subsequently disappeared from rainforests.

Another example we have previously cited (Archer Hand and Godthelp 1988b) concerns the marsupial moles (notoryctids). Although confined today to the central Australian deserts, this habitat is almost certainly relatively recent. We were nevertheless surprised to find abundant notoryctids in the System B units of Riversleigh's Oligo-Miocene deposits (Gott 1989; Gott *et al.* in prep.). Their limb morphology indicates that they were burrowing mammals and their teeth indicate that they were in almost every respect ideal ancestors for the living species. We have suggested that the Riversleigh notoryctids became pre-adapted for a burrowing lifestyle in mesic environments by specialising as burrowing insectivore/carnivores in the possibly mossy floors of the Oligo-Miocene rainforests. As with koalas, we again wonder why notoryctids do not appear to have survived in rainforests.

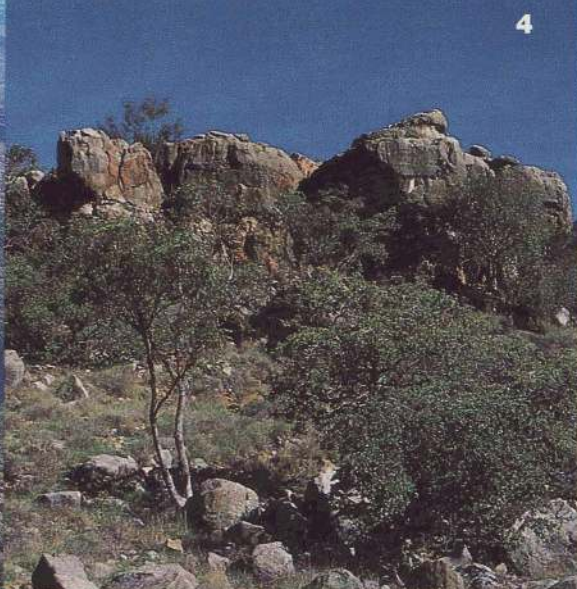
Considering the Riversleigh record as a whole, we are convinced that the Oligo-Miocene rainforests of at least northern Australia were the cradle for all of the mammalian taxa (except murids; see above) that have since adapted to this continent's mesic and xeric environments. This in itself is a very strong argument for conservation of the remnants of this procreative environment throughout Australia and in particular the tropical rainforest refuges of northeastern Queensland.

RIVERSLEIGH STRATIGRAPHY AND PALAEOECOLOGY

Riversleigh presents a vast complex of stratigraphic units and fossil faunas. Any simple model attempting to relate the whole is doomed to an early demise. Although our present understanding (Figs 5-7) is the outcome of 6 years' investigation, we are under no illusions about its probable life span.

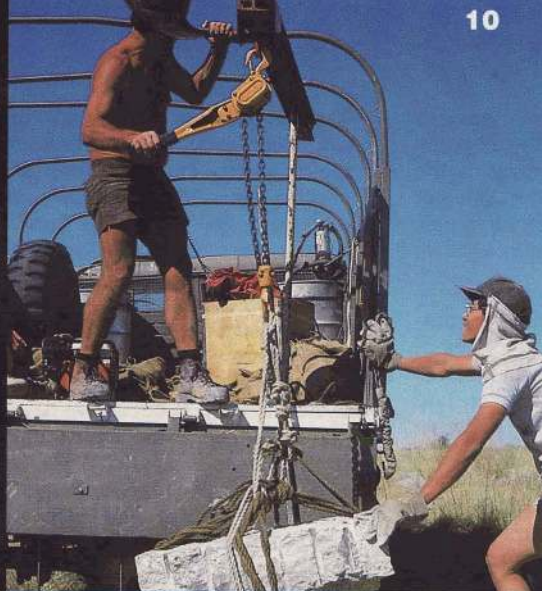
Challenges in defining Tertiary units

While some of Riversleigh's sediments, such as the Thornton Limestone and 'basal conglomerate' (= 'lower





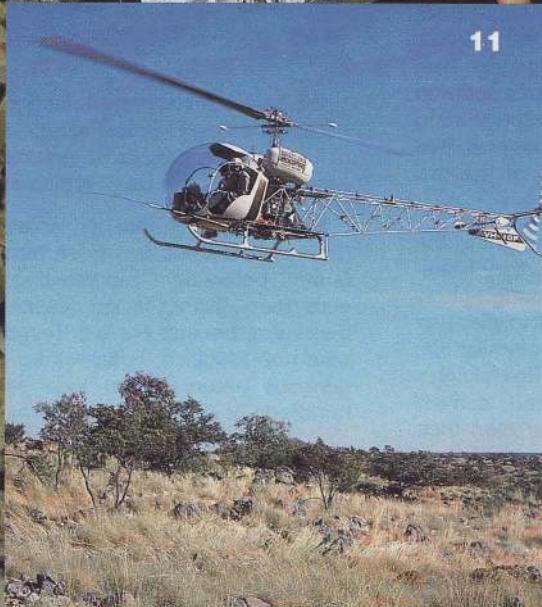
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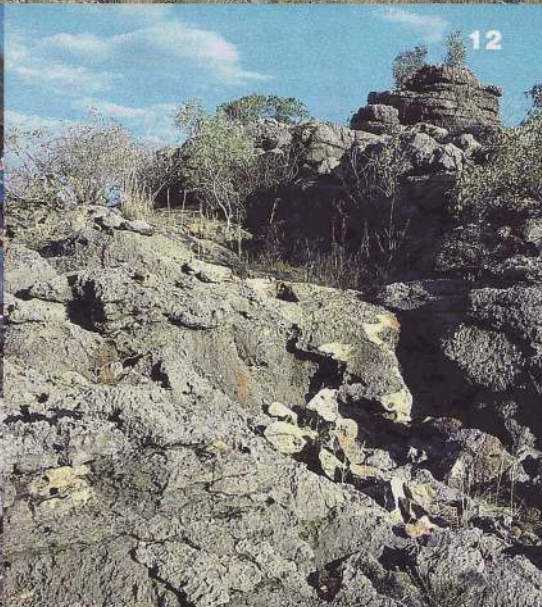
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1. An aerial view of one of the fossil-rich plateaus at Riversleigh. The actual fossil sites occur as relatively small deposits spread unevenly around the edges and tops of these structures.
2. After three weeks of field work, upwards of 15 tonnes of fossil-rich limestone will have been gathered in labelled hessian bags. Volunteers help in all aspects of this work.
3. Fossil bones are clearly visible on the eroded surfaces of grey limestone that preserved them for 20 000 000 years.
4. Site D, one of the first fossil-bearing sites discovered at Riversleigh. The massive grey limestone is approximately 20-25 000 000 years old and contains the bones of giant flightless birds (dromornithids), crocodiles, turtles and rare mammals such as marsupial lions.
5. From the air, the pale fossil-rich System sediments stand out from the surrounding plain of red dust and the darker grey Cambrian limestones in the left foreground.
6. This lower jaw of an extinct balbarine kangaroo is one of many from the Oligo-Miocene local faunas. It appears in Last Minute Site which is among the lowest in the System C sequence on the Gag Plateau.
7. The upper jaw of *Hypsiprymnodon bartholomaii*, an extinct Riversleigh ancestor for the living Musky Rat-kangaroo that today is confined to the rainforests of northeastern Queensland.
8. The most common and widespread mammals in the Riversleigh fossil deposits are bats. In some deposits such as this one (Microsite), their bones occur in the thousands. The most common species in this array of jaws is most closely related to bats previously known only from fossil deposits in Europe.
9. Volunteers, students and professional palaeontologists work together to divide large rock in White Hunter Site. The creatures from this relatively old site are represented by many complete skulls.
10. A block and tackle are used to lift large blocks into the "Bonesmobile", a four-wheel truck provided by the Australian Geographic Society.
11. Helicopter transportation enabled by Wang Australia is sometimes the only way we can reach the more remote deposits and the only way we can retrieve large samples of rocks from the many areas where ground-based vehicles cannot move.
12. Rackham's Roost, unique within the Riversleigh's area because it is so far Riversleigh's only Pliocene site. It preserves the remnants of an ancient cave (one wall is to the right) within which ancestral ghost bats ate their prey. The rocks in the foreground are solid with teeth and bones of small mammals including rodents, bats and dasyurids.

member' of Tedford 1967), appear relatively easy to trace over wide areas, determination of the regional extent and superpositional sequence of many of the Cainozoic deposits has been aggravated by the apparent lack of time-specific macroscopic sedimentary features, a problem noted by Tedford (1967) in regard to what we now call the System A sediments.

Although many of the Tertiary carbonates are complex, we suspect that this complexity reflects cycles of sedimentary events that may have repeated themselves at different times in isolated areas. Thus we often find that different-aged bone accumulations (e.g., Camel Sputum in System B and Henk's Hollow in System C) display a similar lower silt-rich phase containing more complete bones capped by a similar relatively crystalline phase containing more fragmented specimens (see below).

On-going efforts to map contemporaneous units throughout the region are hampered by the isolated nature of many of the bone-bearing exposures (see below). For example, all known System B units occur in a different region of Riversleigh than those representing System C without annectant Tertiary carbonates that could clarify the stratigraphic relationships of the two Systems.

For these reasons, our approach to determining the identity and relationships of most of the Tertiary bone-bearing units has been to treat them as stratigraphers often must treat cave deposits — prepared to discover that non-contemporaneous units may display similar distinctive lithologies. Accordingly, most of Riversleigh's Cainozoic biostratigraphic units have been defined primarily on the basis of their faunas rather than their petrology.

For this reason, for example, we doubt that the 'lower member', a basal conglomerate recognised by Tedford (1967) as a Tertiary unit underlying the Site D limestone, is contemporaneous throughout the Riversleigh region. Such basal conglomerates are widespread and resemble erosional lags of chert nodules of the kind that today carpet the land surface wherever the Cambrian Thornton Limestone (the genetic source of the nodules) has completely eroded away. We suspect that these basal conglomerates have been formed *in situ*, by different cycles of Tertiary sedimentation in the same way that they are forming in local areas of the Riversleigh region today. If so, they may have little biostratigraphic significance beyond representing post-Cambrian erosional surfaces.

Oligo-Miocene sites, faunal assemblages and palaeoenvironments

There are four major regions within Riversleigh Station where most of the Oligo-Miocene sediments have been found: 1, the flat-lying **D-Site Plateau**, to the west of the

Riversleigh/Lawn Hill track, where exposures of late Oligocene-early Miocene units (System A) abound on the southern and eastern margins, 2, early to middle Miocene units (System B) are exposed on the northern edge (possibly including Neville's Garden Site) and western areas (e.g., the discrete Godthelp Hill and Hall's Hill sites) and 'cave' deposits (e.g., Microsite and Bitesantennary Site) of Oligo-Miocene age occur on the southeastern and northern edges respectively; 3, the flat-lying **mesas** to the east of the Riversleigh/Lawn Hill track where additional exposures of what appear to be Systems A and B occur (we have not yet analysed these outlying sites); 4, the slightly dipping **Godthelp Hill and Hal's Hill** series west of Site D where at least 7 metres of System B units lie on D-Site Equivalent units; and 5, the slightly dipping **Gag Plateau** to the northwest of the D-Site Plateau where approximately 12 metres of System C units are superimposed on D-Site Equivalents, in subregions such as Ray's Amphitheatre, Archie's Amphitheatre, Megabyte Hill and Jeanette's Amphitheatre.

We have laser-surveyed many of the sites on Godthelp Hill and the Gag Plateau. Figure 4 is a graphic presentation of the relative heights of selected sites on the north-eastern end of the Gag Plateau and on Godthelp Hill.

Each fossil-rich site, or isolated faunal assemblage (thanatocoenosis), has been treated as a distinct local fauna potentially representing a time-distinct or ecosystem-distinct facies despite the fact that some of these assemblages are less than 5 metres apart in otherwise non-fossiliferous limestone of a seemingly homogeneous nature. Other local faunas are isolated by hundreds of metres from their nearest neighbour.

As seen in eroded or excavated exposures (e.g., Upper Site and Henk's Hollow Site), many of these Oligo-Miocene bone-rich deposits are well-defined laterally, commonly 3-5 metres in diameter, 0.5-1.0 metres in thickness and roughly lens-shaped in cross-section. Our subjective impressions are that in horizontal view these deposits appear to be oval, suboval or arcuate in shape. They appear to grade laterally, albeit rapidly, into non-fossiliferous limestones. Macroscopic lithological discontinuities between the bone-rich and adjacent depauperate limestones are not clear. We are uncertain of the precise shapes of any of the fossiliferous bodies so far sampled because we have left most of each for future investigations.

Often (e.g., Henk's Hollow Site, Camel Sputum Site, Gag Site) the lower levels of these assemblages contain large intraformational clasts or masses of yellowish-white limestone (which experience tells us indicates relatively large amounts of brown silt) cemented by whiter, more crystalline carbonate. These lower levels grade upwards into whiter more homogeneous although sometimes silty limestones. The lower levels often contain more complete

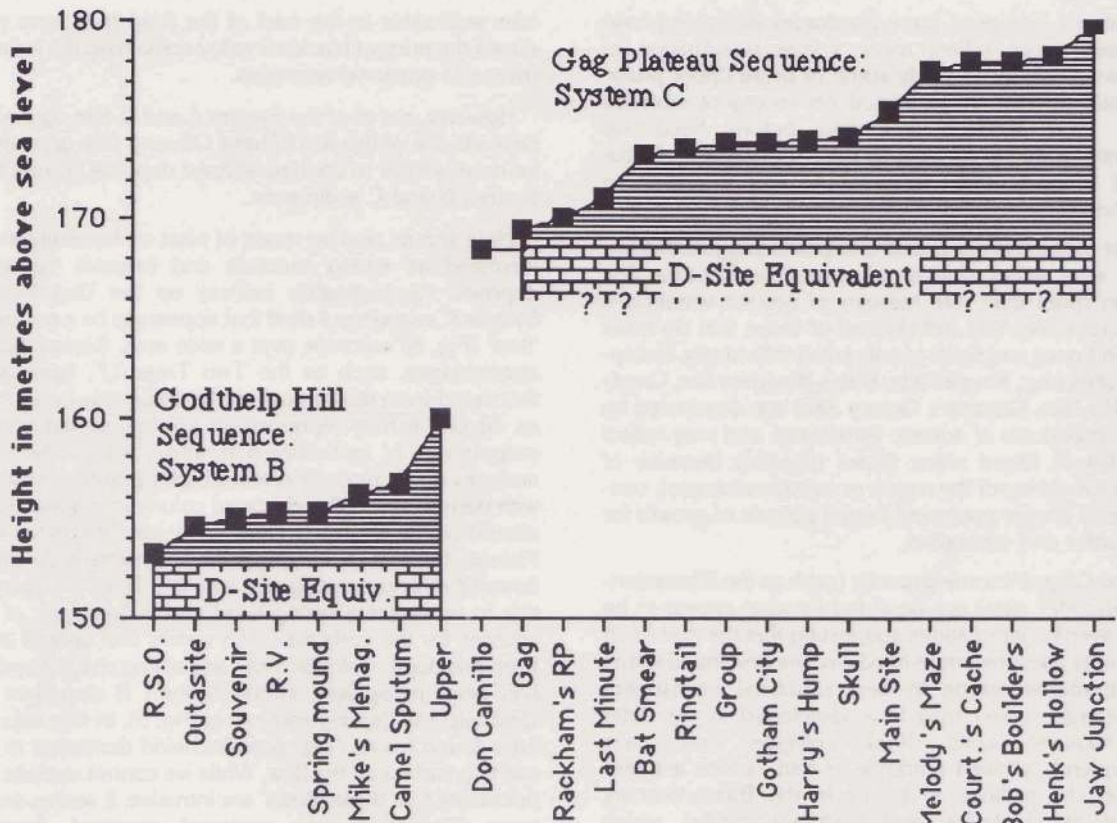


Fig. 5. Laser survey data (per the efforts of M. Bannister, H. Godthelp and A. White) for System B sites on Godthelp Hill and System C sites on the Gag Plateau. Height for the lowest site above mean sea level was calculated using a barometer. Although the two Systems are plotted here together, they are in fact separated geographically. Both sequences also have what we interpret to be D-Site Equivalent units at their base (e.g., Don Camillo exposed on the edge of the Gag Plateau); hence it is unlikely that System B units occur below the System C units exposed in the area of the Gag Plateau. 'Spring Mound' is a geological feature, not a local fauna (see text). The block symbol used here represents the basal relatively homogeneous, thick D-Site Equivalent limestones; the horizontal lines represent the superpositional sediments of System B and C; squares represent the relative heights but not necessarily horizontal proximity of fossil sites within Systems B and C.

skulls and bones while the bones in the higher more crystalline levels are often broken with the 'clean' edges of the breaks lacking abrasion (which might otherwise reflect post-depositional transport).

Although the precise nature of these accumulations is unclear, for some of these sites (e.g., Gag Site in System C) we hypothesise isolated, possibly steep-sided pools of carbonate-rich water accumulating detritus within rain-forest environments. Possibly silt-rich facies accumulating around the edges of deeper pools became periodically unstable and slid *en masse* towards the centre of the pools where the semi-consolidated yellowish clasts were secondarily cemented by more crystalline carbonates precipitating, often with the bones of bats, in the spaces between the clasts. In the final stages of pond filling, the upper units may have become more crystalline as the shallowing water became more concentrated with dissolved calcium carbonate.

In a few sites (e.g., Last Minute Site) the more crystalline phases contain thick sequences of what appear to be shattered evaporite surface crusts that have periodically settled to the bottom with the bones of the animals that may have caused the surface to break. While evaporites are normally associated with saline waters, calcium carbonate evaporites are known to form on the surfaces of cave pools. We have also found evaporite crusts of calcium carbonate on small isolated pools of the modern Gregory River system in open air situations thereby demonstrating that cave environments are not required for the development of animal traps of this kind. Small, still, super-saturated pools surrounded by warm gallery rainforest may well have supported fragile evaporite crusts. These crusts may have been augmented or initiated by floating mats of calcium carbonate-secreting algae of the kind which we appear to have recovered from Upper Site (see the discussion of the Upper Site fauna above).

Relatively increased bone breakages in upper phase materials might reflect more severe bioturbation in shallowing waters. Possibly some of these upper phase materials actually accumulated on emergent surfaces where they suffered trampling before becoming cemented onto the surfaces by travertine deposits. Petrological analyses under way may be able to test these hypotheses.

Most of the System B and C deposits suggest that the pools were either shallow or short-lived because few contain more than rare remains of aquatic vertebrates (fish, crocodiles and turtles) and of those that do most contain bones and teeth of only small individuals. Exceptional sites (e.g., Ringtail Site, Bob's Boulders Site, Crusty Meat Pie Site, Quentin's Quarry Site) are dominated by larger individuals of aquatic vertebrates and may reflect episodes of raised water tables (possibly because of tectonic lowering of the region or eustatic changes), consequently deeper pools and longer periods of growth for fish, turtles and crocodiles.

A few Oligo-Miocene deposits (such as the Bitesantennary and MP² sites) are bounded by what appear to be thin, travertine laminations suggesting that the bone-rich sediments filled travertine-lined cavities developed within the parental limestone. In these situations we visualise that phreatic caves may have developed in the older Oligo-Miocene units. Roof collapse may have subsequently allowed entrance of bats (which are represented by millions of bones in the Bitesantennary deposit; Hand, Archer and Godthelp 1989a), which roosted in the cave, and surface water that accumulated as ponds containing ostracods, snails and possibly rafts of algae. Terrestrial reptiles, birds and mammals may have stumbled over the edge of the cave's mouth or been brought in by mammalian or avian predators to become rare elements in these particular deposits.

The only apparent exceptions to these generalised palaeoecological models may be the faunal assemblages in System A (e.g., Site D) and some of the D-Site equivalents (e.g., Sticky Beak Site and Bone Reef Site). In these the bones are on average larger (almost exclusively fragments of large crocodiles, dromornithids, turtles and diprotodontids) and rarer. The parent limestone in these sites forms thicker units (in Tedford's 1967 Site D the fossiliferous unit is at least 3 metres thick) with some evidence of flysch-like sediments comprising coarser, sometimes better-sorted materials. A palaeoecological model that might explain these features would be a large lake that filled the central basin of the area (through which the Riversleigh/Lawn Hill road now runs) fed by springs, perennial streams or periodic rushes of surface water from the surrounding forested terrain. The western margin of this lake's sediments would have extended at least as far as the thick units containing Tedford's (1967) Sites B-F and possibly further west as the underlying Tertiary sediments of the D-Site Plateau. Erosion of these

lake sediments to the east of the road may have produced the present blacksoil valley containing the isolated mesas as erosional remnants.

However, not all of the System A and D-Site equivalent deposits are of this kind; Burnt Offering Site appears to be more similar to the lens-shaped deposits common in System B and C sediments.

Note should also be made of what we have tentatively identified as spring mounds and massive travertine deposits. Approximately halfway up the Gag Plateau System C sequence a shelf that appears to be a travertine 'flow' (Fig. 6) outcrops over a wide area. Several faunal assemblages, such as the Two Trees LF, have been recovered from this layer which in areas may be as thick as 40 cm. It may represent an episode of widespread outpourings of carbonate-rich spring water. Fractured surfaces of this material reveal a highly porous carbonate with narrow, vertically orientated columns (diagenetically altered calcite crystals?). Near Jim's Jaw Site on the Gag Plateau there is a roughly circular, metre-wide cauliflower structure contiguous with this 'flow'. We interpret this to represent a spring head and at least one of the sources for the carbonate rich waters that spread away from this point. A similar 'flow' and spring mound system has been recognised in the System B sequence on Godthelp Hill ('spring mound' in Fig. 5). In this area we have found fossils (e.g., pseudocheirid dentaries) in the eroding surface of the flow. While we cannot exclude the possibility that these 'flows' are intrusive, it seems much more likely that they represent repeated, possibly regional events that occurred within Systems B and C.

In regard to the spring mounds and travertines, we have previously suggested (e.g., Archer 1988) the possibility that non-contemporaneous spring heads formed part or all of some of the isolated hills capped with System B and C sediments (such as the Gag Plateau and Godthelp Hill). The model involved spring water forced up through the underlying Cambrian and older Tertiary limestones to deposit calcite on the surface as travertine sheets and cauliflowers and then subsequently re-erupting through these deposits to add progressively younger carbonates until the accumulating mass became impenetrable. At that point, the spring water might erupt in another area to start another younger sequence. The faunal assemblages we find might then be interpreted as the cemented contents of isolated rim pools that had developed lateral to the spring head. This might account for the oncolite-like concretions we sometimes find developed around bone fragments in some of the deposits (e.g., Grime's Site on the Gag Plateau). Against this model, however, is the fact that while the Riversleigh limestones are clearly capable of preserving surface features (such as the rippled travertine rims and fragments of straws found in Neville's Garden Site sediments in 1988), these features are unknown from any of the other sites we have so far excavated.

It is clear to us that many different depositional mechanisms were responsible for producing the variety of Oligo-Miocene sediments at Riversleigh. The task now will be to test the competing models and to contrast them with the palaeoecological interpretations independently arising from study of the equally diverse faunal assemblages.

Pliocene sediments, faunal assemblages and palaeoenvironments

The only Pliocene site recognised (Rackham's Roost) appears to be the floor of a long, narrow cave that at one end opened onto a vertical face along the ancestral Gregory River (Godthelp 1988). Another larger, lower opening may have been developed more than 50 metres away in the opposite direction. Most of the millions of bones accumulated in this cave appear to have been brought in by carnivorous megadermatid bats which dropped uneaten bits and defecated the indigestible teeth and bones to the floor below their roosts. There are rarer bones of snakes which may have preyed on the bats and very rare large kangaroos which may have fallen through holes in the roof.

Pleistocene sites, faunal assemblages and palaeoenvironments

The Pleistocene deposits are of two main kinds: isolated cave deposits which have been treated in the same way described above for the Oligo-Miocene units; and perched fluvial terraces. The cave deposits represent fissure fills, megadermatid roosts and/or owl-pellet accumulations of the kind that now accumulate in the general region, for example in the caves around Carnoowear.

In some instances (e.g., at Two Trees Site), what may be Pleistocene (or Pliocene?) fissure-fills have been found as buff- or rust-coloured heterogeneous carbonates intruded into eroded spaces within the Oligo-Miocene sediments. Some of these fissure materials contain murids.

The fluvial terraces are of undetermined extent but each is almost certainly defined by subsequent channeling. Terrace Site, for example, presents an approximately 3 metre thick cross-section through stream bed deposits comprising a basal poorly sorted conglomerate (also containing bone, freshwater mussel shells and charcoal) which grades upwards into finer sands and silts. The bones in the fluvial deposits may represent the carcasses of crocodile meals, accidental drownings or seasonal flushing of the surrounding countryside by rain-fed creeks. Some (but not most) of the bone fragments are very worn which invites an interpretation of long-distance transport and/or re-working from older Cainozoic deposits. The Australian Geographic Society has provided funds to have the charcoal and/or shells from the Terrace Site dated.

Throughout the region there are many other presumably Pleistocene (or late Tertiary) bone-bearing sediments. One of the most widespread is a rust-coloured, possibly indurated soil horizon commonly found on subsoil surfaces or flanks of deeply fissured blocks of the Oligo-Miocene limestones. When it occurs as a cement on the surfaces of bone-rich limestone (e.g., as it does at Helicopter Site), it sometimes contains broken pieces of teeth and bone of Oligo-Miocene taxa. We presume that these had previously been lying free in the soil having been naturally etched from the receding surface of limestone before being re-cemented as an overlying probably Pleistocene soil horizon.

The composite stratigraphic column for Riversleigh

Figure 5 summarises what we now perceive to be the major sedimentary deposits present in the immediate Riversleigh area. Key aspects are:

1. local outcrops (e.g., at the base of the Site D hill along the Riversleigh/Lawn Hill Road, between the Gregory River crossing and Verdon Creek) of an early Proterozoic sediment (Ploughed Mountain Beds) containing conspicuous stromatolite beds;
2. widespread basement of Cambrian carbonate (Thorntonia Limestone characterised by chert nodules and, more rarely, invertebrate remains) which is overlain or cut into by younger sediments;
3. carbonate cemented 'basal conglomerates' mainly containing eroded chert nodules which appear to have accumulated (possibly at different times; see above) as pavements throughout much of the region and which probably represent *in situ* erosion remnants following dissolution of the Thorntonia Limestone and/or older Cainozoic carbonates into which the nodules had previously been reworked;
4. At least five types of Oligo-Miocene bone-rich carbonates:
 - the 'Carl Creek Limestone' [which may more appropriately be called the Verdon Limestone — we are presently considering this problem], a deep-water lacustrine unit that contains, e.g., the Riversleigh Local Fauna from Site D [collectively, these deposits are referred to here as **System A**];
 - the 'D-Site equivalents' which frequently overlie the Thorntonia Lst but are not continuous with the main Site D limestone and which contain, e.g., the Sticky Beak, Pancake, Hiatus 1, Hiatus II, and possibly White Hunter LFs;
 - an at least 7 m thick sequence of lacustrine carbonates best exposed on Godthelp Hill and Hal's Hill which contain *mainly* non-aquatic LFs such as Wayne's Wok, RSO, Outasite, Camel Sputum, Upper Site and Boid Site LFs [collectively referred to here as **System B**];

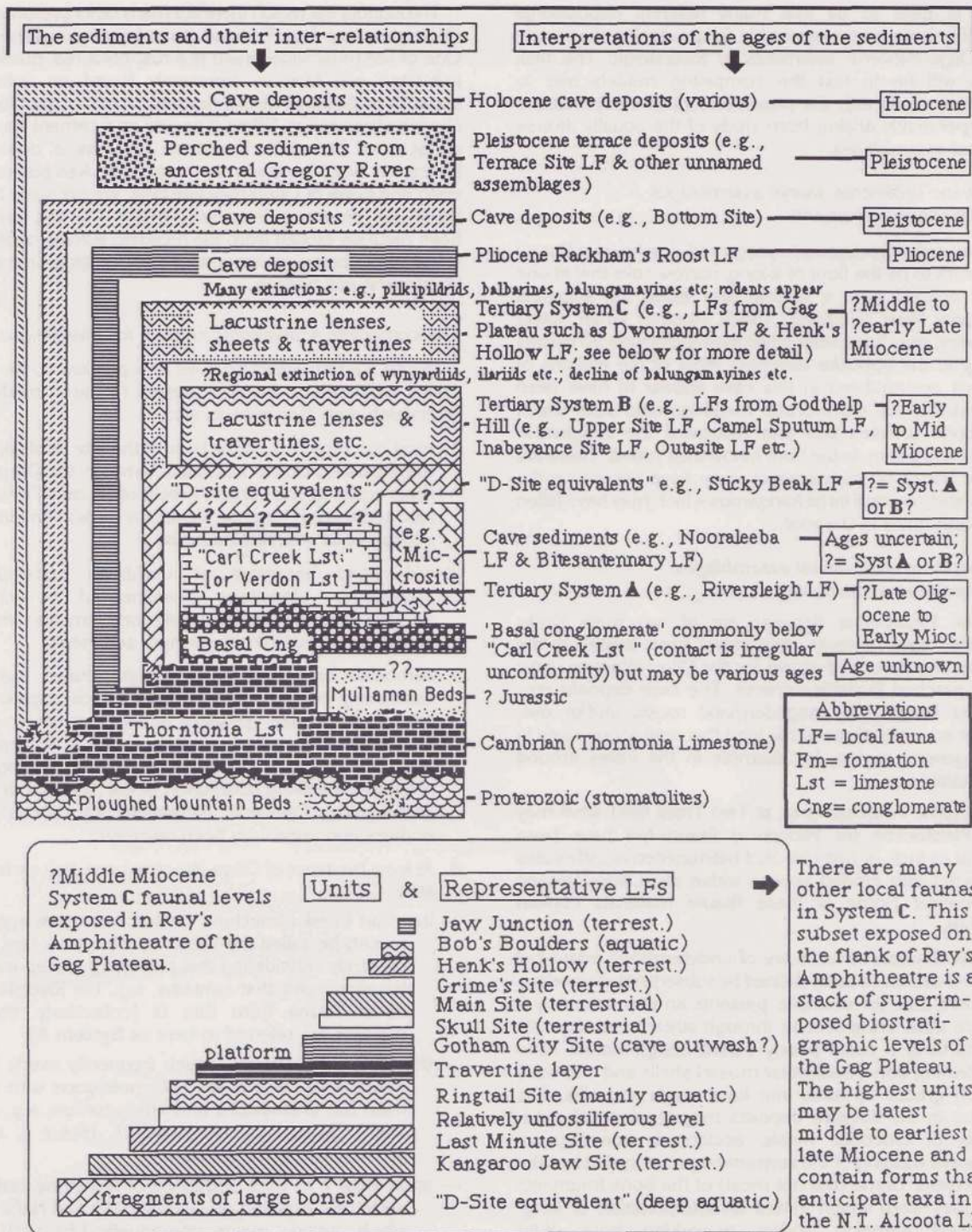


Fig. 6. A composite stratigraphic column for the Riversleigh region depicting what we presently interpret to be the physical and/or temporal relationships of the main sedimentary deposits producing fossils in the area.

- an approx. 10 m thick sequence of lacustrine carbonates (see base of diagram) containing mainly: *non-aquatic* LF's such as Last Minute, Dwornamor from Gag Site, Main Site, Henk's Hollow and Jaw Junction LF's; and largely aquatic LF's such as Ringtail Site, Melody's Maze, Quentin's Quarry and Bob's Boulders LF's [collectively referred to here as **System C**]; and
 - cave deposits such as Microsite (source of the Nooraleeba LF) and Bitesantennary Site which appear to be pool deposits filling caves developed in the 'Carl Creek Lst' and/or D-Site equivalent units;
5. Pliocene cave deposits, Rackham's Roost being the only one so far recognised, that formed from cementation of organic debris on the relatively dry floors of caves cut into the Thornton Lst;
 6. Pleistocene fissure/cave deposits filling spaces in the Thornton Lst probably representing several different episodes of accumulation such as Bottom Site and Outer Limits Site;
 7. Pleistocene fluvial silts, sands and conglomerates, e.g. Terrace Site and other unnamed units of possibly differing ages, exposed as perched and dissected channel deposits accumulated by the ancestral Gregory River system; and
 8. Holocene (i.e., Recent) cave deposits, mostly unnamed, which carpet the floors and fissures of relatively recent fissures developed generally in the Thornton Lst but sometimes in the Tertiary carbonates.

In addition to these deposits presently being examined, we have encountered many others in the region that may prove to be significant when adequately assessed. Most commonly these are fissure deposits of unclear age some of which contain bones. Other presumably Tertiary rock types in the region include zones of secondary ferruginization in isolated patches of Cambrian (and possibly Tertiary) limestones. Wang Site itself appears blackish-grey because of primary deposition or diagenetic concentration of ferromagnesium minerals. We have not seen undoubted exposures of laterite beneath System A units (although they were reported by Tedford 1967) but we have seen a limited exposure of what appears to be laterite immediately north of Megabyte Hill (the location of Wang Site) on the northwestern edge of the primary Gag Plateau. Its stratigraphic relationships to the fossiliferous deposits have not yet been determined.

Work is presently under way to test and refine these preliminary concepts. One of us (Megirian) is concentrating on the geology while about 30 students, colleagues and the rest of us are focusing on the faunas. All of the many kinds of evidence that might clarify understanding about

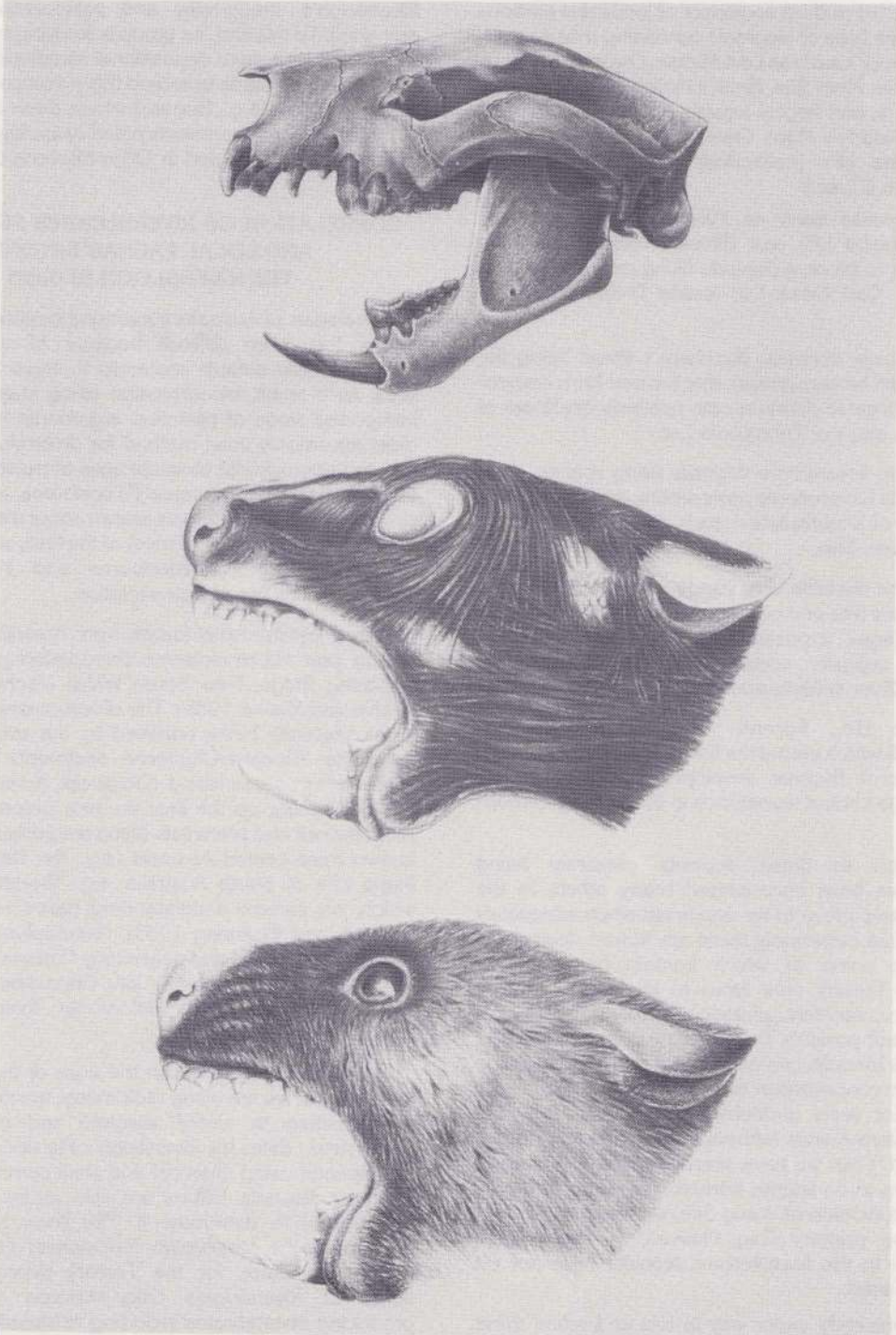
Riversleigh's stratigraphy and palaeoecology will be examined. To this end our group is studying contemporary freshwater carbonate depositional situations throughout Australia and intends to extend this investigation to areas of the Malaysia (e.g., Borneo) where there appear to be contemporary environments possibly analogous to those in the Riversleigh region in Oligo-Miocene times.

CORRELATION OF RIVERSLEIGH'S SEDIMENTS AND LOCAL FAUNAS BEYOND THE RIVERSLEIGH REGION

Correlation of Australia's mammal-bearing fossil sediments has been difficult because of a paucity of radiometrically datable materials in most of the older sites. As a result, biocorrelation using shared taxa and interpreted stage of evolution arguments has been the most commonly used method for determining the relative and approximate absolute ages of most of the previously known assemblages (Woodburne *et al.* 1985). Unfortunately, very little was known about the geographic and/or temporal range of most of the taxa, such as diprotodontoids (Stirton, Woodburne and Plane 1967), involved in studies of biocorrelation.

The oldest mammal known from Australia is the 110 million year old monotreme *Steropodon galmani* from Lightning Ridge, New South Wales (Archer, Flannery, Ritchie and Molnar 1985). The oldest marsupials may be those presently being retrieved by our research group from the ?Eocene/Oligocene sediments of Murgon, southeastern Queensland (Godthelp, Archer and Hand 1989). Coming up the line, the next oldest marsupials, monotremes and placentals (bats) are probably the oldest known from central Australia (e.g., the Ditjimanka and Pinpa LF's of South Australia; e.g., Woodburne 1986) which, on current understanding based on illite dates (Norrish and Pickering 1983), foraminiferal biocorrelation (Lindsay 1987) and palynology (Truswell, Sluiter and Harris 1985), are probably late Oligocene in age (i.e., about 25 000 000 years old; Archer, Every, Godthelp, Hand and Scally 1989).

In our efforts to establish the ages of the Riversleigh local faunas, we are using radiometry, biocorrelation and superposition to clarify absolute and relative ages. Radiometric dates for Riversleigh's Pleistocene units will be obtained using charcoal and shell common in many of these deposits. Efforts are also under way (per G. McNamara) to determine if ¹⁰Be (now known to be present in the Riversleigh limestones) could provide radiometric dates for the Tertiary deposits. Further, some of Riversleigh's Oligo-Miocene deposits are producing invertebrates including ostracods which may be useful for biocorrelation. However, most of our efforts to date the Riversleigh local faunas involve studies of vertebrate biocorrelation within and outside of Australia.



A reconstruction of the head and neck of Wakaleo vanderleuri, a leopard-sized marsupial lion that would have been one of the more efficient carnivores of its day. A related species prowled the older rainforests of Riversleigh as did a tiny cat-sized cousin from the Upper Site Local Fauna. (Drawing by Peter Murray).

The potential of the Riversleigh sequence to serve as a basis for development of a biocorrelation framework for late Oligocene to at least early Quaternary non-marine deposits of Australia is high. Riversleigh's abundant Oligo-Miocene bats (at least 23 species; Hand, Archer and Godthelp 1989b) are enabling intercontinental correlation of Riversleigh's sediments with those from western Europe and other areas of the 'Old World'. For example, in terms of international correlations, the hipposiderid bat *Hipposideros* (*Brachipposideros*) *nooraleebus* from the Nooraleeba (Microsite), Bitesantennary and White Hunter LFs correlates with similar material of Burdigalian age known from France (Sigé, Hand and Archer 1982, Hand 1984, Hand, Archer and Godthelp 1989a). Similarly, a Riversleigh molossid (*Petramops creaseri*) from Gotham City Site resembles Eocene molossids from Europe although this resemblance is almost certainly symplesiomorphic (Hand 1989a).

In terms of intracontinental correlations, the distinctive potoroid *Wakiewakie lawsoni* is now known only from the Upper Site LF of System B in Riversleigh and the Kutjamarpu LF of South Australia (Godthelp, Archer, Hand and Plane 1989). The thylacoleonid *Wakaleo oldfieldi* from the Kutjamarpu LF resembles possibly conspecific thylacoleonid material from Site D and a thylacoleonid from Upper Site appears to be a more derived relative of the Ngapakaldi taxon *Priscileo pitikantensis*. The pseudocheirid genus *Paljara* is similarly only known from the Kutjamarpu LF and System B and C Riversleigh lfs. A balbarine macropodid from some of the System B and C lfs appears to be *Nambaroo*, a genus otherwise only known from the Tarkarooloo and Kutjamarpu LFs of South Australia (B. Cooke, in prep.). The diprotodontid zygomaticurine from one of Riversleigh's highest Oligo-Miocene lfs, the Jaw Junction LF, most closely resembles (but is more plesiomorphic than) *Kolopsis torus* from the Alcoota LF of the southern Northern Territory. The ?wynyardiid genus *Namilamadeta* is now known only from Riversleigh's D-Site Equivalent lfs, System B lfs (and possibly Riversleigh LF) and the Tarkarooloo LF of South Australia. The palorchestid genus *Ngapakaldia*, previously only known from the Ngapakaldi and Tarkarooloo LFs of central Australia is now also known from the Riversleigh LF. The zygomaticurine *Neohelos tirarensis* from Riversleigh System C lfs (e.g., Dwornamor LF) appears to be intermediate in size and morphology between specimens in the Kutjamarpu LF and those in the Bullock Creek LF of central Northern Territory.

Stratophenetic data of this kind are providing the basis for the development of the biocorrelative framework for the Riversleigh local faunas summarised below that encompasses otherwise isolated Cainozoic local faunas from other areas of the continent.

The sequence of sediments in Riversleigh is also providing opportunities to study temporal changes in

lineages, previously only known (if at all) from geographically isolated deposits, such as 'V.D.' perameloids, thylacinids, propleopine, hypsiprymnodontine and balungamayine potoroids, balbarine macropodids, *Neohelos*, *Namilamadeta*, *Wakaleo*, *Paljara*, *Pseudocheirops*, *Macroderma*, pilkipildrids, hipposiderids and molossids. Clarification of sympatric evolutionary trends in these lineages may increase the potential biocorrelative value of these taxa.

Figure 6 summarises some of the evidence we have (only the mammals are considered here) for interpreting the approximate age correlations of key Riversleigh local faunas to those of the rest of Australia and the world in general. Age determinations for the pre-Tertiary sediments (i.e., the early Proterozoic, Palaeozoic [Thorntonia Lst] and Mesozoic [?Mullaman Beds] Eras) are based on previous studies of invertebrates. Our interest focuses on the Tertiary and Quaternary sediments of the Cainozoic.

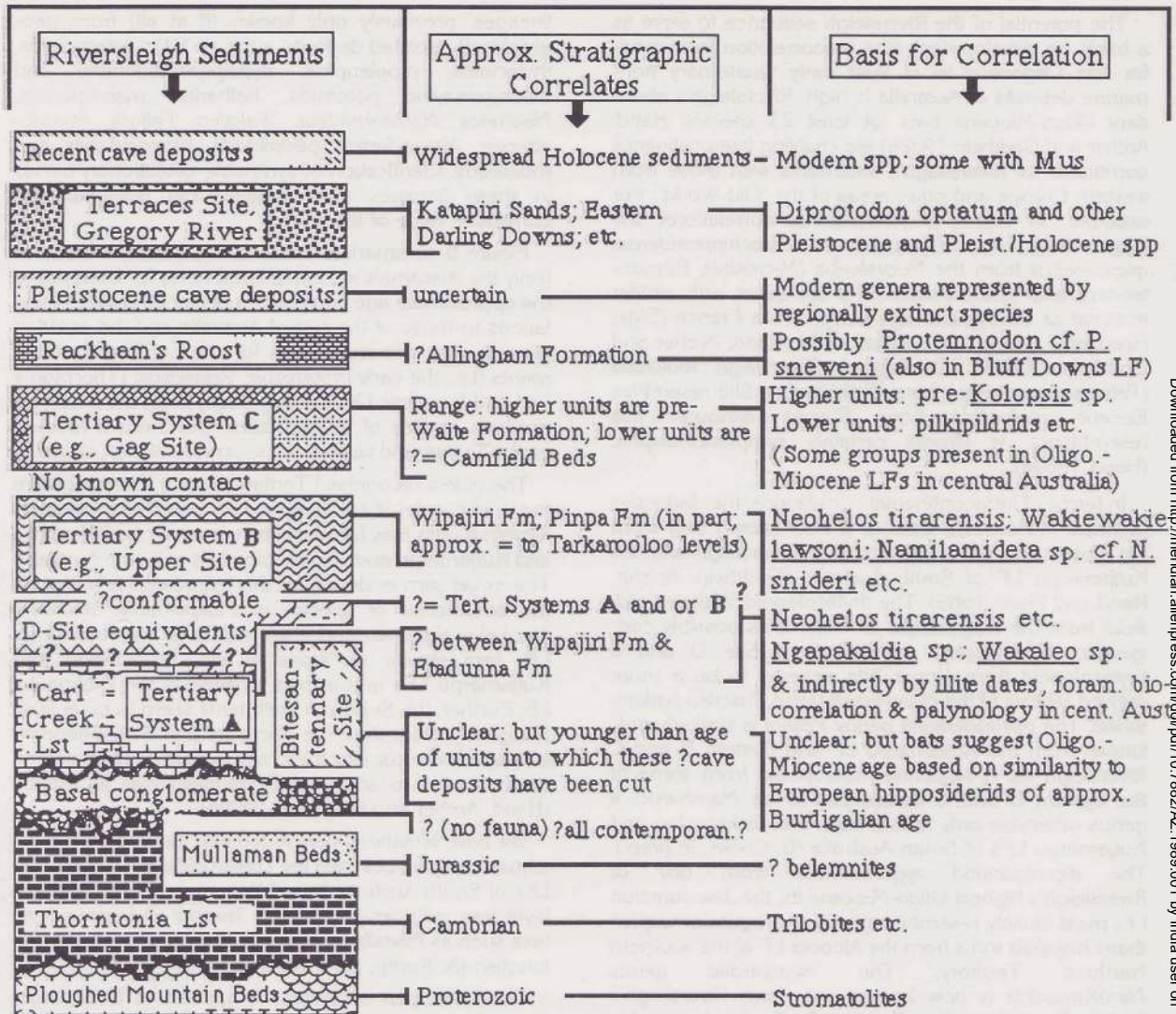
The oldest recognised Tertiary units at Riversleigh are the 'Carl Creek Lst' (or ?Verdon Lst), and System B units. System A units may fall somewhere between the Ditjimanka and Kutjamarpu and Tarkarooloo LFs of South Australia. The as yet slim evidence for this hypothesis is based on the occurrence of species of *Ngapakaldia*, *Wakaleo*, *Neohelos tirarensis* and a wynyardiid in the Riversleigh LF, taxa similar to those in the Tarkarooloo and Kutjamarpu LFs and in part to those in the Ditjimanka LF. Further, the System A sediments seem to be at least marginally older than the Microsite and Bitesantennary LFs which are cut into them and contain a hipposiderid taxon similar to some of Burdigalian age in France (Hand, Archer and Godthelp 1989b).

We have tentatively concluded that the System B local faunas compare best with the Tarkarooloo and Kutjamarpu LFs of South Australia based in part on shared species-level taxa such as *Wakiewakie lawsoni* and genus-level taxa such as *Namilamadeta*, *Nambaroo* and at least one lungfish (A. Kemp, pers. comm.).

The lower part of System C appears to be younger than the Kutjamarpu and Tarkarooloo LFs but older than the Bullock Creek LF based in part on some of the zygomaticurines and thylacinids it contains and its lack of the previously abundant species of *Namilamadeta*. The upper part of System C appears to be close to but older than the Alcoota LF because of the presence of a pre-*Kolopsis*-like zygomaticurine in the Jaw Junction LF of Riversleigh.

The Rackham's Roost LF is interpreted to be Pliocene (probably early Pliocene) because it contains: abundant plesiomorphic rodents (at least 12 spp; Godthelp in prep.); a population of *Macroderma gigas* that retains some features characteristic of the Pliocene *Macroderma koppa* from the Wellington Big Sink Fauna of New South Wales (Hand 1987, Hand, Dawson and Augee 1988); and a macropodid similar to the early Pliocene *Protemnodon sneweni* from the early Pliocene Bluff Downs LF.

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Fig. 7. Our present understanding of the approximate correlation of the main fossiliferous units exposed at Riversleigh. More detail about correlation of the mammal-bearing sediments is given in the text.

The Terraces Site LF is interpreted to be Pleistocene because it contains *Diprotodon optatum*, a taxon otherwise unknown from pre-Pleistocene deposits in Australia.

Other Pleistocene deposits are concluded to be this age on more circumstantial evidence. Bottom Site, for example, contains taxa referable to modern genera but most appear to represent species no longer surviving in the Riversleigh region. Presumably they were present in the area under a different climatic regime, changes which characterised the glacial/interglacial fluctuations of the Pleistocene.

The Recent deposits contain modern taxa still living in the area although some of these sites appear to have been accumulated prior to the introduction of the House Mouse (*Mus musculus*) possibly as early as 400 years ago.

Missing so far from the Riversleigh Oligo-Miocene to Holocene sequence appear to be any local faunas clearly representing the late Miocene and possibly the middle and late Pliocene. Late Miocene local faunas from other areas of Australia include Alcoota (Northern Territory) and Beaumaris (Victoria). The diprotodontids in these local faunas most closely resemble the zygomaturines in Riversleigh's Jaw Junction Site and No-name Site at the top of the System C sequence. These highest local faunas on the Gag Plateau may have been the last to accumulate before deposition on Riversleigh Station shifted to some other as yet undiscovered area. The lack of additional Pliocene sites is similarly probably the result of imperfect knowledge of the area. If one isolated cave accumulated Pliocene materials, surely there were others accumulating at different times in the late Tertiary. For the same reasons, we expect that continued exploration of limestones adjacent to those presently being examined will eventually turn up vertebrate deposits that predate the Oligo-Miocene System A sequence. These are challenges for future Riversleigh expeditions.

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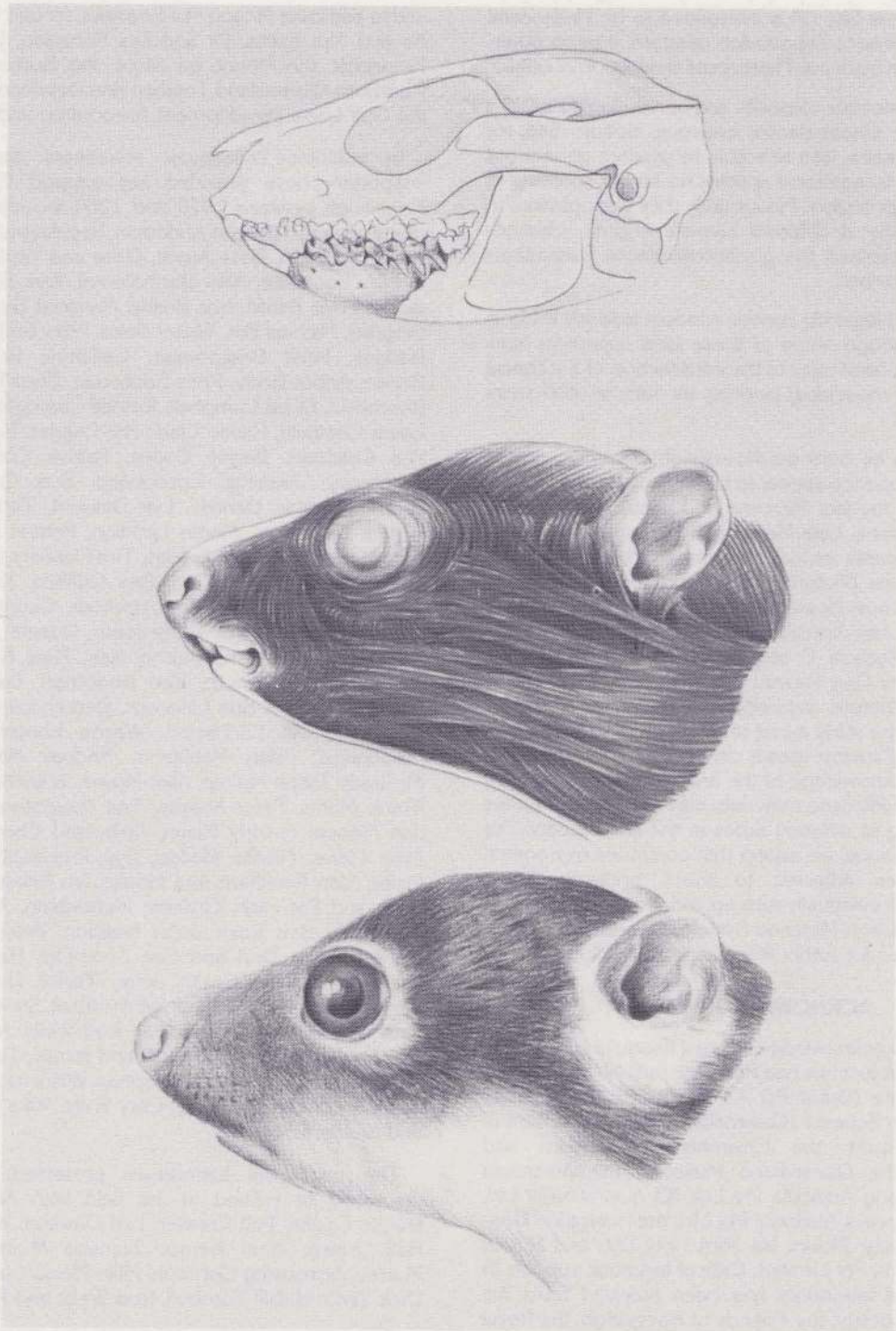
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Reconstruction of the head of an extinct Riversleigh ringtail possum distantly related to the Green Ringtail that survives today in the rainforests of northeastern Queensland. Some Riversleigh local faunas (e.g., the Dwornamor LF) have revealed up to nine distinct sympatric species of ringtails. (Drawing by Peter Murray).

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NOTES PRIMARILY ABOUT ENTRIES IN TABLE 1

- ¹The 'modern' fauna of Riversleigh refers to the whole of the station rather than a single habitat (i.e., from river margins, to clay soil flats, limestone and quartzite ranges) and is thus not strictly comparable with the fossil local faunas which come from single sites.
- ²Footnotes below relate to mammalian diversity within the Riversleigh fossil deposits as a whole.
- ³J. Muirhead, in prep., identifies in the Riversleigh Oligo-Miocene sediments (Systems A-C) approx. 5 species in at least three genera ranging from very generalised to highly specialised (some in press: Muirhead and Archer 1989).
- ⁴J. Muirhead, in prep., recognises several Riversleigh genera in addition to these. One of the Upper Site taxa may be a dasyuroid rather than a dasyurid. Van Dyck and Archer (in prep.) recognise another new dasyurid (Panorama Site, System B) that resembles species of *Antechinus* and *Murexia*.
- ⁵Muirhead (in prep.; noted in Bergdolt and Muirhead 1989) recognises another family of plesiomorphic perameloids (several LFs, Systems A-C).
- ⁶Gott (1989) and Gott *et al.* (in prep.) recognise a new genus and species (several LFs, System B).
- ⁷We recognise *Litokoala* n. sp. and another new taxon (several LFs, Systems B and C).
- ⁸We recognise an enigmatic higher level taxon of uncertain affinities (System B).
- ⁹We recognise new species of *Neohelos* (Systems A-C), *Kolopsis* (System C) and new zygomaturine and diprotodontine genera (Systems A-C).
- ¹⁰S. Creagh *et al.* (in prep.) recognise new species of *Ngapakaldia* (System A) and perhaps *Palorchestes* as well as other genera (several LFs, Systems A-C).
- ¹¹N. Pledge (in prep.) recognises at least 3 species of *Namilamadeta* (several LFs, Systems A and B).
- ¹²We recognise at least three new genera of vombatiform marsupials (several LFs, System B) but no undoubted vombatids.
- ¹³We recognise *Wakaleo* sp. cf. *W. oldfieldi* (Systems A-C) and a genus and new species of cf. *Priscileo* from Upper Site.

- ¹⁴We recognise new species of *Burramys* (several LFs, Nooraleeba LF and Systems B and C, several LFs) and *Cercartetus* (several LFs, System B).
- ¹⁵*Strigocuscus reidi* and *Trichosurus dicksoni* (from several LFs, Systems B and C; Flannery and Archer 1987a); in addition, we recognise a new species of *Wyulda* (in prep.) and additional new phalangerids.
- ¹⁶*Djilgaringa gillespieae* (from several LFs in System C; Archer *et al.* 1987); in addition, we recognise another unnamed taxon.
- ¹⁷We recognise new species of *Paljara*, *Pildra*, *Pseudochirops* and new genera and species representing a considerably wider range of pseudocheirids than exist today in any single fauna (many LFs, System B and C).
- ¹⁸We recognise at least one new species (several LFs, System B).
- ¹⁹We recognise new subfamilies, genera and species of enigmatic ?pseudocheirids (several LFs, Systems B and C).
- ²⁰We recognise a new genus and at least two new species of plesiomorphic petauroids (many LFs, Systems B and C).
- ²¹We recognise new relatively plesiomorphic acrobatids (many LFs, Systems B and C).
- ²²*Wabularoo naughtoni* (balungamayine from D-Site, System A; Archer 1979); *Gumardee pascuali* (balungamayine from D-Site, System A; Flannery, Archer and Plane 1983); *Ekaltadeta ima* (propleopine from many LFs, Systems B-C; Archer and Flannery 1985); *Hypsiprymnodon bartholomaii* (hypsiprymnodontine, many LFs, System C; Flannery and Archer 1987b); *Bettongia moyesi* (potoroine, Two Trees LF, System C; Flannery and Archer 1987c); Cooke *et al.* (in press) recognise many new genera and species of balungamayines and new species of hypsiprymnodontines and propleopines (several LFs, Systems A-C).
- ²³*Balbaroo riversleighensis* (balbarine from D-Site, System A; Flannery, Archer and Plane 1983); Cooke (1989) and Cooke *et al.* recognise other new genera and species of balbarine macropodids (many LFs, Systems A-C). In the Pliocene deposits (Rackham's Roost) there are species of *Protemnodon* and *Macropus*. In the Pleistocene deposits (e.g., Terrace Site) there are species of *Macropus*.
- ²⁴*Yalkaparidon coheni* and *Y. jonesi* (yalkaparidontian marsupials, Systems B and C; Archer, Hand and Godthelp 1988a).
- ²⁵*Yingabalanara richardsoni* (new family; Upper Site, System B; Archer, Every, Godthelp, Hand and Scally, 1989).
- ²⁶*Hipposideros (Brachhipposideros) nooraleebus* (Nooraleeba LF; Sigé, Hand and Archer 1982). Hand (1987), Hand, Archer and Godthelp (1989a,b) and Hand (in prep.) recognise many other hipposiderids (many LFs, Systems B-C and ?A).
- ²⁷*Macroderma godthelpi* (Dwornamor LF etc., System B; Hand 1985). Hand (1987 and in prep.) recognises at least three other megadermatids in various LFs of Systems B and C and two in the Pliocene Rackham's Roost LF (including one that resembles *M. gigas*, the living species).
- ²⁸*Petramops creaseri* (Gotham City LF, System C; Hand, 1989; at least two additional molossidids are present in System B lfs viz. VD Site and Panorama Site).
- ²⁹Godthelp (in prep.) recognises species of some modern genera as well as others representing previously unknown genera.

³⁰*Canis familiaris* dingo.

³¹From other Riversleigh local faunas, we have representatives of the: Ektopodontidae (*Ektopodon* sp.; e.g., Wayne's Wok, System B, Pledge *et al.* in press); Ornithorhynchidae (*Obdurodon* sp., e.g., Ringtail Site, System C; Archer *et al.*, in prep.); ?Miralinidae (e.g., Wayne's Wok, ?System B); ?Ilariidae (new genus and species; e.g., White Hunter, ?System B); a new family of vombatiform diprotodontians (e.g., Boid Site East, System B); another new diprotodontian family (e.g., Hiatus Site 1, ?D-Site Equivalents); a new phalangerid family near to but distinct from phalangeroids (e.g., Wayne's Wok, System B).

³²The Ditjimanka LF of central Australia (e.g., Woodburne *et al.* 1985) is probably slightly older than the Upper Site LF of Riversleigh (if only because of its relatively plesiomorphic ektopodontids and pilkipildrids), but it is not clearly a rainforest local fauna. While it is true that its mammals display no evidence of grazing adaptations, there are proportionately fewer arboreal mammals in this fauna than in any of the Oligo-Miocene Riversleigh LFs or the Pliocene Hamilton LF. Further, while it is true that there is only doubtful evidence for believing that terrestrial grasses were present (*contra* pers. comm. from W. Harris to Woodburne *et al.* 1985), perhaps the Ditjimanka LF represents an open forest environment with a moss, fern and/or shrub understorey. Pollen samples from the Etadunna Formation are being re-examined (H. Martin, pers. comm.).

GLOSSARY OF PALAEOLOGICAL AND GEOLOGICAL TERMS USED

Definitions in double quotes, unless otherwise credited, are those of Bates and Jackson (1984). In these definitions, spellings of the words 'paleontology', 'color' and (where appropriate) the 'ize' endings of words (American spelling) have been altered by us to 'palaeontology', 'colour' and 'ise'.

Assemblage: "... a group of fossils that occur at the same stratigraphic level...". As used here, we intend 'faunal assemblage' to mean 'a group of animals that occur in the same site'. In this sense, a faunal assemblage is the physical basis for what we ultimately interpret to be the 'local fauna'.

Biochronology: "... the relative dating of geologic events by biostratigraphic or palaeontologic methods or evidence; i.e. the study of the relationship between geological time and organic evolution".

Biocorrelation: Demonstration that the same taxon (usually a species or genus) occurs in spatially isolated deposits thus leading to the hypothesis that the isolated deposits are probably similar if not identical age.

Biostratigraphy: "Stratigraphy based on the palaeontologic aspects of rocks; the differentiation of rock units through study of the fossils they contain".

Biostratigraphic unit: "A body of strata that is differentiated from adjacent strata by its fossil content or palaeontological character".

Bioturbation: "The churning and stirring of a sediment by organisms." As used here we suggest that animals walking over previously accumulated bones might break these prior to final entombment by calcium carbonate.

Carbonate: "A mineral compound characterised by... CO₃²⁻. Calcite and aragonite, CaCO₃, are examples of carbonates". As used here it is generally intended as a synonym for limestone.

Chronological: "Having to do with recognising or discriminating intervals of Earth history" (Woodburne 1987).

Correlation: "Demonstration of the equivalence of two or more geological phenomena in different areas...". The correlation may be lithologic or chronologic. However, correlated sediments or local faunas, in the sense used here, imply the conclusion or hypothesis that the objects are approximately the same age.

Diagenetic: Processes that have effected a sediment, fossil or other geological object after it was initially deposited other than weathering or metamorphism.

Eustatic: "Of or pertaining to worldwide changes of sea level". Eustatic changes can bring about renewed deposition or erosion by changing the gradient over which freshwater flows. Raised sea levels commonly reduce erosion and lead to continentally peripheral lakes (e.g., such as we postulate for much of Riversleigh) and estuaries; lowered sea levels revitalise sluggish streams and increase erosion (such as occurs in the Riversleigh region now).

Facies: "The aspect, appearance, and characteristics of a rock unit, usually reflecting the conditions of its origin; esp. as differentiating it from adjacent or associated units." As used here it implies that contemporaneous but isolated local faunas may accumulate in different microenvironments (e.g., a forest floor and adjacent pool) and hence be different in composition.

Fauna: "... an assemblage of fossil vertebrates of specific taxonomic composition obtained from a number of geographically diverse sites" (Woodburne 1987). We do not yet know which Riversleigh assemblages may be composite parts of more widespread, regional faunas hence all that are identified at Riversleigh are called local faunas.

Fissure: An eroded space within a deposit of limestone; generally narrow if vertical or low if horizontal. Our interest in these natural artifacts is that they commonly fill up with new limestone that often contains bones of animals younger than the limestone that originally developed the fissures.

Fluviatile: "Belonging to a river; produced by river action...".

Flysch: "A... sedimentary facies characterised by a thick sequence of poorly fossiliferous, thinly bedded, graded marls and sandy and calcareous shales and muds..." usually interpreted to represent a rapidly moving mud slurry that rushes across a surface or into and through a body of water.

Formation: "A body of rock strata that consists dominantly of a certain lithologic type or combination of types... A lithologically distinct, mappable body of... rock". 'Beds' (e.g., Ploughed Mountain Beds) and 'Limestone' (e.g., Carl Creek Limestone) used in this paper effectively mean the same thing as 'Formation' (e.g., Etadunna Formation).

Intraformational: "Formed within a geological formation, more or less contemporaneously with the enclosing sediments". As used here, it refers to a feature evident in some of the Riversleigh limestones where apparent fracturing of semi-consolidated limy muds was followed by re-cementation of the fractured pieces by marginally younger carbonates.

Lacustrine: "Pertaining to, produced by, or inhabiting a lake or lakes...".

Lithology: "The description of rocks... on the basis of such characteristics as colour, mineralogic composition, and grain size... The physical character of a rock."

GEOLOGICAL TIME SCALE

(after Palaeontology Group, Bureau of Mineral Resources).

	Era	Period	Epoch	Age in years	
PHANEROZOIC	CAINOZOIC	Quaternary	Recent	0-10,000	
			Pleistocene	10,000-2,000,000	
		Tertiary	Pliocene	2-5,000,000	
			Miocene	5-24,600,000	
			Oligocene	24.6-38,000,000	
			Eocene & Paleocene	38-65,000,000	
	MESOZOIC	Cretaceous		65-144,000,000	
		Jurassic		144-213,000,000	
		Triassic		213-248,000,000	
	PALAEOZOIC	Permian		248-286,000,000	
		Carboniferous		286-360,000,000	
		Devonian		360-408,000,000	
		Silurian		408-438,000,000	
		Ordovician		438-505,000,000	
		Cambrian		505-590,000,000	
	PRECAMBRIAN	PROTEROZOIC	Adelaidean		590-1,400,000,000
			Carpentarian		1,400-1,800,000,000
			Lower Proterozoic		1,800-2,300,000,000
ARCHAEAN				2,300,000,000 +	

Limestone: "A sedimentary rock consisting chiefly of the mineral calcite (calcium carbonate, CaCO₃), with or without magnesium carbonate... the consolidated equivalent of limy mud...".

Lst: Abbreviation for limestone.

Local fauna: "... assemblages, containing as few as a single taxon, from a single site or geographically adjacent and temporarily equivalent sites" (Tedford 1967).

Oncolite: "A concentrically laminated, calcareous sedimentary structure, resembling an oöolith, formed by the accretion of successive layered masses of gelatinous sheaths of blue-green algae." Normally these would form in water exposed to sunlight.

Palaeoecology: "The study of the relationship between ancient organisms and their environment".

Petrology: "That branch of geology dealing with the origin, occurrence, structure, and history of rocks...".

Stratigraphy: "The science of rock strata. It is concerned with all characters and attributes of rocks as strata; and their interpretation in terms of mode of origin and geologic history".

Stratophenetics: An integrated approach to the study of the stratigraphic and phylogenetic relationships of evolving organisms. It is done by superimposing sequentially aged faunas and identifying probable ancestral and descendant lineages passing through the predetermined time planes.

Tectonics: "A branch of geology dealing with the broad architecture of the outer part of the earth, that is, the major structural or deformational features and their relations, origin, and historical evolution".

Thanatocoenosis: "A set of fossils brought together after death by sedimentary processes [e.g., stream flow etc.], rather than by virtue of having originally lived there collectively". In the sense used here, it describes the assemblage of normally disaggregated organic remains in a very restricted site (most of which we presume were small pools into which animals fell or into which their bones were washed).

Travertine: "A finely crystalline, massive deposit of calcium carbonate, of white, tan, or cream colour, formed by chemical precipitation from solution in surface and ground waters, as around the mouth of springs... It also occurs in limestone caves, where it forms stalactites and stalagmites".

APPENDIX: LIST OF THE PRINCIPAL RIVERSLEIGH LOCAL FAUNAS AND THEIR RELATIVE AGES

There are in excess of 97 sites and corresponding local faunal assemblages now known from the Riversleigh region. The first of these may have been that which Tedford (1967) described as the Riversleigh Local Fauna, a composite assemblage from his Sites A-E. In the years 1978-1979 and 1983-to the present, expeditions to Riversleigh have yielded many more local faunas the most important of which are listed here.

In what follows, a distinction may be made between the fossil site (e.g., **Microsite**) and its local fauna (e.g., Nooraleeba Local Fauna) as explained in the Introduction. If it is not, the local fauna name is that of the site name listed (e.g., **Bitesantennary Site** contains the Bitesantennary Local Fauna). Local fauna may be abbreviated as LF (LFs for plural).

Apart from the collections made at **Site D** which have been obtained from boulders on a steep scree slope below the **Site D** cliff, we have kept discrete faunal concentrations separate in order to maximise future ability to detect differences in age or palaeoecology. If and when it becomes apparent that some of these assemblages are identical, we shall combine them as regional faunas.

System A: ?late Oligocene to early Miocene

Sites include: **Site A**, **Site B**, **Site C** (type locality for *Bematherium angulum* Tedford, 1967), **Site D**, **Site E**. All of these and several unnamed taxa are described by Tedford (1967). Following that work, we tentatively accept these local assemblages to be approximately contemporaneous and to represent the Riversleigh Local Fauna.

Probable System A local fauna (which may or may not be contemporaneous with the Riversleigh Local Fauna): **Alsite**.

D-Site Equivalents: ?late Oligocene to early Miocene

Limestones tentatively placed in this series are so determined because of their resemblance to the sediments of **Site D** and/or their occurrence as superpositional sediments on the Cambrian Thornton Lst and/or as sediments underlying undoubted System B or C units. Insofar as it has so far been possible to determine, many also share taxa otherwise rare or unknown from System B or C units.

The Azores Site; Bone Atoll Site; Bone Reef Site; Don Camillo Site; Hiatus I Site; Hiatus II Site; Jeanette's Amphitheatre Site; Lockwood's Link Site; Neville's Pancake Site; Sticky Beak Site; White Hunter Site.

Cave deposits: ?Just younger than System A assemblages

These sites are interpreted to have formed as in-fillings of, or out-washings from caves developed in surrounding, older limestone.

Bitesantennary Site (Hand, Archer and Godthelp 1989a); **Microsite** (source of Nooraleeba Local Fauna and type locality for *Hipposideros* (*Brachipposideros*) *nooraleebus* Sigé, Hand and Archer, 1982).

System B: ?early Miocene

These sites appear to represent assemblages accumulated in pools or shallow lakes. **Neville's Garden Site** was undoubtedly formed near caves or limestone overhangs because of the presence of broken 'straws' (speleothems) and *in situ* travertine ridges on what appear to have been irregular surfaces. Because of this it is also possible that some of the vertebrates may have been washed into the deposit from the cave, having been pit-trapped by holes in its roof.

Low assemblages

Bole's Bonanza; D.D.D.D. Site; Female Site; Outasite; Outasite A, B, C, D etc.; RSO Site; Stop Site; Trash Site; Victor's Vacuum Site; Wayne's Wok Site; Wayne's Wok II Site.

Higher assemblages

Boid Site; Boid Site East; CS Site (=Camel Sputum Site; type locality for *Yalkaparidon coheni* Archer, Hand and Godthelp, 1988); **G Spot Site; Helicopter Site; Inabeyance Site; Mike's Menagerie Site; MP² Site; Panorama Site; Paul Willis Site; R.V. Site; Ten Bag Site; Upper Site** (type locality for *Yin-gabalanara richardsoni* Archer, Every, Godthelp, Hand and Scally, 1989); **View Delightful Site.**

Probable System B equivalents

Neville's Garden Site; Souvenir Site; Judy's Jumping Joint Site.

System C: ?middle Miocene to early late Miocene

The sites in this System are interpreted to represent one of three basic environments: deeper pools dominated by aquatic vertebrates (**a**); shallow pools or even emergent accreting surfaces dominated by terrestrial vertebrates; and sites adjacent to cave entrances dominated by what appear to be out-washings from beneath megadermatid roosts (**m**).

Lowest assemblages

Archie's Absence; Bernie's Bedford Site; Gag Site (source of Dwornamor LF and type locality for *Ekaltadeta ima* Archer and Flannery, 1985, *Trichosurus dicksoni* Flannery and Archer, 1987a, *Yalkaparidon jonesi* Archer, Hand and Godthelp, 1988, *Macroderma godthelpi* Hand, 1985, *Hypsiprymnodon bartholomaii* Flannery and Archer, 1987b); **Kangaroo Jaw Site; Last Minute Site** (type locality for *Djilgaringa gillespieae* Archer, Tedford and Rich, 1987, *Strigocuscus reidi* Flannery and Archer, 1987a); **Wang Site.**

Middle assemblages

Bat Smear Site; Bird Bone Site; Courtenay's Cache Site; Gotham City Site (m) (type locality of *Petramops creaseri* Hand, 1989); **Gotham East Site; Gotham North Site; Grime's Site; Group Site; Harry's Hump Site; Incisor Site; Mac's Mound Site; Main Site; Melody's Maze Site (a); Quentin's Quarry (a); Ringtail Site (a;** source of *Obdurodon* sp. skull); **Ringtail East Site; Ringtail East Site 2; Scum Site; Skull Site; Sue's Diprotodontid Site.**

Probable middle assemblage equivalents

Archie's Parlour Site; Jim's Jaw Site.

Highest assemblages

Bob's Boulders Site (a); Crusty Meat Pie Site (a); Fireside Favourites Site; Grimes' Site; Henk's Hollow Site;

Jaw Function Site (source of *Kolopsis*-like zygomaticurine); **Neville's Riches Site; No name Site** (contains large zygomaticurines); **Phalanger Site; Turtle Site; Two Trees Site** (type locality for *Bettongia moyesi* Flannery and Archer, 1987c).

Pliocene Sites

The only undoubted Pliocene site identified from the region is **Rackham's Roost Site (m)** which represents the indurated floor of a cave developed in Thornton Limestone.

Pleistocene Sites

There are many Quaternary deposits in the Riversleigh region. However, few have been more than cursorily examined and none has been precisely dated. Only **Terrace Site**, developed in perched fluvial sediments adjacent to the present Gregory River, has been excavated. The precise age of this site is unclear (see above under Correlation). Other fluvial deposits of probable Pleistocene age are known.

Cave deposits and fissures are also common in the area. Some contain bones but few have been examined. Their ages are likely to vary but have not yet been determined. An example is **Atomic Fissure Site** which is a vertical fissure fill in Thornton Limestone. It contains rodents and a species of *Petrogale*.

Some Quaternary sites are probably late Pleistocene on the grounds that they contain modern species but taxa that no longer survive in this region. Examples would be **Bottom Site** and **Outer Limits Site** developed as fissure fills in Thornton Limestone.

Recent Sites

There are also many sites that appear to represent Recent episodes of accumulation. Most have neither been excavated nor named. Some that have been cursorily examined contain modern taxa appropriate to the region today but lack the introduced House Mouse (*Mus musculus*), a marker which heralds the European invasion of Australia. Other sites have House Mice and are therefore presumably less than 400 years old.

Sites and LFs of (as yet) unclear relationship

ABR Site; Biggles Site (between the Gag Plateau dominated by System C lfs and Godthelp Hill dominated by System B lfs); **Bat Patch Site; Burnt Offering Site; Chinatown Site; Fig Tree Site; M6 Site; Murray B.'s Site; Neo Site; Rackham's Rock Pile Site; Roo Site; Sewer Site; Souvenir Heights Site; Sue's E Site; Sue's Selection Site; Syp's Siberia Site; Upper Burnt Offering Site.**



The spring-fed Gregory River connects the Riversleigh region to the Gulf of Carpentaria. Its banks nourish the last remnants of the lush forests that once dominated the region.