

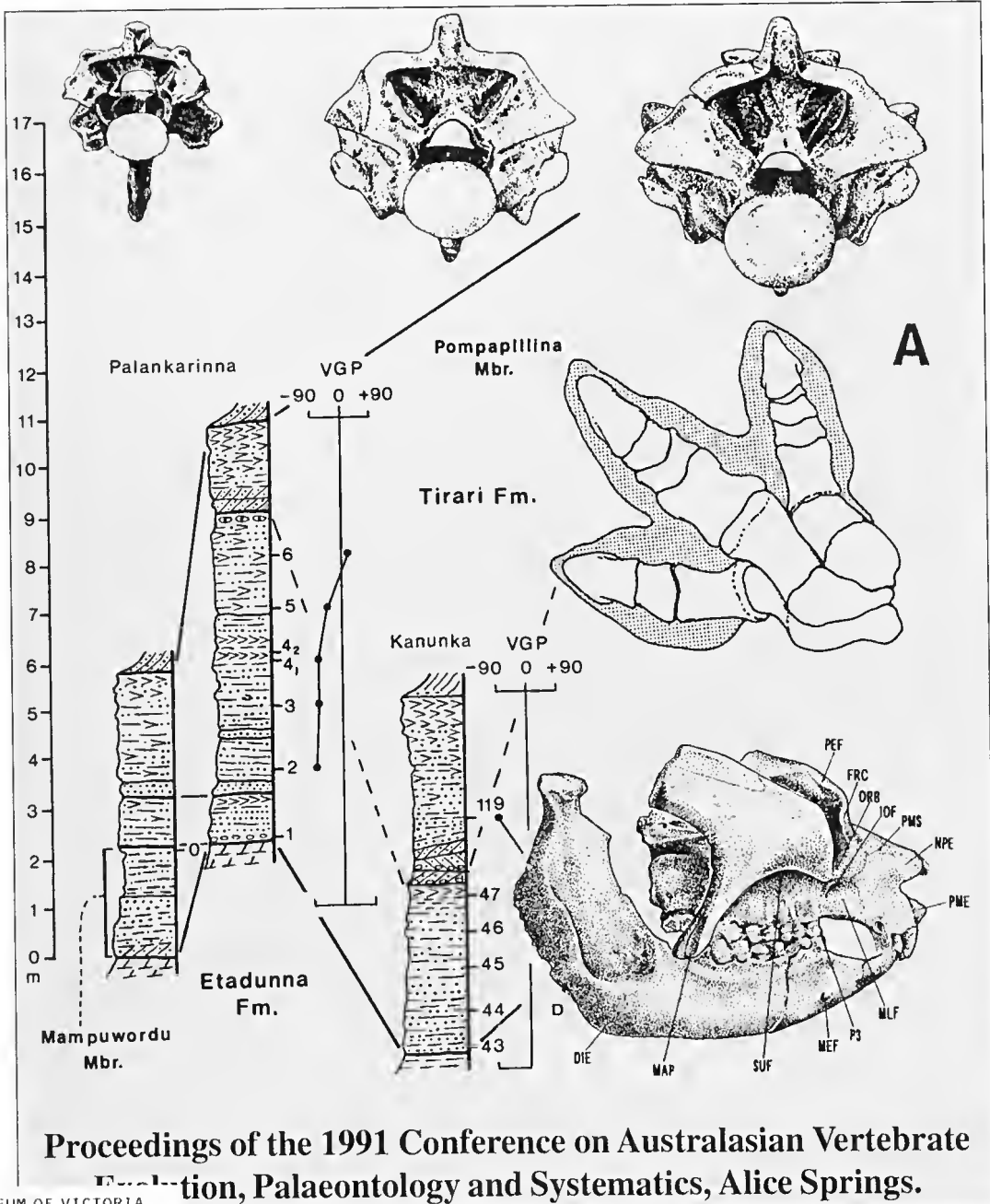
The BEAGLE

Records of the
Northern Territory Museum
of Arts and Sciences

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Proceedings of the 1991 Conference on Australasian Vertebrate
Evolution, Palaeontology and Systematics, Alice Springs.



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Cover: A composition of drawings: top, snake vertebrae by J.D. Scanlon; left, stratigraphic logs by Tedford *et al.*; right center, dinosaur footprint by T. Thulborn; bottom right, Zygomaturine cranium by P.F. Murray.

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PROCEEDINGS OF THE 1991 CONFERENCE ON
AUSTRALASIAN VERTEBRATE EVOLUTION, PALAEOLOGY AND SYSTEMATICS,
ALICE SPRINGS.

CONTENTS

INTRODUCTION	i
HILL, R.S. - Australian vegetation during the Tertiary: macrofossil evidence.....	1
LONG, J.A. - <i>Gogodipterus paddyensis</i> (Miles), gen. nov., a new chirodipterid lungfish from the late Devonian Gogo Formation, Western Australia.	11
LONG, J.A. - First dinosaur bones from Western Australia.	21
THULBORN, T. - The demise of the dancing dinosaurs?	29
GAFFNEY, E.S., ARCHER, M. AND WHITE, A. - <i>Warkalania</i> , a new meiolaniid turtle from the Tertiary Riversleigh Deposits of Queensland, Australia.	35
SCANLON, J.D. - A new large madtsoiid snake from the Miocene of the Northern Territory.	49
HUTCHINSON, M.N. - Origins of the Australian scincid lizards: a preliminary report on the skins of Riversleigh.	61
MURRAY, P.F. - Thinheads, thickheads and airheads - functional craniology of some diprotodontian marsupials.	71
MURRAY, P.F. - The smallest New Guinea zygomaturines - derived dwarfs or relict plesiomorphs?	89
PLEDGE, N.S. - The weird wonderful wombat <i>Warendja wakefieldi</i> Hope and Wilkinson.	111
PLEDGE, N.S. - The Curramulka Local Fauna: a late Tertiary fossil assemblage from Yorke Peninsula, South Australia.	115
TURNBULL, W.D., LUNDELIUS JR., E.L. AND TEDFORD, R.H. - A Pleistocene mar- supial fauna from Limeburner's Point, Victoria, Australia.	143
TEDFORD, R.H., WELLS, R.T. AND BARGHOORN, S.F. - Tirari Formation and contained faunas, Pliocene of the Lake Eyre Basin, South Australia.	173
MURRAY, P.F. AND MEGIRIAN, D. - Continuity and contrast in middle and late Mioene vertebrate communities from the Northern Territory.	195
MEGIRIAN, D. - Interpretation of the Mioene Carl Creek Limestone, northwestern Queensland.	219
JONES, R. - The type and figured collection (excluding plant fossils) in the palaeontology section of the Australian Museum, with special reference to vertebrates.	249
APPENDIX - Abstracts	255

INTRODUCTION

During the Easter break, March 28-30, 1991, more than 40 vertebrate palaeontologists from all states of Australia, from the U.K. and from the U.S.A. overcame the logistics of time and space to convene in Alice Springs, N.T., for the 3rd International Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics (C.A.V.E.P.S.).

The thirty-three papers ranged widely and included palaeobotanical and geological evidence for climatic reconstruction, description of palaeocommunities, locomotion of dinosaurs, anatomy and systematics of fossil marsupials, the earliest bat in the southern hemisphere, Australian lizards, newly discovered dinosaurs, endemic Tertiary crocodylians and turtles, and some of the world's earliest known fishes.

The keynote speech by Dr Robert Hill on the evolution of Australian and Antarctic Tertiary vegetation provided important new insights into the environmental background of vertebrate evolution in Cenozoic Australia. Dr Hill's research on the adaptive significance of leaf form emphasizes the complexity and diversity of vegetational formations throughout the Australian Tertiary. The view that the Australian continent was covered with uniform and widespread rainforest during the Cenozoic is being replaced by evidence of high diversity, adaptability and regionalism in floral communities.

Studies of fossil mammalian systematics and structure emphasized material from mid to late Tertiary localities in Queensland and the Northern Territory. Bernard Cooke described some new kangaroo species from the Miocene deposits at Riversleigh that represent a specialized radiation of early macropodids with serrated incisor margins. Steven Wroe concluded that the unique tooth replacement pattern in the potoroid *Ekaltadeta*, in which the second premolar is retained in mature animals, represents a buttressing mechanism for the large sectorial permanent or third premolar.

Ultrastructure examination of the enamel surfaces of teeth from the Tingamarra deposit, Queensland, by Coral Gilkeson, indicates clear marsupial affinity for some, but not all specimens. Susan Hand *et al.* reported on the discovery of the earliest bat, a microchiropteran, from the Eocene Tingamarra Local Fauna, approximately 55 million years old. The diversity of Oligo-Miocene vombatiform groups represented at Riversleigh was recorded by Michael Archer and Henk Godthelp. The high species diversity of ringtail possums at Riversleigh formed the basis of Michael Archer's hypothesis of greater floral diversity in mid Tertiary Australia than at present. Jeanette Muirhead also emphasized species diversity at Riversleigh in her report on fossil bandicoots. Tertiary bandicoots, though prolifically speciose, show a narrow morphological range until the early Pliocene.

Peter Murray and Phillip Walker described a small, pig-sized, New Guinea Pleistocene zygomatic, concluding that its closest affinity is with the Plio-Pleistocene genus *Zygomaturus*, and that the species may be an example of insular body size reduction. Peter Murray provided an explanation for the extensive sinus developments in the crania of large vombatiforms. Wynyardiid-like features were revealed in Neville Pledge's description of the nearly complete cranium of the plesiomorphic Pleistocene vombatid *Warendja*. The fossil mammals section was concluded by Alex Baynes' criteria-based analysis of the evidence for terminal dates of Late Pleistocene megafauna in Australia.

Tony Thulborn's analysis of dinosaur locomotion cast doubt on Bakker's locomotion-based hot-blooded dinosaur argument. Large boa-like madtsoiid snakes from the Oligo-Miocene were described by John Scanlon. John's analysis indicates that the Madtsoiidae is an ancient lineage of snakes, possibly representing the plesiomorphic sister group of all other boa-like snakes.

Mark Hutchinson raised the possibility that skinks are a Gondwanan reptile group as suggested by their diversity in the Oligo-Miocene at Riversleigh. Gaffney *et al.* presented evidence in support of the presence of horned tortoises (meiolaniids) in Australia at least since the Paleogene and probably in the Mesozoic. John Long reported on the first azhdarchid pterosaur record in Australia. Other recent

dinosaur finds from Western Australia include a possible theropod humerus and a sauropod caudal vertebra. John also described some new dinosaur trackways in the Early Cretaceous Broome Sandstone.

Four new species of Australian crocodiles described by Paul Willis lend support to his hypothesis of an endemic crocodylian radiation in the Australian Tertiary. Thomas Rich and Patricia Vickers-Rich reported on the late survival of labyrinthodont amphibians in Australia. They suggest that the appearance of ecomorphically similar eusuchian crocodylians in the early Cretaceous of Australia may have led to labyrinthodont extinctions through competition. Cold-adapted labyrinthodonts were able to exclude temperature-sensitive crocodylians until the climate became warm enough to recruit widely distributed eusuchian populations in Australia.

Alex Ritchie and Gavin Young provided an update on the prolific fossil fish fauna of the Ordovician-Devonian of central Australia. Additional structural and distributional information on 465 million year old agnathans - the earliest vertebrates in the southern hemisphere - emphasized the national and international importance of research in the region. Some new chirodipterid lungfishes from the Gogo Formation were described in detail by John Long. The monophyly of chirodipterids has only recently been established, and John's excellent reconstructions of the Gogo material are integral to the systematic elucidation of the group.

Two fossil vertebrae representing large (conservatively estimated to have been at least five metres long) lamnoid sharks, from Lower Cretaceous sediments near Darwin, NT, were described by Susan Turner and Andrew Rosenfelds. Along with ichthyosaurs and plesiosaurs, these giant lamnoid sharks were among the top Albian marine predators, and may have rivalled or even out-sized the giant Great White Sharks of the Tertiary-Recent.

Andrew Constantine and Dirk Megirian provided geology-based interpretations of Australian vertebrate faunas. Andrew's study of the taphonomy of dinosaur fossils in the Otway Group examined the factors involved in predicting the location of fossil-bearing sediments in complex fluvial horizons. Dirk's paper on the Carl Creek Limestone focussed on the processes of carbonate deposition at Riversleigh, providing new evidence for climatic reconstruction and taphonomic interpretations.

Eocene to Pleistocene-aged Australian local faunas from Tingamarra, Qld; Alcoota, NT; Camfield, NT; Eyre Basin, SA; Curramulka, SA and Limeburner's Point, Vic, were described in individual papers by Godthelp *et al.*, Tedford *et al.*, Murray and Megirian, Pledge, and Turnbull *et al.* The Eocene Tingamarra fauna's greatest similarity is with the Australian biota, indicating a high endemicity of the Australian fauna early in the Tertiary.

Both the Bullock Creek Local Fauna and the Alcoota Local Fauna show evidence of encroaching aridity in the mid to late Miocene of central Australia. Magnetostratigraphic studies of the Tirari Formation have helped to refine the ages of its faunas. The Curramulka fauna, from joint-controlled caves in the Yorke Peninsula, is considered to be early Pliocene on biochronological evidence. A mid Pleistocene date for the local fauna at Limeburner's point is supported by magnetic polarity stratigraphic analysis.

Overall, the symposium represents a varied and balanced contribution to Australasian palaeontology. Several presentations provide tantalizing prognostications of discoveries yet to come: among these, the Eocene Tingamarra assemblage, the recently recognized giant sharks from the Cretaceous of the Northern Territory, the high prospects for finding the best preserved, if not the earliest remains of the world's oldest vertebrates in central Australia and the new dinosaur discoveries in Western Australia.

The convergence of evidence from palaeobotany, sedimentary geology, plate tectonics, biogeography, systematics and morphology was implicit in many of the presentations. The ingenious labyrinthodont extinction hypothesis, the systematics of Australian Tertiary crocodiles, the diversity of Oligo-Miocene skinks, the early radiation of meiolaniid turtles and the uniqueness of the Paleogene Tingamarra LF all raise new questions about the position and nature of connections of the Australian plate between the late Mesozoic and the early to mid Tertiary.

Several contributions indicate that significant progress has been made in the field of Tertiary biostratigraphy. Stratigraphic refinements, particularly through the use of palaeomagnetic correlation, have greatly improved the resolution of late Tertiary biostratigraphy in Australia. As it eventuated, there was little discussion of "stage of evolution" biochronology, and we missed a contribution to the palaeontology of birds. A symposium on monotremes was held within days of the C.A.V.E.P.S. meeting, consequently a contribution on monotreme palaeontology was understandably wanting.

I take this opportunity to congratulate all the contributors to the symposium, and those who participated in the sometimes vigorous discussions, for making the conference an intellectually satisfying, scientifically enlightening and socially enjoyable experience. I also thank Dirk Megirian, Karl and Bobbi Roth, all the Spencer and Gillen Museum attendants, Jens Pederson, my Flinders University Honours students, Leanne Dansie and Susan Jennings, for their help in organizing and supporting the conference. I am especially indebted to Leanne, who postponed her studies to devote full time to the organization of the conference activities. It could not have been done without her. Preparations for the 4th International C.A.V.E.P.S. has passed over to Drs Rod Wells and Neville Pledge. I wish them every success in the endeavour and look forward very much to seeing you all again next time, in Adelaide.

Peter Murray
Convener, 3rd International C.A.V.E.P.S.

AUSTRALIAN VEGETATION DURING THE TERTIARY: MACROFOSSIL EVIDENCE.

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ABSTRACT

The Australian Tertiary plant macrofossil record, although very incomplete, offers a unique insight into past vegetation composition and dynamics, and the effect of changing climate both on vegetation composition and plant evolution. During the Early Tertiary, southeastern Australia supported complex rainforests with a very high diversity of woody plant species. The prevailing climate included a moderate mean annual temperature and, more importantly, very little temperature variability away from the mean. As well as this, rainfall was high throughout the year, and humidity was also very high. There is no extant analogue either for this climate or for the vegetation it supported. As the climate cooled and temperature extremes developed, and rainfall declined and became more seasonal, rainforests in southeastern Australia declined in species numbers. Many taxa became extinct or migrated (or were restricted in range) northwards into the mid-high elevation equatorial rainforests where they, or their descendants, still occur. Some rainforest taxa evolved in response to the changing climate in southeastern Australia, although many of these were ultimately unsuccessful and became extinct in the region. As the climate further deteriorated, non-rainforest vegetation expanded in the drier and colder areas, although many of the taxa present in these expanding ecosystems may have had their origin in nutrient-poor rainforests.

KEYWORDS: Plant macrofossils, Tertiary, Australia, plant-climate interaction, vegetation reconstruction.

INTRODUCTION

The extant Australian vegetation is a complex mixture of types, which interact over large and small scales both spatially and temporally. It is generally considered that much of this complexity has a recent origin, resulting from the extremes of the rapid glacial cycles and the catastrophic effects of the arrival of Aboriginal and then European man. The magnitude of these causative factors has probably been overestimated, partly because the prevailing view has been that Tertiary vegetation in Australia was largely uniform, and varied only on very broad latitudinal and altitudinal scales. This view is still held by some palaeobotanists, but the emerging and more realistic view is that Australian vegetation has been enormously dynamic over a very long period of time, and, rather than seeing it at its most complex today, much of the landscape has suffered a substantial reduction in floristic diversity since the Early Tertiary.

Unfortunately, macrofossil evidence is still scarce, but it is accumulating rapidly, and from much farther afield than the traditional southeastern Australian coastal belt, which until recently provided almost all the data from which reconstructions of vegetation over the entire continent were based. The palynological data base is also expanding quickly, especially into central Australia. Palynological evidence provides us with the broad picture, since pollen is widely dispersed (Kemp 1978; Martin 1982; Kershaw 1988). However, this has its drawbacks when attempting to reconstruct local communities, and this is exacerbated by the current lack of taxonomic resolution in many pollen forms. The macrofossil record is much less extensive than the palynological record, but it represents local vegetation and communities and taxonomic resolution is often much greater. This allows far more detailed reconstructions of local plant communities. In this review of the available evidence the macrofossil record will be favoured for both of

these reasons, and to complement the reviews of palynological evidence already presented by several authors (e.g. Kemp 1978; Martin 1982; Kershaw 1988).

DIFFERENTIATION OF THE VEGETATION DURING THE TERTIARY

Few macrofossils of angiospermous affinity have been published from the Australian Cretaceous, and with the exception of that of Taylor and Hickey (1990) there is a lack of detailed work on these fossils. Therefore we have little real idea of the form of the vegetation prior to the Tertiary. However, it is clear that by the Early Tertiary the vegetation had differentiated, at least on a regional scale, and probably on a much finer scale as well. The oldest Tertiary macroflora known to date is in Late Paleocene sediments at Lake Bungarby in southern N.S.W. This site occurs in the eastern highlands and was deposited at an altitude of 400-800m (Taylor *et al.* 1990). The macroflora largely awaits description, but it is diverse, very large-leaved, and contains an interesting mixture of taxa. Among the angiosperms which have been identified are elements which are regarded as microthermal rainforest taxa (e.g. *Eucryphia* (Hill 1991b), *Nothofagus*, and microthermal sclerophyllous taxa (*Banksiaeaphyllum*). There are other angiosperms which have been identified (e.g. Lauraceae), which are typical of all except the coolest rainforests, and which have such wide extant ecological tolerances that it is difficult to speculate on their palaeoecological significance. The relatively large leaf size in this deposit suggests a high mean annual temperature, but the age of this site and its high palaeolatitude means that other factors, and in particular photoperiod, may have been playing an important role in determining leaf size. This flora also contains a high diversity of small-leaved conifers, which appear to have had a significant role in cooler forests in this region during the Early Tertiary.

The plant macrofossil record of the Early Eocene is not well known, with only a few poorly described sites in southeastern Australia yielding data to date. This includes sites in Tasmania which are notable for their high conifer diversity (Townrow 1965a, 1965b; Bigwood and Hill 1985; Hill and Bigwood 1987; Hill and Carpenter 1991) and the predominance of small to medium sized angiosperm leaves, at least some of which have microthermal living relatives (e.g.

Eucryphia (Hill 1991b)). The Early Eocene Deane's Marsh locality in Victoria is of particular interest. The only macrofossil described from this site is a *Banksiaeaphyllum* species (Hill and Christophel 1988), but Christophel and Greenwood (1989) consider that the leaf size of the fossils most closely allies the vegetation with microphyll mossy forest, thus making this site particularly cool for the time. Unfortunately, they did not publish any of the data associated with this conclusion, so the details are uncertain.

Middle Eocene macrofloras on the coastal margin of southeastern Australia are notable for their extraordinary complexity (Christophel and Blackburn 1978; Christophel *et al.* 1987; Christophel and Greenwood 1987), but it is interesting that conifers are relatively scarce, and their diversity is low in comparison to both earlier and later macrofloras (Table 1). No microthermal elements have been described from these floras, although taxonomically they are very poorly understood. The Early-Middle Eocene boundary Nerriga macroflora occurs further inland and at a higher elevation and has a lower diversity, with clear dominants present (Hill 1982, 1986, 1989). However, there is no evidence for microthermal taxa in this deposit either.

Middle-Late Eocene macrofloras from Vegetable Creek (northern NSW) and Tasmania once again have a microthermal angiosperm element (e.g. *Nothofagus* (Hill 1988), *Eucryphia* (Hill 1991b)) and a prominent and diverse conifer element (Ettingshausen 1888; Hill and Carpenter 1991). Because of their geographical separation it is not yet clear whether the coastal Middle Eocene floras (Anglesea, Maslin Bay, Golden Grove) represent a genuine shift in vegetation at that time away from microthermal taxa, or whether they reflect a coastal vegetation type which persisted for a much longer time both before and after the Middle Eocene.

Oligocene rainforests are only known from Tasmania, where several deposits demonstrate a shift towards even more microthermal vegetation, with a reduction in the number of taxa which have their extant relatives at low latitudes. There can be little doubt that this floristic shift is a direct response to climatic change, most probably a slight decrease in mean annual temperature coupled with the development of a more seasonal climate, with the consequent onset of frost as an important environmental determinant. However, even during the Tasmanian Oligocene there is a mixture of species in single

vegetation types which now occur over a very wide latitudinal range (about 40°). This is interpreted as being due to the presence of a climate which was more equable than any now occurring in the region (Hill 1990b). Mainland Oligocene vegetation is represented by the Latrobe Valley coal (Duigan 1966; Blackburn 1985) and possibly a site at Westdale in Western Australia (Hill and Merrifield in press). Both sites have a distinctive sclerophyllous element, which may be representative of a general shift towards a more xeric climate on mainland Australia. Although the data are too sparse to emphatically support this as a general conclusion, it is clear from palynological evidence that such environments were expanding at this time.

Miocene macrofloras are rare in Australia and are, in general, poorly studied. The Latrobe Valley coal is an exception, and again provides strong evidence of at least localised sclerophyllous (nutrient-poor) and occasional xeric conditions (Blackburn 1985). Other macrofloras are suggestive of microthermal *Nothofagus*-dominated rainforest in southeastern and eastern Australia (Baechus Marsh (Christophel 1985), Vegetable Creek (Eutinghausen 1888; Hill unpublished data), and in Tasmania there is evidence for the presence of complex subalpine woodland at high altitude by the onset of the Miocene (Hill and Gibson 1986; Macphail *et al.* 1991).

Pliocene macrofloras are unknown in Australia, but an Early Pleistocene macroflora on the west coast of Tasmania is providing abundant evidence for the importance of the Quaternary glacial cycles as agents of ecological sifting (Hill and Macphail 1985, in press; Jordan and Hill 1991). Many taxa have been recovered from

these sediments which are now extinct in Tasmania and which have their nearest living relatives on mainland Australia, sometimes far removed from Tasmania (G.J. Jordan pers. comm.). This suggests that at least some of the complexity present in Eocene-Oligocene rainforests in the region was still present in the Pleistocene and was progressively reduced with succeeding glacial cycles.

Thus the general picture which emerges of Tertiary rainforest in southeastern Australia is of a very complex mosaic in the Early Tertiary, containing microthermal and mesothermal lineages. This rainforest has no modern analogue and is presumed to have developed under an extremely equable climate which similarly has no modern analogue. The mean annual temperature was probably higher than at present, but not excessively so. The important feature of temperature was more likely to have been a lack of extremes and certainly frost is unlikely to have been an important environmental factor. Part of the reason for the lack of temperature extremes was probably the high year round rainfall and humidity. Nix (1982) provides a very good summary of the important factors of Tertiary climates from the perspective of plant growth, and predicts climatic zones for the Tertiary right across Australia. Later in the Tertiary, when temperature declined and became more variable, and rainfall declined and became more seasonal, the Early Tertiary rainforest elements separated. Some appear to have "followed" the most suitable climate, and now occur at moderate to high altitudes in New Guinea. Others remained in the region and in many cases evolved substantially in response to the changing climate. Some examples of these taxa are consid-

Table 1. Species numbers in selected genera and families (in brackets) which are prominent in Tasmanian fossil deposits. The Tasmanian sites are Regatta Point (Early Eocene), Cethana (Early Oligocene), Pioneer and Little Rapid River (Oligocene) and Monpeelyata (Late Oligocene-earliest Miocene). Three Eocene sites from southeastern mainland Australia (Maslin Bay, Anglesea and Nerriga) are shown for comparison. Data from Blackburn (1981), Carpenter (1991), Christophel *et al.* (1987), Greenwood (1987), Hill (1990b, 1991), Hill and Bigwood (1987), Hill and Carpenter (1991), Hill and Christophel (1988), Wells and Hill (1989).

Site (estimated total species diversity in brackets)	<i>Banksiaephyllum</i> / <i>Banksiaeformis</i> (Proteaceae)	<i>Nothofagus</i> (Fagaceae)	<i>Araucaria</i> (Araucariaceae)	<i>Dacrycarpus</i> (Podocarpaceae)
Regatta Point (> 40)	1 (2)	0	≥ 4 (6)	2 (6)
Cethana (> 100)	7 (≥18)	≥ 5 (5)	≥ 2 (5)	1 (≥ 12)
Pioneer (> 25)	1 (2)	1 (1)	0 (1)	2 (6)
Little Rapid River (> 40)	0 (2)	≥ 4 (4)	1 (2)	5 (13)
Monpeelyata (> 20)	0 (1)	2 (2)	3 (3)	3 (5)
Maslin Bay (> 200)	2 (3)	0	0 (1)	0 (1)
Anglesea (> 80)	1 (5)	0	0	1? (6)
Nerriga (> 25)	0 (1)	0	0	0 (1)

ered in the next section. Some taxa migrated northwards, but also remained in the region, evolving substantially in response to climate change. However, in most of these cases, they appear to have been ultimately unsuccessful, probably disappearing from southeastern Australia during the Late Tertiary or during the Quaternary glaciations.

One of the particularly interesting features of Tertiary vegetation in southeastern Australia is that not only is the species diversity usually very high, but the diversity within particular genera is also often high. Examples of this include the angiosperm genera *Nothofagus* and *Banksiaephyllum* (*Banksia/Dryandra*) and the conifer genera *Dacrycarpus* and *Araucaria* (Table 1). This is particularly interesting, since it is rare to see such a diversity within single genera in a single catchment area today, even when the regional diversity of a genus is high (e.g. *Banksia* in southwestern Australia or *Araucaria* in New Caledonia). The reason(s) behind this high diversity of species within single genera are uncertain, but there is no doubt that it was highly significant for animal species which depended upon them as food sources or for other aspects of their ecological niche.

PLANT EVOLUTION IN RESPONSE TO CLIMATE CHANGE

Many of the changes in diversity described above are simply a result of changes in species' distributions in response to climate change. However, there is abundant evidence for plant evolution during the same time period, and most of it can be closely related to climatic change. Within rainforest vegetation in Tasmania there is clear evidence for evolution of leaf form in response to changes in both temperature and rainfall. Leaves are the most common plant macrofossils, and as the physiological work-houses of the plant they are also the most sensitive to climate change. In the past this has often led to the conclusion that leaves are unreliable taxonomic units, since they are so morphologically responsive to local microclimate, but it is now becoming clear that this responsiveness is a very useful tool for the analysis of past climates.

The most obvious change in leaf morphology in southeastern Australia during the course of the Tertiary is a reduction in leaf size. Paleocene-Eocene rainforests generally had large leaf sizes (Fig. 1), and although this may be partly a result

of the unusual photoperiod at very high latitudes, there is no doubt that the over-riding factor controlling this was temperature. It has been known for a long time that large leaf size is correlated with a high mean annual temperature and that leaf size generally declines with increasing latitude as long as rainfall is not limiting. It is also clear that the living relatives of many of the Eocene species now occur in meso-megathermal forests at low latitudes, which is in accord with this conclusion. In many cases the transition from large- to small-leaved plants during the Tertiary in southeastern Australia is the result of species replacement, but in some cases there are clear phylogenetic lines involved.

The best documented example is within the *Nothofagus moorei*-*N. cunninghamii* complex. *Nothofagus moorei* is a large-leaved, evergreen species which occurs today in small pockets of high altitude rainforest in northern New South Wales and southern Queensland, while *N.*

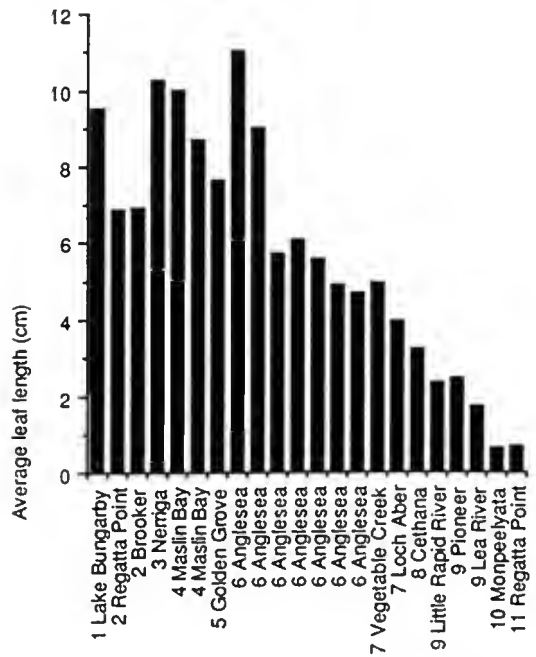


Fig. 1. Histogram showing average length of angiosperm leaves from Tertiary sediments in southeastern Australia. Note the general trend towards decreased leaf size in more recent sediments. The ages of the sites shown are: 1 = Late Paleocene; 2 = Early Eocene; 3 = Early-Middle Eocene boundary; 4 = early Middle Eocene; 5 = Middle Eocene; 6 = late Middle Eocene; 7 = Late Eocene; 8 = Early Oligocene; 9 = Oligocene; 10 = Late Oligocene-earliest Mioocene; 11 = Early-Middle Pleistocene. Data derived from Christophel and Blackburn (1978), Christophel (1981), Christophel and Greenwood (1987, 1988, 1989), D.R. Greenwood (pers. comm.) and Hill, Carpenter and Jordan (unpublished data).

cunninghamii is a small-leaved evergreen rainforest dominant in Tasmania and parts of Victoria (Table 2). Paleocene and Eocene leaves from southeastern Australia which are related to these extant species all closely resemble *N. moorei* in leaf size and morphology (Hill 1988, 1991a). However, during the course of the Tertiary in Tasmania this lineage decreased in leaf size and changed in morphology until by the close of the Tertiary it is recognisable as *N. cunninghamii* (Hill 1983, 1991a). During this time period in New South Wales, more limited evidence suggests that the fossils more or less retained their original form, resulting in the extant *N. moorei*. Thus the Tasmanian lineage has evolved considerably in leaf size and morphology, presumably in response to the decrease in mean annual temperature which took place in Tasmania during the Tertiary. Although the fossil evidence for other taxa is limited, there is compelling evidence from the leaf size of closely related species in temperate rainforests of New South Wales and Tasmania to suggest that this leaf size reduction was a general phenomenon (Table 2).

There is also evidence to suggest that evolution in leaf form took place in response to changing rainfall patterns. This evidence is best documented in the conifer family Podocarpaceae, but is supported by evidence from angiosperm leaves as well. The podocarp genus *Acmopyle* is very restricted today, with one species in New

Caledonia and the other known from only six collections in Fiji. However, it is known as a macrofossil from several Early Tertiary sites in southeastern Australia and demonstrates an elegant pattern of evolution in response to declining water availability.

The oldest *Acmopyle* macrofossils (Late Paleocene) are fully amphistomatic, i.e. they have stomates equally distributed over both leaf surfaces. This suggests that water was plentiful throughout the year for this species and that water loss was never a serious problem (Hill and Carpenter 1991). Therefore the plant has maximised its stomatal distribution in an attempt to maximise photosynthesis and growth. By the Early Eocene *Acmopyle* had begun to lose stomates on one leaf surface, suggesting that control of water loss was developing as a serious problem, and the species had adapted morphologically by reducing its stomatal distribution, presumably with the consequence that net photosynthesis was also reduced (Hill and Carpenter 1991). That is, the plant was adapting to a harsher environment, but at a cost in terms of potential growth. This trend continued throughout the Eocene, and by the Late Eocene one species of *Acmopyle* had evolved to the point where stomates were reduced to one leaf surface. The last record of *Acmopyle* in southeastern Australia is from the Early Oligocene, and it can be assumed that at about this time the climate changed to such a degree that *Acmopyle* was no longer able to evolve a competitive response to it and thus became extinct in the region. It is interesting that the two living species of *Acmopyle* both have a stomatal distribution similar to that of the Early Eocene species in Tasmania: there are stomates on both leaf surfaces, but they are relatively restricted on one of them. This suggests that the prevailing climate over the range of living *Acmopyle* is suboptimal, but that it is not as severe as the genus can withstand.

The podocarp genus *Dacrycarpus* illustrates an interesting combination of response to both temperature and rainfall changes. *Dacrycarpus* has two foliage types. In one type the leaves are bilaterally flattened, so that each functional leaf surface is composed of both adaxial and abaxial leaf surfaces. Furthermore, the whole short shoot (a single season's growth) is flattened into two dimensions, so that the short shoot probably functions like a single broad angiosperm leaf. As well as this, *Dacrycarpus* produces small, scale-like bifacially flattened leaves, which are arranged spirally around the axis in an imbricate

Table 2. Mean leaf area (mm²) of species in common genera from temperate rainforest in Tasmania or northern New South Wales (standard deviation in brackets). *Nothofagus cunninghamii* is separated into Victorian and Tasmanian populations. In each case, the species from lower latitudes has a significantly higher leaf area. Glasshouse experiments demonstrated that a large part of this difference in leaf area is genetically fixed. Adapted from Hill and Read (1987).

Species	(location)	Leaf area	(standard deviation)
<i>Acradenia euodiformis</i>	(N.S.W.)	9817	(3424)
<i>A. frankliniae</i>	(Tas.)	756	(338)
<i>Anopterus macleayanus</i>	(N.S.W.)	13846	(3326)
<i>A. glandulosus</i>	(Tas.)	3420	(1664)
<i>Eucryphia moorei</i>	(N.S.W.)	2278	(1024)
<i>E. lucida</i>	(Tas.)	405	(140)
<i>E. milliganii</i>	(Tas.)	75	(33)
<i>Nothofagus moorei</i>	(N.S.W.)	1649	(692)
<i>N. cunninghamii</i>	(Vic.)	130	(59)
<i>N. cunninghamii</i>	(Tas.)	83	(36)
<i>Trochocarpa laurina</i>	(N.S.W.)	566	(310)
<i>T. disticha</i>	(Tas.)	62	(20)
<i>T. gunnii</i>	(Tas.)	31	(10)
<i>T. cunninghamii</i>	(Tas.)	24	(12)

arrangement. In most living species these two foliage forms appear at random on the plant, although the bilaterally flattened foliage is often considered to represent juvenile foliage.

Dacrycarpus macrofossils are particularly abundant in Early Tertiary sediments in Tasmania (Wells and Hill 1989; Hill and Carpenter 1991), and demonstrate a clear trend in foliage evolution. In Early Eocene sediments, both foliage types are very common, and stomates occur all over both leaf surfaces. However, in progressively more recent sediments there is a trend in two aspects of leaf morphology. Firstly, the bilaterally flattened foliage becomes less common, and by the end of the Oligocene is no longer present as a macrofossil. Secondly, in the bifacially flattened foliage stomates become progressively more restricted to the inner (adaxial) leaf surface, and by the end of the Oligocene are only found in that position. No *Dacrycarpus* macrofossils have been found in Tasmania after the earliest Miocene, but pollen is recorded up until the Early-Middle Pleistocene (Hill and Macphail 1985, in press), suggesting that *Dacrycarpus* may have been a victim of the Quaternary glacial cycles. Thus in this genus we see the reduction in leaf area noted earlier for *Nothofagus*, and presumably a response to declining mean annual temperature, as well as a restriction in the distribution of stomates, which is interpreted as a response to the onset of seasonal rainfall and possibly a decrease in total annual rainfall as well. The other interesting feature of *Dacrycarpus* is that these trends are seen in more than one phylogenetic line, suggesting that these were general convergent trends in foliage in response to common external factors (Hill and Carpenter 1991).

There is also some evidence for evolution or possibly species replacement in response to far more pronounced changes in water availability during the Tertiary. In Early Tertiary rainforest floras there is often an element present which, in terms of its taxonomic affinity and its leaf structure, is best considered as sclerophyllous. This group is most prominently represented by the Casuarinaceae and Proteaceae (particularly the genus *Banksiaeaphyllum*). Sclerophylly is presumed to be a primary response to low soil nutrient levels (e.g. Loveless 1961), although it is also frequently observed as a xeromorphic response. In the Early Tertiary representatives it is probable that low nutrient levels were the only factors acting, since it has already been noted

that water was plentiful in these sites, and in all fossil leaves examined there are no morphological adaptations to protect the stomates. Such adaptations would be expected if lack of water was an important factor. However, there is no doubt that some of the sclerophyllous characteristics of these plants (thick cuticles, small leaves, large proportion of water conducting tissue etc.) preadapted these plants to decreased water availability when lower and more seasonal rainfall developed later in the Tertiary (Hill 1990a). Therefore these plants would have been able to exploit marginal rainforest habitats and probably quickly evolved more xeromorphic adaptations to exploit the developing arid regions. Thus in the later Tertiary we see similar leaves to those sclerophylls which were present in the Early Tertiary, but they have developed more obvious stomatal protection mechanisms.

While the Tertiary evolution of xeromorphic characters seems to be a viable hypothesis, it is equally if not more likely that what we see in the fossil record is not evolution in response to developing aridity, but radiation of a previously restricted flora. It is probable that during the Early Tertiary there were dry microsites (e.g. sand dunes, ridgetops) which would have been populated by a highly xeromorphic flora, possibly closely related to the less xeromorphic sclerophylls which were present in and around rainforest. These xeromorphs were in sites where fossilisation was highly unlikely, and coupled with their restricted distribution this means that they have not left a detectable macrofossil record to date. As the climate dried these xeromorphic plants radiated rapidly, and supplanted rainforest in many areas, in the process appearing for the first time in the macrofossil record. Thus these plants did not evolve xeromorphic adaptations during the onset of widespread aridity during the Late Tertiary, but simply expanded their range. It is probable that macrofloras away from the coastal southeastern Australian region hold the best hope of determining between these two hypotheses.

The role of xeromorphic preadaptation may also have been important in the early development of the Australian alpine flora. The best macrofossil example of this is at Monpeelyata, at about 900m ASL in central Tasmania. The Late Oligocene-earliest Miocene lake sediments contain abundant plant macrofossils (Hill and Gibson 1986; Hill 1990a; Macphail *et al.* 1991), many of which are extremely small sclerophyllous leaves,

reminiscent of the present Tasmanian alpine flora. The presence of a small log at Monpeelyata demonstrates that it was below the tree-line, but there is no doubt that many of the plants present would have been well suited to treeless vegetation at high altitude when the appropriate conditions developed. It is probable that the species involved had a similar origin to the xeromorphic sclerophylls described earlier, since many of the sclerophyllous responses would preadapt a plant to cold as well as dry conditions.

One interesting feature of the macrofossil record of scleromorphic plants in Australia is the apparent scarcity of *Eucalyptus*. Although a Tertiary macrofossil record for this genus is now well established (Lange 1978; Holmes *et al.* 1983), it appears to have been a relatively minor component of most Tertiary ecosystems, especially in comparison with its abundance under a wide diversity of conditions today. There is compelling evidence to suggest that increasing fire frequency within the relatively recent past (<200,000 years) has been a major factor in the rise to dominance of *Eucalyptus* (Singh *et al.* 1981), and there is certainly evidence to suggest that an absence of fire sees the removal of *Eucalyptus* from at least some ecosystems (Withers 1978). The source of this increased fire frequency is uncertain, but the options appear to be climatic change or the introduction of fire by Aborigines as part of their food gathering regime. However, it would be unwise to discount the significance of rapidly changing climates during the glacial cycles as an agent for the rapid increase in *Eucalyptus* biomass in Australia, and possibly also a rapid increase in species numbers as new habitats were exploited. Whatever the explanation, it is clear that the current dominance of the Australian landscape by eucalypt communities is a recent event, which masks much of the underlying long term evolution which formed the basis of the Australian vegetation.

CONCLUSION

Although the Tertiary plant macrofossil record is incomplete, there is strong evidence for several general conclusions. During the Early Tertiary, southeastern Australia supported complex rainforests with a very high diversity of woody plant species present. These forests undoubtedly occurred under very equable conditions, with a

moderate mean annual temperature and, more importantly, very little temperature variability away from the mean. As well as this, rainfall was high throughout the year, and humidity was also very high. There is no extant analogue of this climate and hence no living vegetation which can be regarded as particularly similar to these forests, at least floristically and probably also structurally. There was altitudinal and latitudinal zonation of vegetation, and probably a reasonable degree of regionalisation of vegetation under similar climatic zones. High latitude and/or high altitude sites had a microthermal element prominent, with *Nothofagus* usually present, and often dominating the macroflora. This feature extended to moderate latitudes in Tasmania following the cooling event during the Late Eocene. Another interesting feature of these cooler climate floras is the high generic and specific diversity and number of specimens of conifers, both in comparison with lowland coastal Middle Eocene sites and also most rainforests in Australia today. At their peak in Oligocene sites in Tasmania and high latitude Eocene sites, conifers had a diversity which is unmatched in any vegetation type worldwide today, and probably was rarely, if ever surpassed in any vegetation in the past. A further point of interest is that the high species diversity in these floras often included large numbers of species from single genera, a phenomenon which has not been adequately explained and which is rarely seen today.

As the climate cooled and temperature extremes developed, and rainfall declined and became more seasonal, rainforests declined in species numbers as many taxa became extinct or migrated (or were restricted in range) northwards into the mid-high elevation equatorial rainforests where they, or their descendants, still occur. Many rainforest taxa evolved in response to the changing climate in southeastern Australia, although many of these were ultimately unsuccessful and became extinct in the region. As the climate further deteriorated, non-rainforest vegetation expanded in the drier and colder areas, although many of the taxa present in these expanding ecosystems may have had their origin in nutrient poor rainforests. It is probable that during the Early Tertiary, before the development of widespread arid and semi-arid conditions, much of central Australia was covered with a peculiar form of sclerophyllous and/or "xeromorphic" rainforest, which probably has no modern analogue. The history of this vegeta-

tion is largely unknown, although some evidence for it exists (Lange 1978; Hill and Merrifield in press).

Much more evidence is required before the microfossil record can supply detailed regional vegetation reconstructions. However, there is no doubt that the evidence available at present has allowed the generation and testing of important hypotheses concerning the origin and evolution of some of the important vegetation types which could not have obtained in any other way.

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GOGODIPTERUS PADDYENSIS (MILES), GEN. NOV.,
A NEW CHIRODIPTERID LUNGFISH FROM THE LATE DEVONIAN
GOGO FORMATION, WESTERN AUSTRALIA.

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ABSTRACT

A new genus of chirodipterid lungfish, *Gogodipterus* gen. nov., is erected for *Chirodipterus paddyensis* Miles, 1977, after further preparation of the holotype revealed that the palate has an unusual parasphenoid with a raised buccal lozenge that participated in the reduction of food. Other major differences between *Gogodipterus* and *Chirodipterus* are in the dentition and features of the braincase. A revised classification of the chirodipterid group is proposed in which the families Chirodipteridae Campbell and Barwick, 1990, and Stomiahykidae Bernaeseck, 1977 are placed within the superfamily Chirodipteroidea superfam. nov. The family Chirodipteridae contains two subfamilies: the Chirodipterinae subfam. nov. and the Pillararhynchinae subfam. nov. *Gogodipterus* is regarded as a sister genus to *Chirodipterus* based on synapomorphies of the palate, dentition and scales, and absence of more specialized characters seen in *Pillararhynchus* and *Sorbitorhynchus*.

KEYWORDS: Devonian, Gogo Formation, Western Australia, Dipnoi, *Gogodipterus* gen. nov., Chirodipteroidea superfam. nov., Chirodipterinae subfam. nov., Pillararhynchinae, subfam. nov.

INTRODUCTION

The genus *Chirodipterus* Gross, 1933, includes two species known only from holotype material, *C. wildungensis* Gross from the Late Devonian of Germany, and *C. onawayensis* Schultze, 1982, from the Middle Devonian of the USA, and two species from the Late Devonian Gogo Formation of Western Australia, *C. australis* Miles, 1977, and *C. paddyensis* Miles, 1977. *Chirodipterus paddyensis* was described from two specimens, a partial body and skull (the holotype) and a single right ramus of a lower jaw; because the holotype was embedded in resin the palate and lower jaw dentition was not revealed. Smith and Campbell (1987) further described the histology and mode of growth of chirodipterid toothplates and figured the isolated lower jaw of *C. paddyensis*.

The holotype (Western Australian Museum (WAM) 70.4.250) has been further prepared with acid to remove all matrix from the palate and braincase, and the resin slab cut in order to separate the lower jaw from the skull, revealing for the first time the nature of the palate, upper

jaw dentition and posteroventral face of the braincase (Fig. 1) as well as the lower jaw and parts of the visceral skeleton (Fig. 2). In this paper the specimen is redescribed and comparisons made with other chirodipterids. A revised classification of chirodipterids is proposed based on the phylogenetic conclusions of Campbell and Barwick (1990) and this paper.

Terminology for cranial bones follows Forster-Cooper (1937). Institutional prefixes to catalogue numbers: BMNH, British Museum (Natural History), London; WAM, Western Australian Museum, Perth.

SYSTEMATIC PALAEOLOGY

Superfamily Chirodipteroidea nov.

Diagnosis. Dipnoans with dental tuberosities arranged radially or subradially; discontinuous basal pulp cavities; hypermineralized dentine in tuberosities and flat parts of plates; buccohypophysial foramen absent; bone A in contact with bone B, but bone A still carries

occipital commissure; pineal foramen absent; anterior furrow on mandible not confined laterally by dentary; jaw suspension moved forwards, quadrate inclined.

Remarks. The diagnosis is taken from characters listed in Campbell and Barwick (1990) to define the monophyly of the chirodipterid group. As their family Chirodipteridae refers only to an advanced set of taxa on their cladogram (*Chirodipterus*, *Palaedaphus*, *Sorbitorhynchus* and *Pillararhynchus*), and excludes the Stomiahykidae, it is necessary to place the two families into a new superfamily, Chirodipteroidea.

Referred genera. *Chirodipterus* Gross, *Pillararhynchus* Campbell and Barwick, *Sorbitorhynchus* Wang *et al.*, *Gogodipterus* gen. nov., *Palaedaphus* Traquair, *Stomiahykus* Bernacsek, *Archaeonectes* Meyer.

Family Stomiahykidae Bernacsek, 1977

Diagnosis. Chirodipteroid lungfishes having elongated pterygoid dental plates with pointed anterior tuberosities, most of which remain isolated, arranged in rows; large tusk-like tuberosity at anterior end of mesial row.

Remarks. Bernacsek (1977) did not provide a diagnosis of the family, as it was monotypic as proposed, based on the characters of the genus *Stomiahykus*. The above synapomorphies are from Campbell and Barwick (1990:162).

Referred genera. *Stomiahykus*, *Archaeonectes*.

Family Chirodipteridae Campbell and Barwick, 1990

Diagnosis. Chirodipteroid lungfishes having pterygoid dental plates approximately as wide as long, and with an obtuse or rounded anterior end; tuberosities closely spaced or fused along the radial rows; large areas of plate without tuberosities; sutures present between parasphenoid and pterygoids; dermopalatines and anterior median plate not fused to pterygoids; adsymphyseal plate free; spiracular recess absent; cleithrum with buried concave external face; scales not rhombic and lacking articulatory pegs.

Remarks. The above characters are listed in Campbell and Barwick (1990:162) for defining the clade containing higher chirodipterids. Other features used to define chirodipterids (Long 1988) include the cheek with long 10 bone which contacts bones 5-7 (seen only in *Chirodipterus*

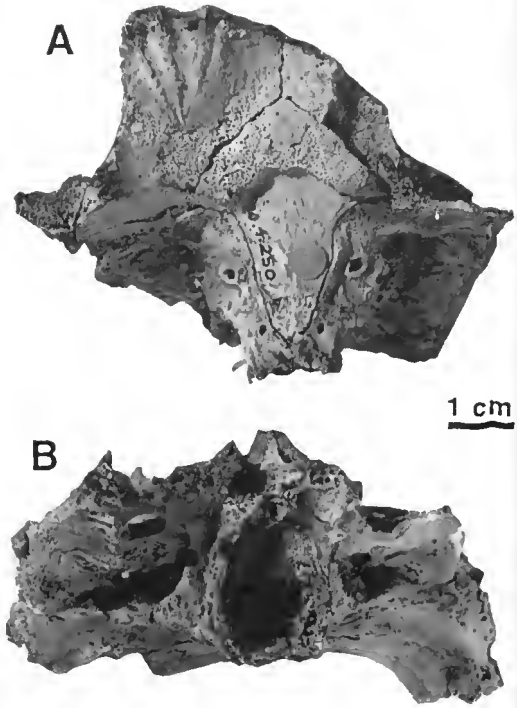


Fig. 1. *Gogodipterus paddyensis* (Miles) gen. nov., holotype WAM 70.4.250. A, palate and braincase in ventral view. B, braincase in posterior view.

and *Pillararhynchus*), and the ploughshare-shaped parasphenoid. As this last feature is only seen in *Chirodipterus* it must now be regarded as an autapomorphy of that genus.

Referred genera. *Chirodipterus*, *Pillararhynchus*, *Sorbitorhynchus*, *Gogodipterus*, *Palaedaphus*.

Subfamily Pillararhynchinae nov.

Diagnosis. Chirodipterid lungfishes having a lower jaw with long median symphysis, and only two or three infradentaries; supra-Meckelian vacuity almost closed; preglenoid process long and high; glenoid fossa restricts lateral movement of jaw.

Remarks. The above characters are from Campbell and Barwick (1990: 162), with the additional character of the long median symphysis (48-56% of lower jaw length for the two genera). Other derived features of the new genera *Pillararhynchus* and *Sorbitorhynchus* will no doubt be included to expand this diagnosis after they have been formally described.

Referred genera. *Pillararhynchus*, *Sorbitorhynchus*.

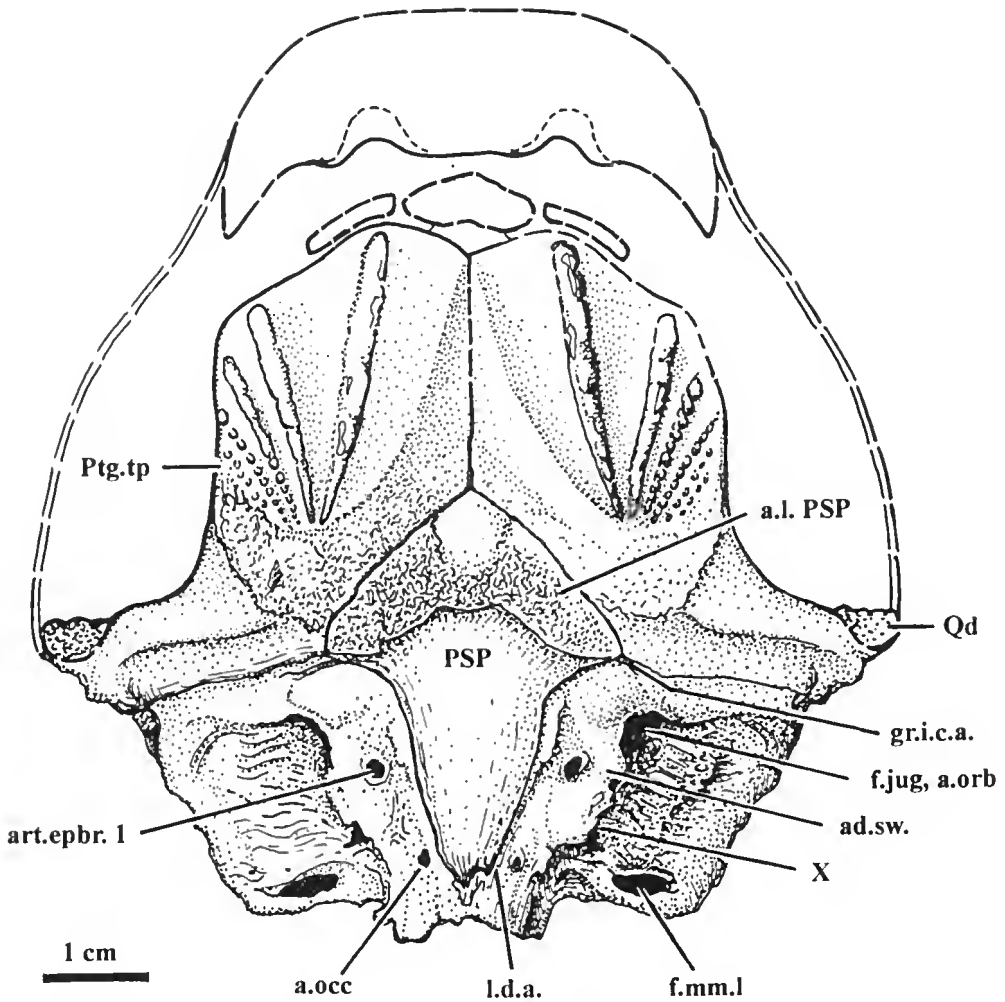


Fig. 2. *Gogodipterus paddyensis* (Miles) gen. nov., reconstruction of the palate and braincase in ventral view, based on the holotype, WAM 70.4.250.

Subfamily Chirodipterinae nov.

Diagnosis. Chirodipterid lungfishes that retain a large supra-Meckelian vacuity and have a median symphysis on the lower jaw of about 40-43% of total jaw length.

Remarks. The presence of the large supra-Meckelian vacuity and the smaller median jaw symphysis are not regarded as derived features within the clade, but serve only to distinguish the genera *Chirodipterus* and *Gogodipterus* from the Pillararhynchines.

Gogodipterus gen. nov.

Type species. *Gogodipterus paddyensis* Miles, 1977.

Diagnosis. Chirodipterine lungfish having parasphenoid with an anterior division with raised anteriorly pointing V-shaped ridge bearing enamel-covered dentine confluent with medial crushing surfaces of the pterygoid toothplates; dentition consists of three well-spaced high ridges which cross from labial to lingual surface and converge on the posteromesial angle, and up to three smaller outer rows of individual, non-coalescent tuberosities; small process on dorso-lateral edge of prearticular which projects over the supra-Meckelian fossa of mandible at base of the toothplate; shorter region on posterior face of braincase dorsal to foramen magnum, transverse processes lateral to foramen magnum are large.

Remarks. The new genus is readily distinguished from all other chirodipterids because of

the shape of the parasphenoid and the extensive, dentine-covered ledge along its anterior margins. The dentition is also unique amongst chirodipterids, all others having rows of cusps which may coalesce to form low tooth-ridges, as distinct from the sharp, high tooth-ridges separated by deep furrows seen in *Gogodipterus* gen. nov. Other characters listed by Miles (1977:12) for separating the species from *Chirodipterus australis* are now included as generic features due to the discovery of a second new species of *Chirodipterus*, from south of Lloyd Hill at Gogo, currently being studied by the author.

***Gogodipterus paddyensis* (Miles, 1977)**
(Figs 1.2, 3A, 4A, 5, 6, 7C)

Chirodipterus paddyensis Miles, 1977, pp.1, 3, 12-13, 38, 45-46, 66, 69, 83, 96, 113, 115-116, 132, 153, 167, 182, 200, 204-207, 231, 236-7, 247-248, 253, 255, 259, 273-274, 276-279, 293; Figs. 3a,b: 19-2, 38, 85, 107, 121 b-h, 145-146, 148.

Chirodipterus paddyensis - Smith, 1977, p.53

Chirodipterus paddyensis - Schultze, 1982, p.161.

Chirodipterus paddyensis - Marshall, 1987, p.19

Chirodipterus paddyensis - Smith and Campbell, 1987, p.333, 339, 342-343; Pl.3, Figs 14-17, Fig.32.

Chirodipterus paddyensis - Long, 1987, p.310.

Chirodipterus paddyensis - Long, 1988, p. 440.

Chirodipterus paddyensis - Long, 1991, p. 395.

Chirodipterus paddyensis - McNamara, Long and Brimmell, 1991, p. 88, 89 Fig.3.

Description. Miles (1977) has described and figured much of the anatomy of *Gogodipterus paddyensis*, including the posterior and lateral surfaces of the braincase, the lower jaw (based on BMNH P56034), the subopercular and opercular bones, and parts of the visceral skeleton. The following new features are described herein: the parasphenoid (ventral surface), pterygoid toothplates, hyomandibular and new observations on the lower jaw (based on holotype) and the ceratohyal are included. Comparisons are made directly with other chirodipterids, based on the descriptions of *Chirodipterus wildungensis* (Gross 1933; Säve-Söderbergh 1952; Jarvik 1967), *C. australis* (Miles 1977, Campbell and Barwick, 1982a, 1982b, and several specimens in the Western Australian Museum), *Stomiahykus* (Bernacsek 1977; Smith and Campbell 1987); *Pilliarhynchus* (Campbell and Barwick 1990), *Archaeonectes* (Meyer 1859), *Palaedaphus* (Traquair 1878) and *Sunwaptia* (Thomson 1967).

The braincase. Miles (1977) gave a detailed description of the dorsal, posterior and postero-lateral regions of the braincase, as these were the only exposed surfaces on the holotype. The specimen now also shows the ventral surface of the braincase posterior to the pterygoid toothplates. In general, the braincase of *Gogodipterus* (Fig. 3A) is not as deep as that of *Chirodipterus australis* (Fig. 3B) or *Pilliarhynchus* (Fig. 3C). The ventral surface of the braincase exposed posterior to the quadrates is proportionally broader (Breadth/Length index = 250) than for *Chirodipterus australis* ($B/Li = 225$) or *C. wildungensis* (c.195).

Most of the anatomical features of the ventral surface correspond well to those described for *Chirodipterus australis*, except for the development of the foramina interpreted by Miles as for the lateral division of the masseter muscle (l.mm.l, Fig. 3B). In modern lungfish (e.g. *Neoceratodus*) the masseter muscles pass posterodorsally from the lower jaw, in front of the quadrate to insert on the rear dorsal region of the braincase, not onto the posterior face of the braincase. It seems more likely that these foramina are for venous drainage of the braincase. In *Chirodipterus australis* this foramen is clearly shown in ventral view, and in posterior view is barely visible. In *Gogodipterus* this foramen has more of a posteroventral orientation, and is only partially seen in ventral view, being more clearly shown in posterior view (Fig. 3A).

The articulation for the first epibranchial is large on *Gogodipterus* (art.epbr 1, Fig. 2) relative to that in *Chirodipterus australis*, and the adotic swelling (ad.sw, Fig. 2) has a small lateral groove developed in *Gogodipterus* which is absent in *Chirodipterus*. The foramen for the jugular vein (f.jug, Fig. 2) is preceded by a well-defined entrance groove in *Gogodipterus*, but not in *Chirodipterus*.

In posterior view, the area of hypaxial trunk muscle attachment dorsal to the foramen magnum and ventral to the fossa for the temporalis muscle is proportionately much shorter in height on *Gogodipterus* than for *Chirodipterus* or *Pilliarhynchus* (Fig. 3). There is no occipital crest present in *Gogodipterus* (Miles 1977: Fig. 19) as is developed in *Chirodipterus australis* (cro, Fig. 3B). The transverse processes (tr.pr, Fig. 3A) developed lateral to the foramen magnum are larger and more distinct in *Gogodipterus* than in *Chirodipterus australis* (Fig. 3B).

The features of the lateral surface of the braincase of *Gogodipterus* is very similar to

those of other *Chirodipterus* species as far as is known. However, on the diagram of Miles (1977: Fig. 21) the foramen labelled as the optic nerve (II) is here interpreted as being the foramen for the ophthalmic artery (Fig. 4A, a.om). This is because on all other chirodipterids where the braincase is preserved (*Chirodipterus australis*, *C. wildungensis*, *Stomialykus*, Fig. 4C-D) the

first foramen anterior to the profundus canal (VI) and foramen jugulare is always the ophthalmic artery. The position of the optic nerve foramen in *Gogodipterus* would be slightly anterodorsal to the ophthalmic artery foramen, and this area is not preserved on the specimen.

In addition to these differences in braincase anatomy, Miles (1977:45-46) notes the following differences between *Gogodipterus paddyensis* and *Chirodipterus australis*: the lateral occipital fissure is closed immediately behind the foramen jugulare, but is open more dorsally, and extends upwards well into the midline; the foramen jugulare shows weakly defined subdivision into nervous and venous openings, as distinct from *Chirodipterus australis* in which the two openings are well-defined.

The parasphenoid. The parasphenoid of *Gogodipterus* (PSP, Fig. 2) measures 39.6mm long by 29 mm wide. The anterior division, as exposed ventrally, measures 16mm in length, being approximately 40% of the bone's length (in *Chirodipterus australis* this is 36%, in WAM 86.9.692). The anterior edge of the bone is formed into a raised platform that forms an inverted V-shape, and this ledge (a.l.PSP, Fig. 2) rises approximately 3.3 mm high from the level of the midline of the ventral surface of the bone. This raised ledge is covered by 'vermiform dentine' made up of enamel-covered denticles (Smith and Campbell 1987: 343) which is covered in the middle of the ledge by small blebs of smooth enamel-covered dentine, confluent with the level of the mesial edges of the pterygoid toothplates.

It is clear that the raised ledge of the parasphenoid was actively used in crushing food, greatly enlarging the crushing surface of the palate beyond the area of the toothplates. This utilisation of the parasphenoid in feeding is otherwise only seen in few dipnoans: the chirodipterid *Pillararhynchus longi* (Campbell and Barwick 1990), the chirodipterid *Stomialykus* (Campbell and Smith 1987, fig.18) and the Permian *Conchopoma* (Schultze 1975). In addition to these, a new species of *Chirodipterus* being studied from the Gogo fauna by the author also has small blebs of dentine on the parasphenoid, but in its dentition and overall morphology it closely resembles *Chirodipterus australis*. The damaged areas of the braincase on the holotype of *Gogodipterus paddyensis* reveal that the anterior end of the parasphenoid is not plough-share shaped as in *Chirodipterus australis*

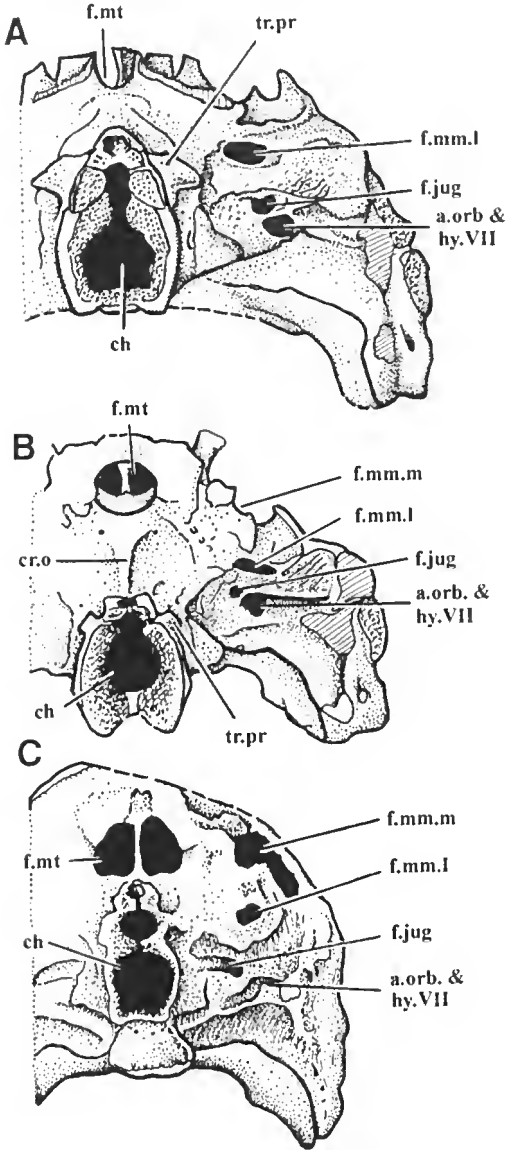


Fig. 3. Chirodipterid braincases in posterior view. A, *Gogodipterus paddyensis* (Miles) gen. nov., holotype WAM 70.4.250. B, *Chirodipterus australis* (after Miles, 1977: Fig. 16). C, *Pillararhynchus longi* (after WAM 86.9.695).

(Campbell and Barwick 1982a: Fig. 6). The thickness of the parasphenoid at its anterior extent is 4.7mm.

Pterygoid toothplates. Much of the right pterygoid toothplate is preserved (Figs 1A, 2. Ptg.tp), lacking only the anterior margin. It shows three well-developed tooth ridges, the mesial row is inclined anteromesially at an angle of 5° from the midline; the second and third tooth rows are directed anterolaterally, the second forming an angle of 13° , and the third, or outermost row,

forms and angle of 31° with the midline axis. Three small rows of isolated cusps form tooth-rows 4 - 6. The first tooth row shows wear of individual cusps down to a smooth ridge, yet cusp boundaries are still clearly defined. The second and third toothrows show less wear of individual cusps, and it is clear from tooth-row 3, which is completely preserved, that about 11-13 cusps are present. The pterygoid toothplate is covered in smooth shiny dentine mesial to the tooth-rows, and with vermiform enamel-cov-

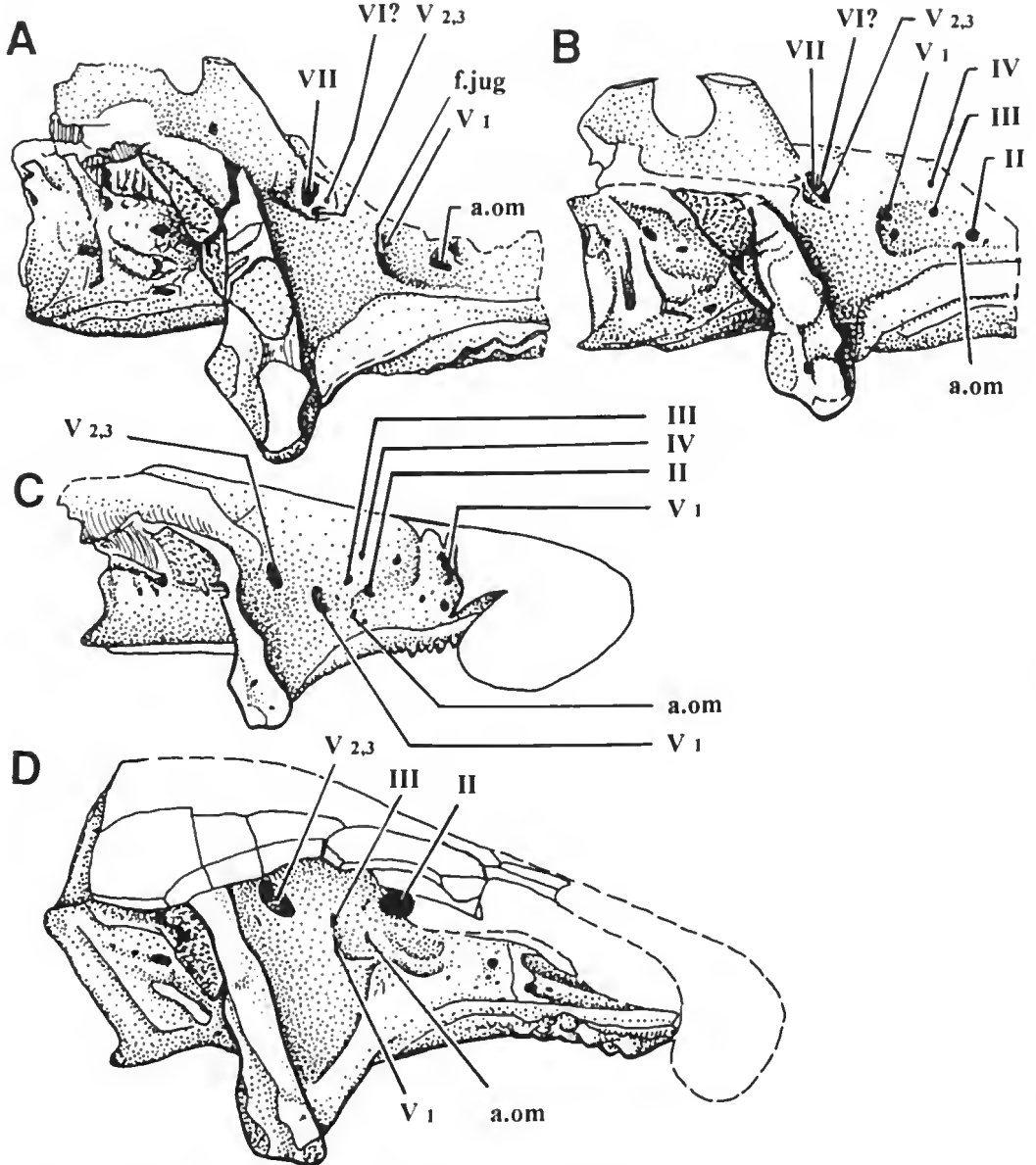


Fig. 4. Chirodipteroid braincases in right lateral view. A, *Gogodipterus paddyensis* (Miles) gen. nov., holotype WAM 70.4.250. B, *Chirodipterus australis* (after Miles, 1977, fig. 35). C, *Chirodipterus wildungensis* (after Säve-Söderbergh 1952: Fig. 5, sagittal section of skull). D, *Stomiahykus thlaodus* (after Bernacsek, 1977: Fig. 9).

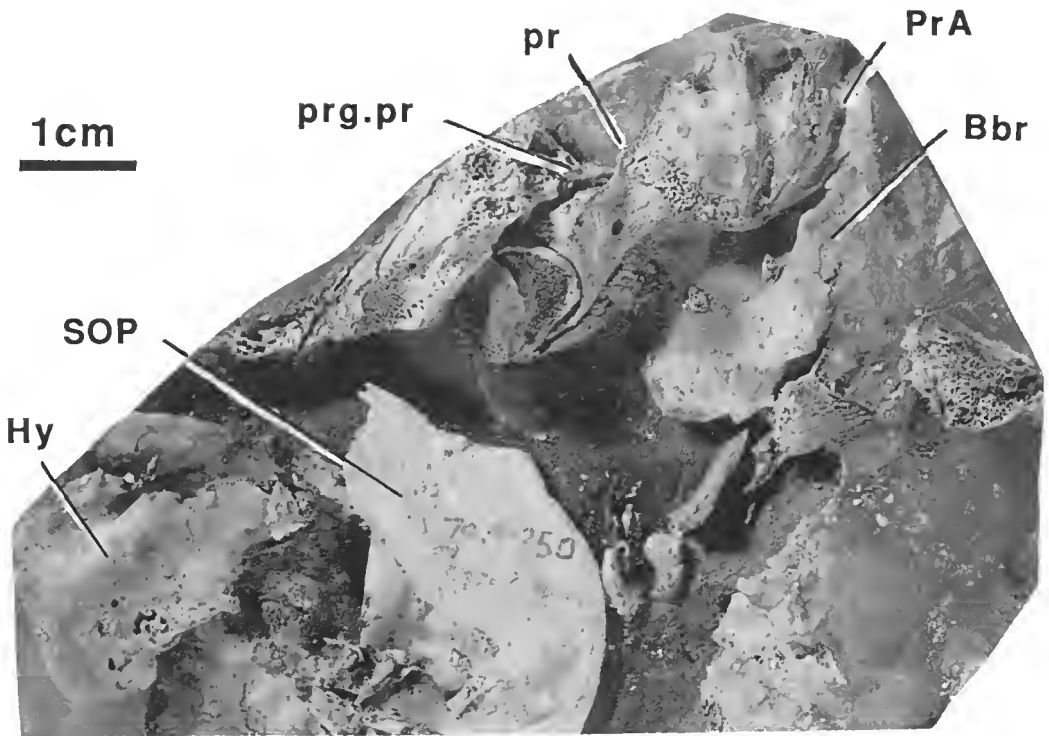


Fig. 5. *Gogodipterus paddyensis* (Miles) gen. nov., holotype WAM 70.4.250, lower jaw (left ramus), hyomandibular, subopercular and basibranchial, as prepared in situ in resin slab.

ered denticles posterior to the tooth-rows. This vermiform dentine coalesces with similar tissue on the anterior ledge of the parasphenoid.

The dentition of *Gogodipterus* differs markedly from that of *Chirodipterus australis* (as noted by Miles 1977: 293; Campbell and Smith 1987: 339), although Campbell and Smith also comment that "the plate type and structure and mode of formation of the tuberosities leave no doubt that the two species are closely related". This holds true for many of the chirodipterid group and no doubt also applies to the genus *Pilliarhynchus*, whose toothplates more closely resemble those of *Chirodipterus australis* in their wear patterns and general shape than those of *Gogodipterus*.

Hyomandibular. Miles (1977:273) described the hyomandibular of this species, but was unsure whether the truneus hyomandibularis VII nerve passed through a foramen in the bone (as in *Chirodipterus australia* and *Griphognathus*) or passed through a notch on the anterior margin. The new preparation has shown both sides of the hyomandibular well-preserved (e.g. Fig. 5, Hy) indicating that it bore a strong notch for the

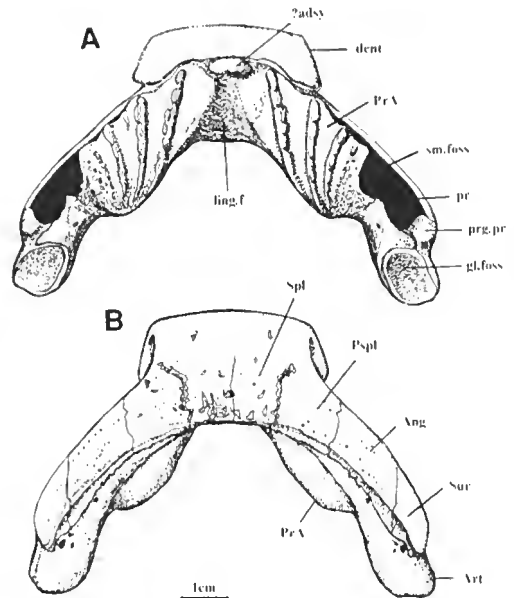


Fig. 6. *Gogodipterus paddyensis* (Miles) gen. nov., reconstruction of mandible in dorsal (A) and ventral (B) views, based on holotype WAM 70.4.250 and isolated lower jaw ramus P. 56034 (from Miles, 1977: Fig. 107).

passage of the nerve. In all other respects it is similar to that of *Chirodipterus australis*.

Ceratohyal. As described and figured by Miles (1977: Fig. 145), the ceratohyal of this species closely resembles that of *Chirodipterus australis* except for the fact that it is more robust and is said to lack a lateral endochondral attachment area. Miles (1977:275) suggested that the equivalent area on the lateral crest of the ceratohyal has coarse depressions and ridges which probably served the same function. Although the figure of the ceratohyal in Miles (1977: Fig. 145) shows the right element, his description is actually based on the left bone, as the right ceratohyal was only recently prepared, and it is poorly preserved. The lateral crest of the left ceratohyal shows that it bears a well-defined groove along its equivalent to the groove above the lateral crest on the ceratohyal of *Chirodipterus australis* (Miles 1977: Fig. 142). The ceratohyal of *Gogodipterus* is also slightly more elongated, having a height to length index of 39 compared to that of c. 43 in *C. australis*.

Basibranchial. Two of the basibranchial bones are preserved in the holotype, situated mesial to the left lower jaw ramus. The anterior basibranchial (B.br, Fig. 5) is missing the anterior third of its length, but when reconstructed

appears to be of similar shape and proportions to that of *Chirodipterus australis* (Miles 1977: Fig. 147e). A small bone can be seen lying ventral to the anterior basibranchial, it is approximately 13 mm in length, and is probably the posterior basibranchial. It is not as highly arched anteriorly as that of *C. australis* (Miles 1977: Fig. 149), being about one third as high as it is long. In all other respects it is similar to that of *C. australis*.

Lower jaw. The nearly complete right ramus of this species was described by Miles, based on P56034 (Miles 1977: Fig. 107), and a further description of the dentition of this specimen was given by Smith and Campbell (1987). The left lower jaw ramus of the holotype shows clearly the posterior end of the jaw, enabling a restoration of the entire lower jaw to be accurately made by combining features of P 56034 with those of the holotype (Fig. 6), and matching these to the lower jaw tooth-ridges of the palate. The most notable features are the great width of the mandible and its well-developed lingual furrow (ling.f, Fig. 6A). The supra-Meckelian fossa (sm. foss, Fig. 6A) is invaded by a short process (pr) emerging from the prearticular (PrA), which presumably divided the jaw muscles into the anterior suborbital fibers and the larger adductor

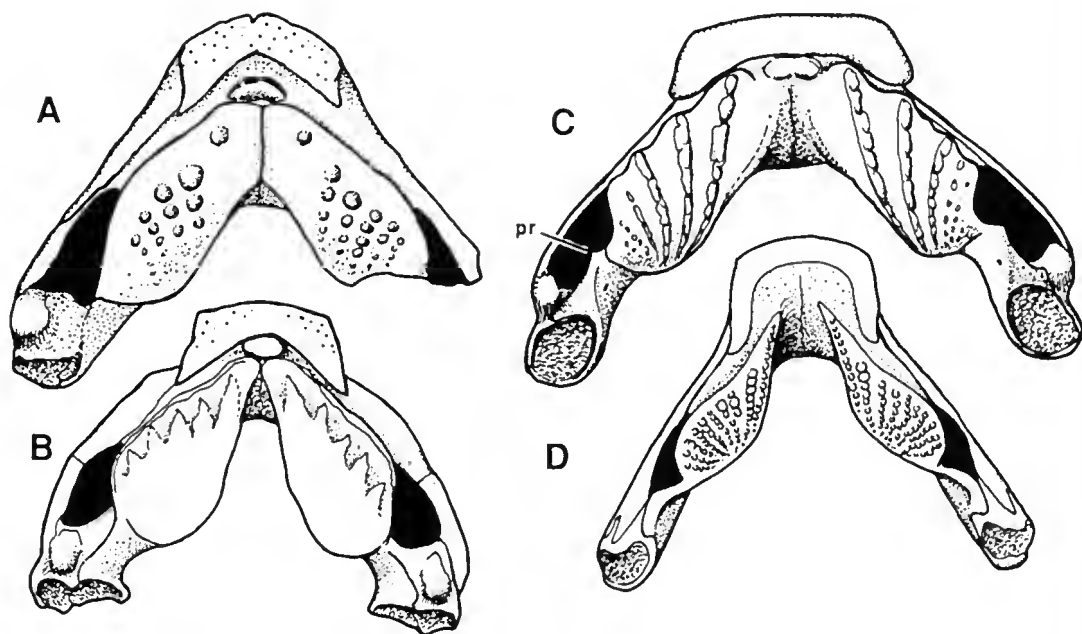


Fig. 7. Dipnoan lower jaws in dorsal view, A-C, chirodipterids, D, dipterid. A, *Chirodipterus wildungensis* (after Jarvik, 1967). B, *Chirodipterus australis*, WAM 86.9.692. C, *Gogodipterus paddyensis*, reconstructed from holotype, WAM 70.4.250. D, *Dipterus valenciennesi* (after Jarvik, 1967).

mandibulae fibers (Lauder 1980). In dorsal view the glenoid fossa (gl.foss) is well-exposed, having a more dorsally facing orientation than for other chirodipterids. It does not restrict the lateral movement of the jaw as occurs in *Sorbitorhynchus* and *Pillararhynchus* (Campbell and Barwick 1990). The preglenoid process (prg.pr) is well-developed as in other chirodipterids, but is not as high as in pillararhynchines (Campbell and Barwick 1990). The dentary (dent) is a very broad bone as shown in the reconstruction, and matches well the overall broad proportions of the palate and skull.

Etymology. After the Gogo Formation (named after Gogo Station) of the Canning Basin, Western Australia, and the well known Devonian lungfish genus *Dipterus*.

RELATIONSHIPS OF *GOGODIPTERUS* GEN. NOV.

The chirodipterid group was considered to be monophyletic by Long (1988:445) who suggested that *Pillararhynchus* ("new chirodipterid", WAM 86.9.695) was a primitive sister taxon to *Chirodipterus* plus *Stomiahykus*, based on the

shared feature of the notochordal pit being separated from the foramen magnum. There was a misprint in this work which should have said that the condition was opposite to what was stated, as in *Chirodipterus* the foramen magnum has merged with the notochordal pit. However, on the evidence of primitive dipnorhynchids having a similar condition to that of *Chirodipterus* and *Stomiahykus* (Campbell and Barwick 1982a: Figs 1-3), I now see the condition in *Pillararhynchus*, where the foramen magnum is separated from the notochordal fossa, as a specialised condition, probably related to the fact that *Pillararhynchus* has an extremely deep braincase.

A more detailed list of synapomorphies defining the chirodipterid group was given recently by Campbell and Barwick (1990). Their phylogenetic results are embodied in the classification presented in the front of this paper. Campbell and Barwick erected the new family Chirodipteridae, based on the synapomorphies given in the diagnosis in this paper. Both *Chirodipterus* and *Gogodipterus* are more advanced phylogenetically than the stomiahykids in a number of characters, such as closed pineal foramen, jaw suspension moved more anteriorly etc. (listed in Campbell and Barwick 1990:162).

These two genera are regarded as more plesiomorphic than *Pillararhynchus* and *Sorbitorhynchus* in lacking the synapomorphies of the pillararhynchines (e.g. almost closed supra-Meckelian vacuity, very large preglenoid process). It is not clear at present whether *Gogodipterus* and *Chirodipterus* share any synapomorphies that might define them as a monophyletic group (Chirodipterinae), or are sister taxa to each other plus the Pillararhynchinae. For convenience they have been placed in the new subfamily Chirodipterinae because of similar shared vascular and nervous foramina pattern seen on the lateral surface of the braincase in the orbital region. Figure 4 shows that the exit foramina for the profundus nerve (V1) is situated higher on the lateral wall than the optic foramen (II) in *Chirodipterus* species (Fig. 4B, C) and presumably in *Gogodipterus* (Fig. 4A), than for *Stomiahykus* (Fig. 4D). Another feature that might unite the *Chirodipterus* species with *Gogodipterus* is the shape of the foramen for the lateral division of the masseter muscle (Fig. 3, f.mm), which is slit-like in these forms but more rounded, and smaller in overall size, on *Pillararhynchus* (Fig. 3C).

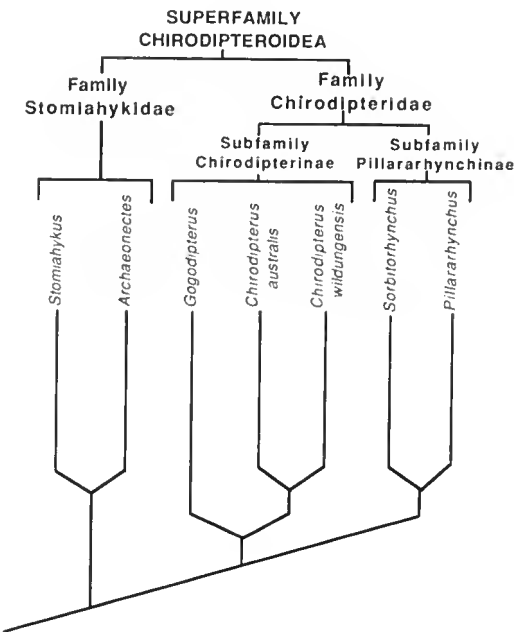


Fig. 8. Interrelationships and classification of chirodipteroids, based on characters discussed in the text (synapomorphies given in diagnoses of higher taxonomic groups).

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FIRST DINOSAUR BONES FROM WESTERN AUSTRALIA.

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ABSTRACT

A proximal end of a reptilian right humerus from the Late Maastrichtian Miria Formation, Carnarvon Basin, is identified as possibly belonging to a theropod dinosaur, based on the shape of the deltopectoral crest and the slender shaft. A small caudal vertebra from the Middle Jurassic Colalura Sandstone, near Geraldton, may belong to the Dinosauria on the basis of its overall similarity with caudal vertebrae of sauropod dinosaurs. These are the first recorded bones of dinosaurs from Western Australia.

KEYWORDS: Cretaceous, Jurassic, dinosaurs, Western Australia, Miria Formation, Colalura Sandstone.

INTRODUCTION

Dinosaurs have been known from Western Australia since the mid 20th century from footprints in the Lower Cretaceous Broome Sandstone (Glauert 1952, Colbert and Merrilees 1967). Despite numerous finds of Mesozoic reptile bones from throughout the State, nearly all of these are readily identified as ichthyosaur or plesiosaur remains (Teichert and Matheson 1944, Long 1990). A specimen which lay unrecognised in the collections of the Western Australian Museum for over 30 years was recently recognised as a partial humerus of a large pterosaur (Bennett and Long 1991), this being Australia's largest known pterosaur, and from Australia's youngest known Mesozoic vertebrate fauna.

Further discoveries of dinosaur footprints in the Broome area by local naturalist Mr. Paul Foulkes have recently been examined by the author, and these extend the known fauna of dinosaurs from Western Australia to include theropods, sauropods, ornithopods, and possibly stegosaurs (Long 1990). In this paper two more bones are described which are believed to be from dinosaurs, despite poor preservation, thus representing the first record of dinosaur bones from the western half of the Australian continent.

Institutional prefixes to catalogue numbers are as follows: Western Australian Museum, WAM; University of Western Australia, UWA.

A LATE CRETACEOUS THEROPOD HUMERUS

The theropod humerus (WAM 90.10.2) was discovered by Mr. George Kendrick, of the Western Australian Museum, from a gully near West Tank, Giralda Station (Fig. 1) in August 1990. The specimen (Fig. 2) shows typical preservation of bone from the late Cretaceous Miria Formation, and there is no evidence to the contrary that the bone had not been derived from that unit. Many fossils such as ammonites, molluscs and shark teeth weather out of the soft sediments of the Miria Formation and are found littering the gullies of the region.

The Miria Formation represents a lag deposit which contains phosphate nodules (Henderson and McNamara 1985). It is richly fossiliferous, containing many forms of ammonites, gastropods, bivalves, rare echinoderms, shark teeth and reptile bones, including those of mosasaurs. The only other outcropping sedimentary units in the area are white chalks of the Wadera Calcareenite (also Upper Cretaceous) and the Palaeocene Boongerooda Greensand. The Wadera Calcareenite represents deeper water, and quiet sedimentation, and to date has not yielded any vertebrate remains, so derivation from that unit is unlikely. The identification of the specimen as most likely belonging to a dinosaur also supports its derivation from the Miria Formation.

The specimen (Fig. 2) shows a slender shaft with an expanded articular end. As preserved, the specimen is 21 cm long, the shaft measures 3.4 cm by 2.6 cm at its smallest cross-section, and clearly shows that the bone was hollow, having a bone thickness of 5.5 mm. The slender proportions of the shaft, and its hollowness, precludes its identification as either ichthyosaur, plesiosaur, mosasaur or chelonian, all of which tend to have robust, stoecky limb elements (Romer 1956, Carroll 1988), and lack hollow cavities inside limb bones. The ratio of bone diameter to its wall thickness in a wide variety of vertebrates has been studied by Oxnard (1992). In agile cursorial animals, the ratio is as high as 7, ranging down to 4 in large graviportal animals like elephants. Pterosaurs, birds and bats have high ratios (14-45), whereas aquatic animals tend to lack hollow cavities in bones. The Miria bone has a mean ratio of 5.5 (average diameter), placing it in the main category for terrestrial agile animals, thus supporting the identification of the bone as being that of a dinosaur.

The expanded end of the bone shows a well-developed flange which is damaged, but if reconstructed would probably taper out to form a broad flat area for muscle attachments. This bone has been compared with many types of reptile limb elements and most closely matches that of the humerus in theropod dinosaurs. The broad muscle attachment surface represents the deltopectoral crest which is well-developed in bipedal dinosaurs, and especially so in the theropods (Ostrom 1969, Madsen 1976, Harrison and Walker 1973, Molnar *et al.* 1990). Bipedal ornithomimids tend to have stoeckier, robust humeri because the forearm is generally used to take the weight of the animal when on all fours (e.g. *Muttaburrasaurus* Bartholomai and Molnar, 1981; *Camptosaurus* Marsh (Galton and Powell 1980). Large carnosaurs tend to have more robust humeri with thicker shafts (Molnar *et al.* 1990). The bone may superficially resemble that of a partial sauropod ischium (e.g. *Camarasaurus* Cope; see Cope, Osborn and Mook, 1921: Figs 96-100) but differs in lacking a prominent ischial surface or ridge on the shaft, in not being solid bone, and in the more robust development of the head (or iliac border in ischia).

The combination of having a slender, gracile shaft with a greatly expanded humeral head is restricted amongst large Mesozoic vertebrates to certain families of theropod dinosaurs: coelurosaurs, some carnosaurs (e.g. *Liliensternus*

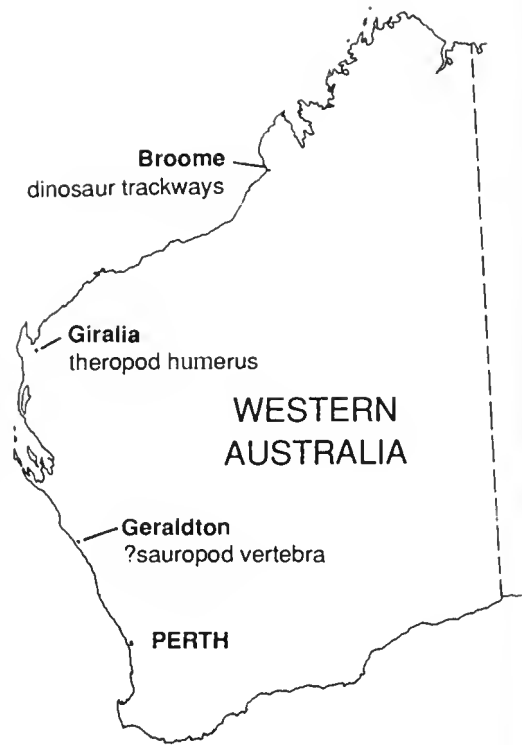


Fig. 1. Locality map showing occurrences of dinosaur remains or traces in Western Australia.

Welles, ornithomimosaurs, oviraptorids and dromaeosaurs. From biogeographic data it is clear that some dinosaur groups which first evolved late in the Cretaceous and were restricted to North America and Asia (such as hadrosaurs and ceratopsians) would not be expected to occur in Australia, due to the splitting up of landbridges as Gondwana rifted apart. Therefore, we may exclude the presence of oviraptorids, ornithomimosaurs and dromaeosaurids from Australia, but expect the presence of those groups which had evolved by the end of the Jurassic and had opportunity to disperse to Gondwana. These include coelurosaurs (e.g. *Kakuru* Molnar and Pledge 1980; *Skartopus*, Thulborn and Wade 1984) and carnosaurs (e.g. *Allosaurus* Marsh, Molnar *et al.* 1981, 1985; Welles 1983; Long 1990). Abelisaurids, once thought to be endemic to Gondwana, are also known from Europe (LeLoeuff, 1991), and their presence in Australia is at most tentative, based on one metacarpal bone of *Rapator ornitholestoides* Von Huene (Molnar 1991). The humerus of the abelisaur *Carnotaurus sastrei* Bonaparte is somewhat stoecky and robust (Bonaparte *et al.* 1990: Fig.28), quite unlike WAM 90.10.2.

Figure 3 shows a comparison between WAM 90.10.2 and the humerus of *Deinonychus antirrhopus* Ostrom, an Early Cretaceous dromaeosaur from North America. The W.A. bone matches closely the shape of the proximal

portion of the humerus as far as reconstruction permits. It is clear that the proximolateral flange would correspond to an area of attachment for deltoid and humeroradialis muscles, and the distal projection of that flange of bone would be

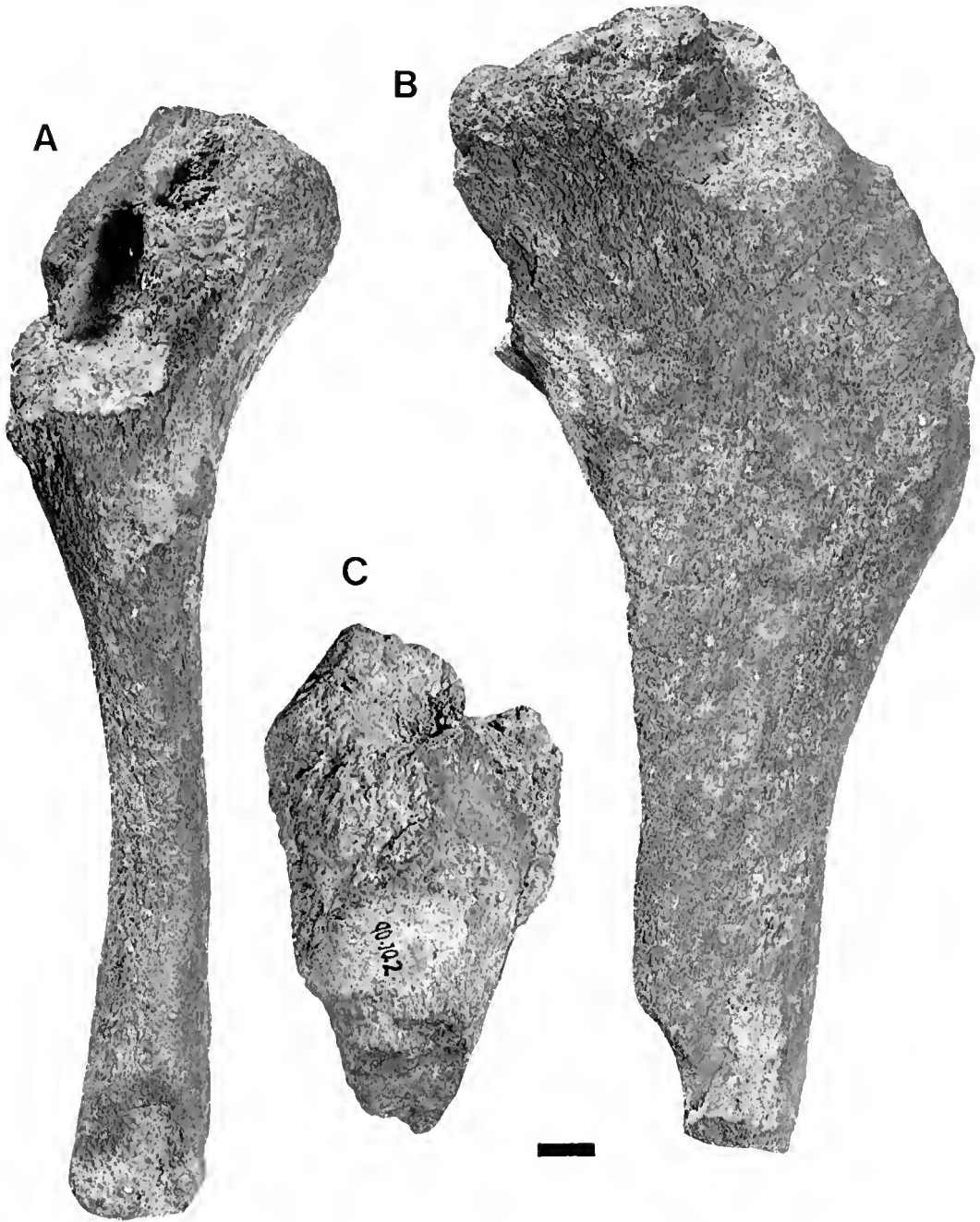


Fig. 2. WAM. 90.10.2., proximal half of left humerus of a theropod dinosaur from the Late Maastrichtian Miria Formation, Western Australia. **A.** anterior view. **B.** lateral view. **C.** dorsal view. Bar scale 1cm.

the deltopectoral crest. The head of the humerus is partially preserved, but can be confidently restored from the specimen. It shows the supporting buttress of a robust caput humeri, angled in mesially from the long axis of the shaft. An internal tuberosity was probably developed, as seen on the outline of the bone, and an attachment area for scapulo-humeralis muscles is also clearly defined. In proximal view, the head of WAM 90.10.2, as much as is preserved, has a moderate curvature not as pronounced as the Z-shaped proximal head of the humerus in *Deinonychus* (Harrison and Walker 1973: Fig. 6).

If the bone was reconstructed with similar proportions as the dromaeosaur *Deinonychus*, it would have an estimated total length of about 32-35 cm. As theropod dinosaurs exhibit a great range of forearm sizes, from small dinosaurs with large arms (e.g. *Deinonychus*) to gigantic forms with tiny arms (e.g. *Tyrannosaurus* Osborn), it is difficult to estimate the size of the Western Australian theropod without more tangible anatomical features to narrow down its identification.

In summary, the Western Australian bone most likely comes from a theropod dinosaur

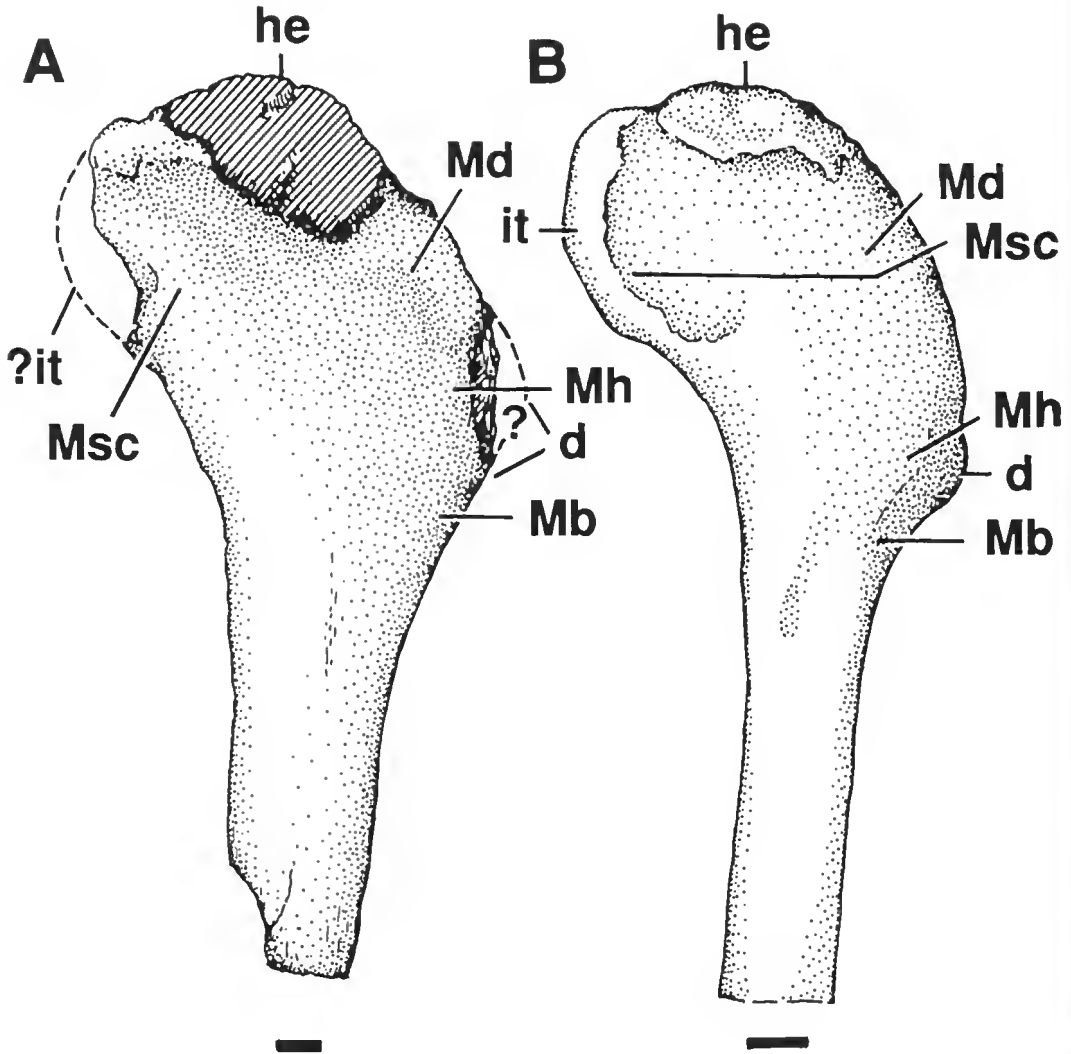


Fig. 3. Comparison between A, WAM 90.10.2 and B, left proximal part of left humerus from the dromaeosaur *Deinonychus antirrhopus* (after Ostrom 1969). Abbreviations: d, deltopectoral crest; he, head of humerus; it, internal tuberosity; Mb, attachment surface for brachialis muscle; Md, attachment surface for deltoid muscle; Mh, attachment surface for humero-radialis muscle; Msc, attachment surface for scapulo-humeralis muscle. Bar scale 1cm.

aving slender forearms, possibly one of the rger coelurosaurs. The presence of large mososaurs and coelurosaurs in the Early Cretaceous of Western Australia is known from footprints in the Broome area. Although coelurosaurs came extinct by the end of the Early Cretaceous in North America, it would not be unusual for the group to have survived later in Australia, other Australian dinosaurs, like *Allosaurus*, have been shown to persist to later times when compared with their relatives in the northern hemisphere.

A MIDDLE JURASSIC SAUROPOD VERTEBRA?

A small vertebra from the Middle Jurassic (Bajocian) Colalura Sandstone was found at

Bringo Railway Cutting, about 20km east of Geraldton, by students from the Geology Department of the University of Western Australia, back in the mid 1970s. The specimen (UWA 82468) was labelled in the collections as a possible plesiosaur vertebra. Several well-preserved vertebrae of plesiosaurs have been found from that unit (Long 1990, p. 53).

The specimen (Figs. 4, 5) is a distal caudal vertebra measuring 6.3 cm in length, 4.7 cm wide, with centrum height of 4.3cm. It is almost complete, missing only part of the anterior central surface and the top of the neural arch. Both of the central surfaces are strongly concave, and the posterior surface has a well-developed posteroventral surface for chevron bone articulation. The neural arch encloses a canal 1 cm in breadth. (1.96 cm total breadth of neural arch) and the neural arch arises 1.9 cm from the

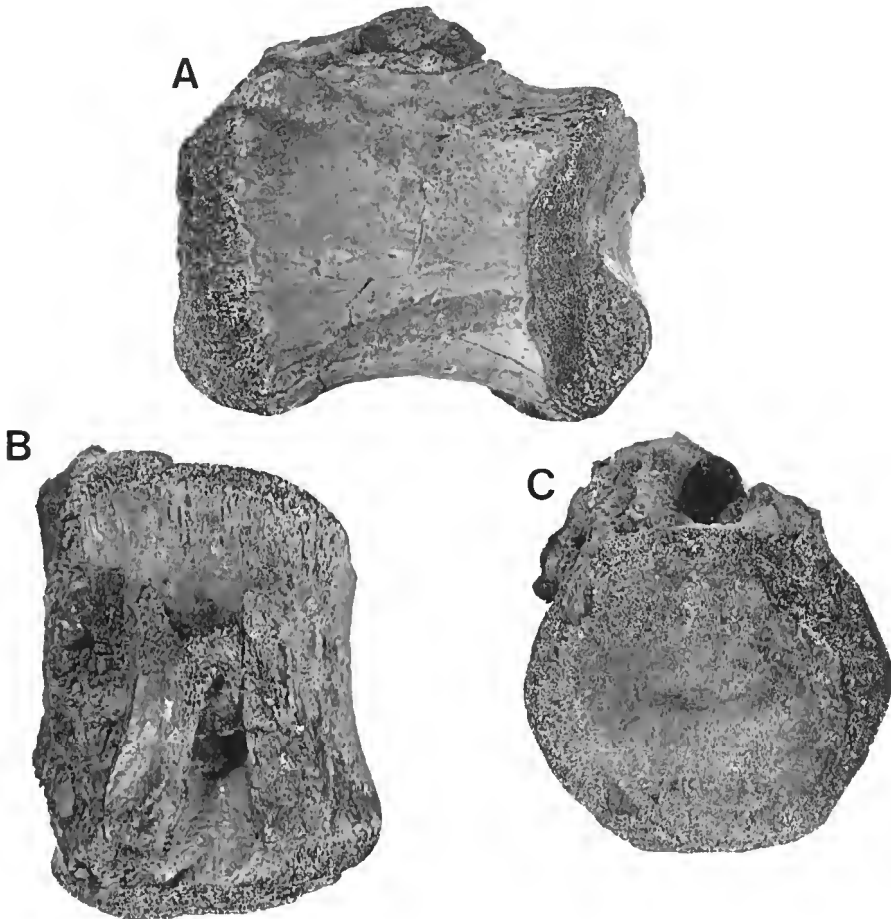


Fig. 4. ?Sauropod caudal vertebra from the Middle Jurassic Colalura Sandstone of Western Australia, UWA 82468. A, right lateral view; B, dorsal view (anterior towards top); C, posterior view. Natural size.

anterior of the bone where it continues to its posterior extent, broadening posteriorly (neural arch 2.88 cm wide). In lateral view, the bone shows strongly concave ventral margins, and in dorsal view the lateral margins are also strongly concave. Small nutritive foramina are visible on the ventral and lateral surfaces of the bone, but these are not regularly placed nor as proportionately large as those seen in plesiosaur vertebrae.

The bone has been shown to a number of fossil reptile experts and, using the literature, compared with numerous reptile vertebrae from a diverse range of taxonomic groups. Although essentially lacking synapomorphic features which could unite it with certain groups of dinosaurs, it can only be generally said that it closely resembles the distal caudal vertebrae of sauropods. A caudal vertebra of *Austrosaurus Longman* sp. (QM F 7292) was borrowed from the Queensland Museum for comparison. Both show similar general proportions: spindle shape, strongly concave central surfaces; chevron facets on the presumed posteroventral margins, similar development of neural arch shape (basal attachments only). A distal caudal vertebra of *Austrosaurus* sp. from Queensland figured by Coombs and Molnar (1981: Plate 1,5) is also very similar in the relative shape and placement of the neural arch on the vertebral centrum. There is nothing to preclude the Western Australian specimen from belonging to another group of dinosaurs, although lack of representative material in Australia has prevented more extensive comparisons from being made. At this stage it is tentatively identified as dinosaurian, cf. sauropod.

The significance of the specimen lies in that if it is a dinosaur it represents only the second known Jurassic occurrence of skeletal material of dinosaurs in Australia, the other being the sauropod *Rhoetosaurus brownei* Longman, discovered in the 1920s near Roma, Queensland (Longman 1926, 1927). The potential for more discoveries of dinosaurs in the Geraldton area is not great however, as outcrop of the Colalura Sandstone is not very extensive. To date, the only known vertebrate remains from this unit have all come from the small railway cutting at Bringo.

ACKNOWLEDGEMENTS

For helpful correspondence on the two Western Australian specimens, and for looking at one

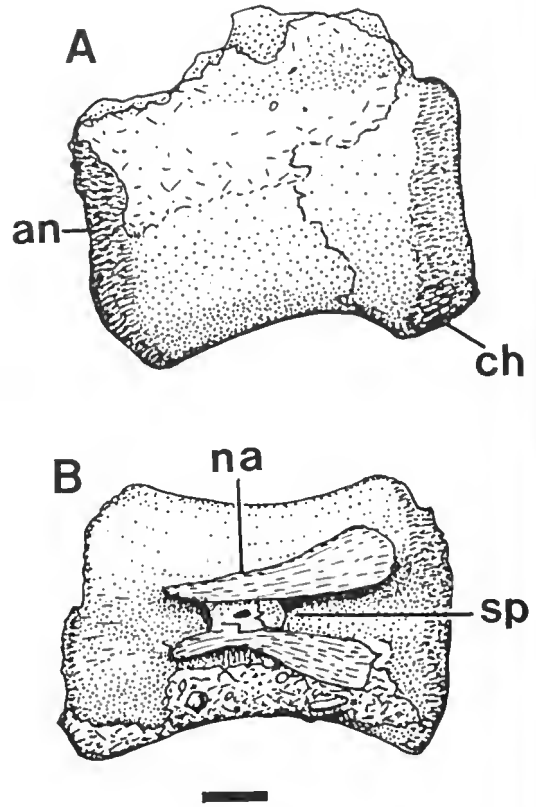


Fig. 5. ?Sauropod caudal vertebra from the Middle Jurassic Colalura Sandstone of Western Australia, UWA 82468. A, left lateral view. B, dorsal view. an, anterior face of centrum; Abbreviations: ch, chevron articulation surface; na, neural arch; sp, cavity for passage of spinal cord. Bar scale 1cm.

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THE DEMISE OF THE DANCING DINOSAURS?

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ABSTRACT

Speed-estimates derived from fossil trackways have recently been used to support the claim that dinosaurs were warm-blooded. Critical examination of those speed-estimates reveals no basis for the claim that "dinosaurs cruised at warm-blooded speeds": the speeds of dinosaurian track-makers appear to have been consistently overestimated, and comparisons of absolute speed are inappropriate because they make no allowance for differences in size of the track-makers. If size-differences are taken into account, dinosaurs do not appear to be significantly faster, or slower, than other terrestrial vertebrates.

KEYWORDS: dinosaurs, tracks, speed, locomotion, thermal physiology.

INTRODUCTION

The protracted and lively debate about "warm-blooded" *versus* "cold-blooded" dinosaurs was initiated nearly 20 years ago in a provocative paper by Bakker (1972). Despite a great deal of discussion, the issue remains unresolved and continues to generate controversy (e.g. Thomas & Olson 1980; Bakker 1986a; Ostrom 1987; Reid 1987, 1990).

Bakker's original argument for dinosaurian endothermy (1972) drew on three categories of evidence - (1) bone histology, (2) features of gross anatomy (e.g. locomotor adaptations, pneumatopores, secondary palate), and (3) community structure. Evidence from those same three sources has been amplified considerably and combined in various permutations in Bakker's subsequent publications on dinosaur biology (e.g. Bakker 1974, 1975a, 1975b, 1980, 1986a).

More recently, the claim that dinosaurs were warm-blooded has been bolstered with the evidence of speed-estimates derived from fossil trackways (Bakker 1986a, 1986b, 1987; Paul 1988). The fullest treatment of this evidence is given in Bakker's article titled "The Return of the Dancing Dinosaurs" (1987). Briefly, Bakker ascertained that the average walking speeds ("cruising speeds") of dinosaurs and thecodontians were at least as great as those of

existing mammals. By contrast, average walking speeds were found to be "much lower" among undoubted ectotherms (living amphibians and reptiles, along with a variety of Permian and Carboniferous tetrapods). In Bakker's estimation these findings (Fig. 1) demonstrate that "dinosaurs cruised at warm-blooded speeds" (1987: 39).

Although the evidence of dinosaur tracks is only a small ingredient in the overall argument favouring dinosaurian endothermy, it does nevertheless comprise hard quantitative data and should, for that reason, provide some fairly robust conclusions. Moreover, a recent resurgence of interest in the study of dinosaur tracks and their biological significance (Haubold 1984; Gillette and Lockley 1989; Thulborn 1990; Alexander 1991) provides a satisfactory background for appraising the validity and the significance of Bakker's findings.

VALIDITY OF SPEED-ESTIMATES

Bakker estimated the speeds of dinosaurs and other extinct tetrapods by means of a method pioneered by Alexander (1976). That method certainly seems to provide realistic estimates of speed, though Alexander conceded (1989: Fig. 6) that it might tend to underestimate moderate speeds and to overestimate higher ones. In this

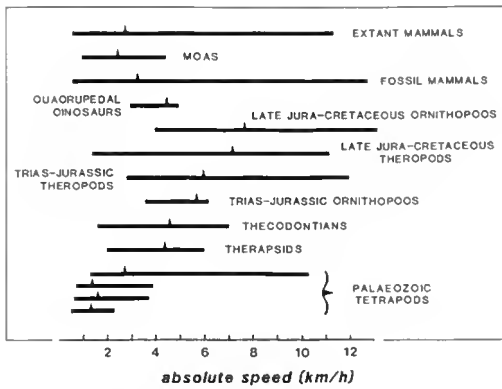


Fig. 1. Estimated 'cruising speeds' of extinct tetrapods and observed 'cruising speeds' of living mammals. Range and median indicated for each group. Diagram adapted from Bakker (1987: Fig. 7), with sample for 'Late Jura-Cretaceous thropods' excluding an outlier of speed estimates for running animals (Farlow 1981).

context it may be noted that the highest estimates of speed obtained by Bakker are those for dinosaurs (Fig. 1).

In order to check the accuracy of Alexander's (1976) method, Bakker plotted predicted speeds against observed speeds for a range of extant tetrapods (1987: Fig. 4). This test revealed that "ninety-five percent of the predictions fell within 2 times the actual speed" (Bakker 1987: 48). While this test confirmed the value of Alexander's method as a generalization, it did not sanction the uncritical application of that method to "cruising speeds" in particular. Here it must be observed that Bakker's test confirmed the reliability of Alexander's method over a very wide range of speeds, from about 0.7 km/h (walking lizard, *Teratosciurus*) to more than 90 km/h (fast-running cheetah). But within the restricted range of "cruising speeds" discussed by Bakker (approximately 0.5 to 12.1 km/h), Alexander's method would seem to be a far less reliable predictor of actual speed. And within the extremely narrow range of median "cruising speeds" calculated by Bakker (approximately 1.3 to 7.7 km/h), Alexander's method appears to be a very poor predictor indeed.

Thus, Bakker's (1987) predictions of speed for dinosaurs and other extinct tetrapods are not necessarily accurate, despite the fact that Alexander's (1976) method was confirmed as a reliable generalization. Unfortunately, Bakker's presentation of his findings (Fig. 1) gave no indication of the possible margins of error. The reliability of those findings would have been

more readily apparent had they been presented as mean values with confidence limits, rather than simple histograms with median values.

Prerequisites for the use of Alexander's method are measurements of stride length, SL , and of the track-maker's height at the hip, h . Stride length is measured directly on the trackway, but height at the hip must be estimated, usually from the size of the track-maker's footprints. Obviously the dimension h must be estimated with care, since any error may have a substantial effect on the ratio SL/h and, hence, on the final prediction of the track-maker's speed.

Numerous methods, some more reliable than others, have been used to estimate h for dinosaurian track-makers (Thulborn 1990: 249-256). Bakker estimated h by means of simple morphometric ratios, where "hind-limb length" (equivalent to h) was expressed as a multiple of "foot breadth across the metatarsals" (1987: 48). So, for instance, sauropods (brontosaurus) were estimated to have hindlimbs equivalent in length to about 4.8 times the width of the metatarsus. Unfortunately, Bakker's list of such ratios was neither complete nor very detailed: it gave no ratio(s) for theropod dinosaurs, and it specified a wide range of ratios for ornithopod dinosaurs - from 5.8 in hadrosaurs to 8.0 in fabrosaurs. Nor did Bakker explain how estimates of "foot breadth across the metatarsals" were derived from fossil footprints. Such explanation is essential because there seems to be no immediately obvious corre-

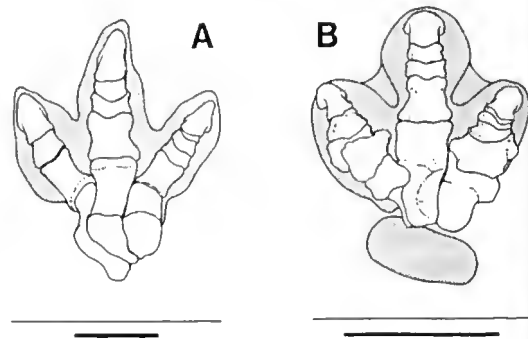


Fig. 2. Foot skeletons of large ornithomorph dinosaurs superimposed on corresponding footprints. A, Foot skeleton of the early Cretaceous ornithomorph *Iguanodon* superimposed on footprint from rocks of similar age (adapted from Dollo 1906). B, Foot skeleton of the hadrosaur *Hypacrosaurus* superimposed on a suspected hadrosaur footprint from the Upper Cretaceous of Alberta, Canada (adapted from Langston 1960). Note that there is no straightforward correspondence between the maximum width of the metatarsus (thick bar) and the maximum width of the footprint (thin bar).

lation between the width of a dinosaur's footprint and the width of its metatarsus (Fig. 2).

Bakker's reliance on morphometric ratios disregards the prevalence of allometry within dinosaur taxa: it assumes that all individuals within a dinosaur taxon will share an identical ratio of foot breadth/hindlimb length, regardless of their size or ontogenetic status. That assumption is unrealistic and is likely to generate some spurious estimates of h and, therefore, of the track-makers' speeds (Thulborn 1989, 1990). While estimates of h derived from morphometric ratios are undeniably convenient for preliminary analy-

ses of tracky data, they are probably less reliable at the level of accuracy required by Bakker's investigation.

Moreover, it is difficult to confirm the absolute values of the morphometric ratios cited by Bakker (1987). For example, the only well-known skeleton of a fabrosaurid dinosaur, *Fabrosaurus australis* (*Lesothosaurus diagnosticus*) has a skeletal hip height of 30.2 cm, representing the combined lengths of femur, tibia and metatarsus (Thulborn 1972); the maximum width of the metatarsus is 2.3 cm, indicating that the ratio of hindlimb height to metatarsus width is roughly 13/1 and not, as Bakker suggested, 8/1. Measurements from two specimens of the primitive-looking ornithopod dinosaur *Hypsilophodon foxii* (Galton 1974) provide ratios of 9/1 and approximately 10/1. In the case of these smaller ornithopods, including fabrosaurids, it appears that Bakker has underestimated the length of the hindlimb, thus generating overestimates of speed. (I assume that estimates of hindlimb height exclude the digits; if the digits are included, the discrepancies are even more pronounced, with *Fabrosaurus* having a ratio of nearly 16/1.)

Similar queries arise over Bakker's estimates of hindlimb length for sauropods (brontosaurus) and hadrosaurs (duck-billed dinosaurs). Among the hadrosaurs, for instance, one survey of osteometric data indicates that h is approximately 5.9 times the length of the metatarsus (Thulborn 1989: 42). Since the hadrosaurian metatarsus is between 1.1 and 1.3 times wider than long, h might be estimated at roughly 6.4 to 7.5 times metatarsus width. By contrast, Bakker (1987: 48) cited a figure of 5.8 times metatarsus width. Here, again, it seems that the morphometric ratio used by Bakker would consistently generate underestimates of size and overestimates of speed.

SIGNIFICANCE OF SPEED-ESTIMATES

Bakker claimed that cruising speeds were much lower among cetotherms than among living mammals (1987: 49), yet this is clearly not the case. Figure 1 shows that the median cruising speed of existing mammals (nearly 3 km/h) is not significantly higher than among Palaeozoic tetrapods (with median predictions ranging from about 1.5 km/h to 3 km/h). Here it should be recalled that the the predictions in Fig. 1 were guaranteed to be no more accurate than "within 2 times the actual speed" (Bakker 1987: 48).

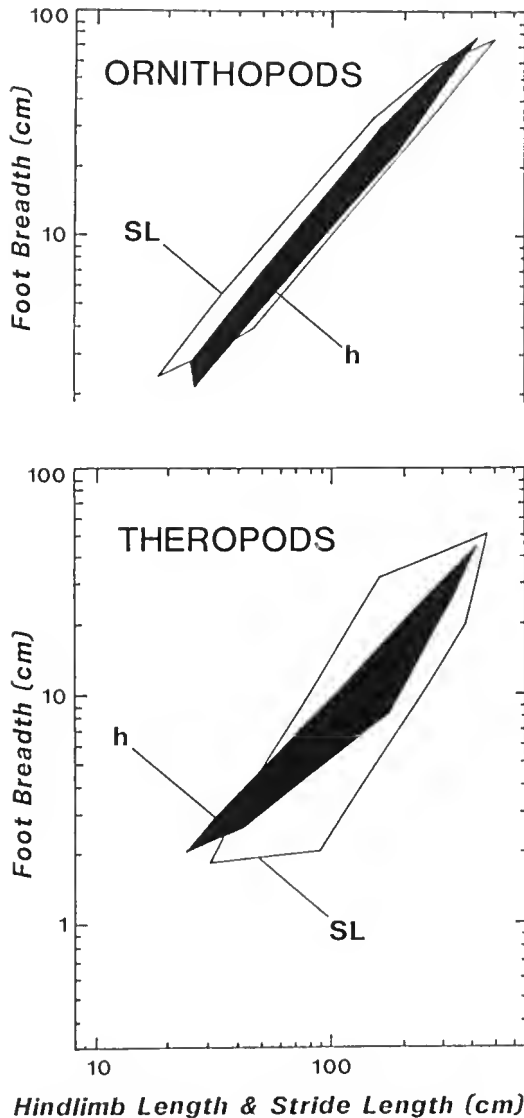


Fig. 3. Relationship of stride length (SL) to hindlimb length (h) in ornithopod dinosaurs and theropod dinosaurs. Both diagrams adapted from Bakker (1987: Fig. 6).

Thus, Bakker's basic assumption - that endothermic tetrapods *should* cruise at higher speeds than ectothermic tetrapods - seems less than convincingly demonstrated.

It is well known that a small animal needs to achieve a higher level of locomotor performance (i.e. a faster gait) in order to match the speed of a bigger animal (Heglund et al. 1974; Thulborn and Wade 1984). This point is easily appreciated by small children, who are often obliged to trot alongside their walking parents. Nevertheless, Bakker (1986a, 1987) compared estimates of absolute speed for dinosaurs and other tetrapods regardless of their body size (Fig. 1). Bakker clearly appreciated the significance of size, since he claimed (1987: 48) that "dinosaurs had cruising speeds as high or higher than that [sic] of mammals with comparable body size". Yet, even so, his findings were presented (1986a,b, 1987) only in terms of absolute speed. Those findings might be expressed more appropriately, and more meaningfully, in terms of dimensionless speed ($u[gh]^{-0.5}$), Froude number (u^2/gh) or relative stride length (SL/h) - where u is velocity (m/s) and g is the gravitational constant (Alexander 1976, 1977, 1991; Thulborn and Wade 1984). Any of these various measures will permit more equitable comparisons of locomotor performance among animals of different size. Here it is most convenient to make comparisons in terms of relative stride length (SL/h), because estimates of this ratio are commonly cited in studies of dinosaur tracks.

In terms of relative stride length, Bakker's findings (1987) appear to be entirely consistent with other studies on dinosaur locomotion (e.g. Thulborn 1982, 1984). For instance, Bakker showed (1987: Fig. 6) that stride length (SL) is roughly equivalent to hindlimb length (h) throughout the bipedal dinosaurs, both ornithomorphs and theropods (Fig. 3); this finding is in fair agreement with the observation that average stride length was equivalent to about $1.3h$ among bipedal dinosaurs in general (Thulborn 1984).

In addition, a definite pattern begins to emerge if one compares estimates of size and stride length for the smallest animals and the largest. For the smallest animals considered by Bakker (Permo-Carboniferous tetrapods), stride length is consistently as great or greater than height at the hip; by contrast, the biggest animals (quadrupedal dinosaurs and elephants) took strides noticeably shorter than their height at the hip (Fig. 4). The changeover from long strides in small animals to progressively shorter strides in bigger animals is also apparent within Bakker's sample of data for theropod dinosaurs alone (Fig. 3). These findings confirm the existence of a negative correlation between relative stride length and body size (Thulborn and Wade 1984: 448), and they underline the need for Bakker's estimates of absolute speed to be scaled or adjusted in accordance with body size.

The real significance of Bakker's findings (1986a, 1987) is most easily appreciated from

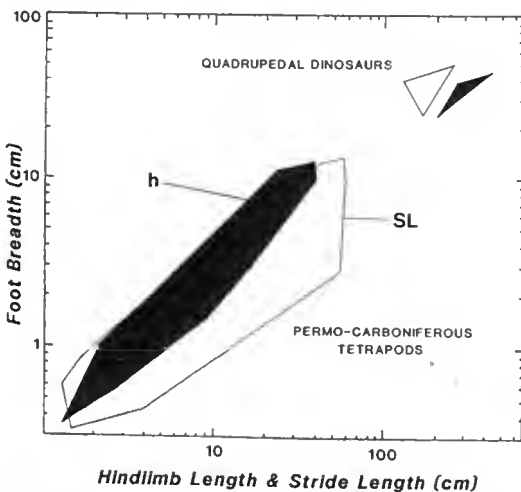


Fig. 4. Relationship of stride length (SL) to hindlimb length (h) in Palaeozoic tetrapods and quadrupedal dinosaurs. Note progressive decrease in relative stride length (ratio SL/h) in bigger animals. Adapted from Bakker (1987: Fig. 6).

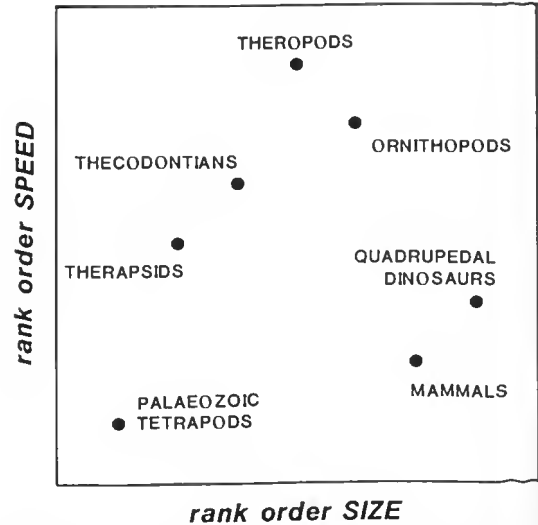


Fig. 5. General relationship of absolute speed (median estimate) to body size (median estimate of h) in dinosaurs and other tetrapods. Derived from data presented by Bakker (1987: Figs 6 and 7).

Fig. 5, where median estimated speed is plotted against median body size. Evidently the smallest and largest animals have the lowest absolute speeds whereas animals of intermediate size (which happen to be dinosaurs) attain the highest absolute speeds. This pattern of relationship between size and speed probably reflects the well-known fact that there is an optimal body size for terrestrial locomotion. In terms of running ability for tetrapods in general, Coombs (1978) considered the optimum to be about 50 kg; for mammals alone, Garland (1983) specified an optimum of 119 kg. The optimal body size probably furnishes an advantageous ratio of muscular power to body mass (proportional to the ratio of cross-sectional area to volume); the power/weight ratio is advantageous in the sense that it can be exploited by means of cursorial adaptations (Coombs 1978). Smaller animals have an even more favourable ratio of power to weight, but they do not attain very high speeds on account of their small absolute size - which probably restricts maximal stride length. At the other extreme, big animals tend to be relatively underpowered, since the power/weight ratio declines rapidly as body mass increases.

In short, Bakker's study of fossil trackways (1986a, 1987) does not support the claim that dinosaurs were warm-blooded. Bakker's estimates of absolute speed may not be sufficiently reliable to demonstrate meaningful similarities or differences; moreover, there is some likelihood that the speeds of dinosaurian track-makers have been consistently overestimated. Even if all Bakker's findings (Fig. 1) were acknowledged to be unquestionably correct, they still would not demonstrate that dinosaurs were warm-blooded; those findings merely demonstrate the well-known fact that there is an optimal body size for terrestrial locomotion (Fig. 5).

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WARKALANIA, A NEW MEIOLANIID TURTLE FROM THE TERTIARY RIVERSLEIGH DEPOSITS OF QUEENSLAND, AUSTRALIA.

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ABSTRACT

Warkalania carinaminor sp. nov., is based on posterior skull elements from the (?) Oligocene - early Miocene Carl Creek Limestone, Paneake Site of Riversleigh Station, northwest Queensland. *Warkalania* is a meiolaniid cryptodire because it has the synapomorphies of the squamosal produced into posteriorly and posterolaterally directed processes and an extensive squamosal-quadratojugal contact beneath the eavum tympani. Within meiolaniids, *Warkalania* is unique in having the squamosal processes formed into low, horizontal ridges, small and roughly similar to each other in size, rather than having one or more of these seale areas extending prominently away from the skull, as in all other meiolaniids.

KEYWORDS: *Warkalania carinaminor* gen et sp. nov., new genus, new species, Meiolaniidae, horned turtle, Oligocene, Miocene, Carl Creek Limestone, Queensland.

INTRODUCTION

Turtles and other vertebrates were discovered in the Carl Creek Limestone at Riversleigh Station in northwestern Queensland by Tedford in 1968. Further work by teams led by M. Archer, S. Hand, and H. Godthelp resulted in the discovery of nearly 100 additional sites spanning in time the Oligocene to Pleistocene, and the recognition of a relatively rich turtle fauna (Gaffney *et al.* 1989). A review of the Riversleigh localities and an introduction to the growing literature on Riversleigh and its fossils can be found in Archer *et al.* (1989). The first turtles described from Riversleigh Tertiary sites were three genera of chelids based on fragmentary material (Gaffney *et al.* 1989). Meiolaniids in the Riversleigh Tertiary were first recognized by A. Ritchie (pers. comm.) on the basis of tail ring fragments (see below) in 1987. One of us (ESG) found more meiolaniid fragments in Riversleigh collections in 1989 but it was not until Neville Pledge's discovery of a partial skull, that diagnosable meiolaniid material was recovered from Riversleigh Tertiary deposits. This material represents a new genus of meiolaniid (Fig. 1) and is described here.

The reader should refer to Figures 5-7 and Gaffney (1983) for scale terminology of meiolaniid skulls. Descriptions of the skull of *Meiolania platyceps* Owen can be found in Gaffney (1983). Institutional prefixes to catalogue numbers are as follows: AMF, Australian Museum, Sydney; BMNH, British Museum of Natural History, London; QMF, Queensland Museum, Brisbane.

SYSTEMATICS

Order Testudines
Megaorder Cryptodira
Capaxorder Selmaeryptodira
Hyperorder Daiocryptodira
Parvorder Eueryptodira
Suborder Meiolanoidea
Family Meiolaniidae

Type Genus. *Meiolania* Owen, 1886b.

Known Distribution. Pre-Oligocene ("Cretaceous or Eocene", Simpson 1938) of Argentina, Miocene to Pleistocene of Australia, Pleistocene (or younger) of Lord Howe Island, Walpole Island, and New Caledonia.

Previous work. Gaffney (1983) relates the long and complex history of work on the meiolaniids, beginning with Owen's (1881) identification of the first known meiolaniid as a giant horned lizard. Recent papers are Megirian (1989, 1992), Gaffney and McNamara (1990), and Gaffney (1992).

Revised Diagnosis. Eueryptodiran turtles with the squamosal and supraoccipital uniquely produced into posteriorly and posterolaterally directed processes, three scale areas (A,B,C in Gaffney, 1983) being most prominent; temporal emargination completely absent and related to extensive squamosal-supraoccipital contact and relatively small parietal; supraoccipital with large horizontal plate on skull roof; nasal bones unusually large; sinus formed from nasal and maxilla lateral to, and communicating with, apertura narium externa (determinable only in *Meiolania platyceps* and *Ninjemys oweni*); broad squamosal-quadratojugal contact ventral to completely enclosed incisura columellae auris which contains both stapes and eustachian tube; medial plate of pterygoid separated ventrally from basisphenoid to form intrapterygoid slit; palate concave ventrally with vomerine ridge on midline; well developed labial and lingual ridges not greatly expanded; tail partially or completely

surrounded by dermal ossifications; tail club formed by fusion of terminal caudal vertebrae and osteoderms (at least in *Ninjemys oweni* and *Meiolania platyceps*); cervical formula is $(2((3((4)5)6)7)8)$; free cervical ribs present on cervicals 2-6; caudal vertebrae opisthoecelus with well developed haemal spines; plastron lacking axillary and inguinal buttresses; no mesoplastra present; plastron with fontanelles on midline; first thoracic of the carapace facing anteriorly, and first thoracic rib long and reaching plastron laterally; posterior peripherals scalloped; adults usually with cranial and shell sutures fused; carpal and tarsal formula 2-2-2-2-2.

It should be noted that most of these characters are known only in *Meiolania platyceps* (Gaffney, 1983, 1985).

Discussion. The higher phylogenetic relationships of meiolaniids and the higher classification of cryptodires is discussed in Gaffney (1983), Gaffney and Meylan (1988), Gaffney *et al.* (1991), and Gaffney (1992).

Warkalania gen. nov.

Type Species. *Warkalania carinaminor* sp. nov.

Known Distribution. Mid Tertiary, north-west Queensland.

Diagnosis. Meiolaniid with B scale area (encompassing the largest horn in other meiolaniids), delimiting a low, horizontal ridge, not a recurved horn as in *Meiolania* nor a large lateral projection as in *Niolania* (including *Crossocheilus*) and *Ninjemys oweni*; A, B, and C scales formed into low, horizontal ridges, small and roughly similar in size to each other, in contrast to all other meiolaniids; A scale area not as protuberant as in *Niolania* and *Ninjemys oweni* but more protuberant than in *Meiolania*; C scale area a low ridge, higher than in *Meiolania* but lower than in the other meiolaniids; X scale small, and D scales in midline contact as in *Ninjemys oweni* and *Meiolania*.

Etymology. *Warka*, Queensland aboriginal for turtle; *lania*, in reference to the usual endings for meiolaniids (*Lanius* is Latin for "butcher" but Owen (1886b) gave no indication of an etymology when he erected *Meiolania*).

Warkalania carinaminor sp. nov.

Type material. HOLOTYPE QMF 22649, a right squamosal (Fig. 2). This fragment includes the posterior margin of the cavum tympani, all of

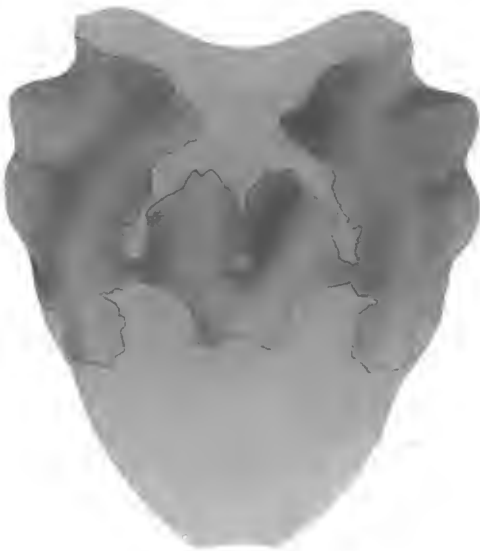


Fig 1. *Warkalania carinaminor* gen. et sp. nov. Dorsal view of skull based on QMF 22649, 22650, and 22651, partially restored by transferring side to side. See Figure 5 for scale labels.

scale C, most of scale K, and parts of scales B,H, and D. It is likely, but not definitely demonstrable, that QMF 22650-22653 and 22682 belong to the same individual.

Type locality. Paneake Site, Riversleigh Station, northwest Queensland, see Archer *et al.* (1989).

Horizon. “? late Oligocene to early Mioene” Archer *et al.* (1989:64).

Other material. Referred specimens, all from the type locality: QMF 22650, left squamosal with complete scale areas A,B, and C plus part of scale D (Fig. 3). A fragment of the posterior wall of the antrum postoticum is preserved internally; QMF 22651, central section of right and left parietals, bearing on its dorsal surface scale X and surrounding portions of scales G and D; QMF 22652, nearly complete right quadrate; QMF 22653, right exoccipital and basioccipital lacking ventral surface; QMF 22682, part of right supraoccipital containing semicircular canals, small portions of prootic and opisthotic; QMF 22654, left squamosal with scale areas B and C complete portions of scale areas A and K (Fig. 4).

Discussion. An important question to be dealt with in the proposal of *Warkalania* as a new genus of meiolaniid, is: do the seven skull fragments actually belong to one species or one specimen? It is apparent that at least two individuals are present because QMF 22650 and

22654 consist of the same bone elements. The remaining fragments, QMF 22649, 22650, 22651, 22652, 22653 and 22682, come very close to actual contact, show no overlap, and can be restored as a reasonable skull from one individual. However, the type specimen chosen, QMF 22649, has enough diagnostic characters so that it can stand alone as a new taxon of meiolaniid, even if the composite reconstruction is in error due to the mixing of more than one individual and more than one species. The holotype QMF 22649, shows the large squamosal, enclosed incisura columellae auris, and development of protuberances identifiable as B and C horns, diagnostic of Meiolaniidae. But the B and C horns of QMF 22649 differ significantly from all other meiolaniids. The C horn is cone shaped (or flat in *Meiolania*) in all other meiolaniids, but in *Warkalania* it is a horizontal ridge directed anteroposteriorly. The B scale of QMF 22649 is also a flattened ridge in strong contrast to the cow-like, recurved B horn core synapomorphic for *Meiolania*. The B horn cores of *Ninjemyx oweni* and *Niolania* are much larger, laterally directed spines, rather than the relatively low, horizontal ridge of *Warkalania*.

The other cranial fragments identified here as belonging to *Warkalania* allow the diagnosis to be extended to the X scale area, the A and D scales, and the posterior parts of the braincase.

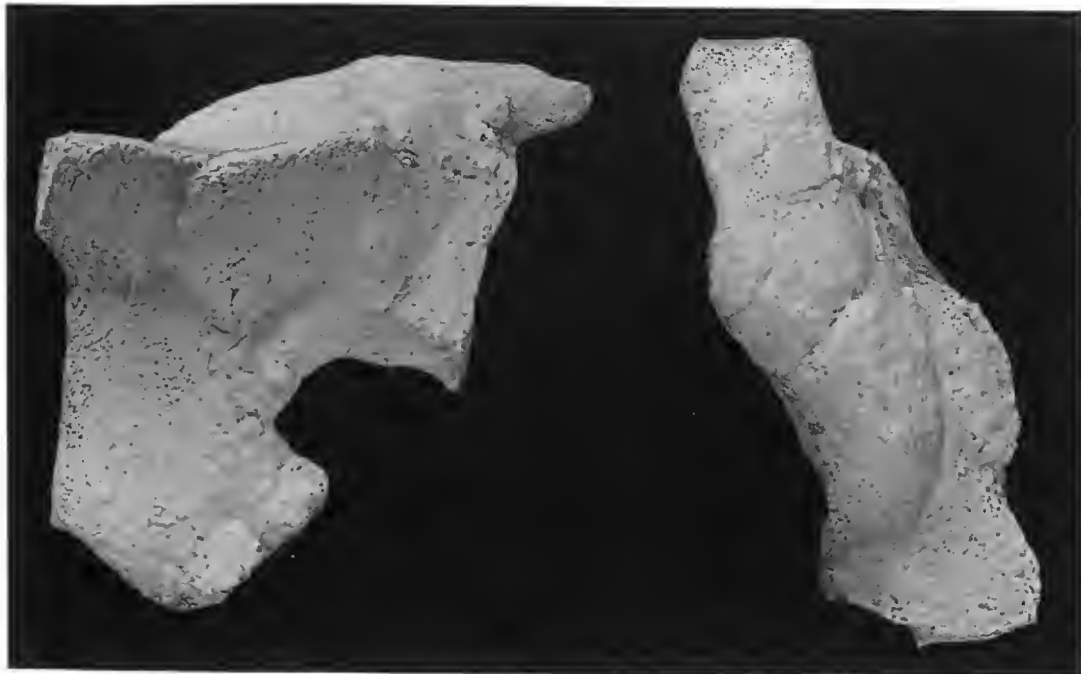


Fig 2. *Warkalania carinaminor* gen. et sp. nov. QMF 22649, type specimen, right squamosal. Left, lateral view; Right, dorsal view.

Diagnosis. Same as for genus.

Description. Because there are no bone sutures preserved in the *Warkalania* material, the description uses the scute areas as homologous entities that are hypothesized as suitable for comparisons. The scute terms and the order is from Gaffney (1983).

The areas preserved in *Warkalania* only include the posterior parts of the skull. The overall proportions and size of the *Warkalania* specimens are roughly the same as *Meiolania platyceps* (Figs 5,6). In most *Meiolania platyceps* skulls the scute areas are delimited by raised ridges, while in *Ninjemyx oweni* and *Niolania* the scales

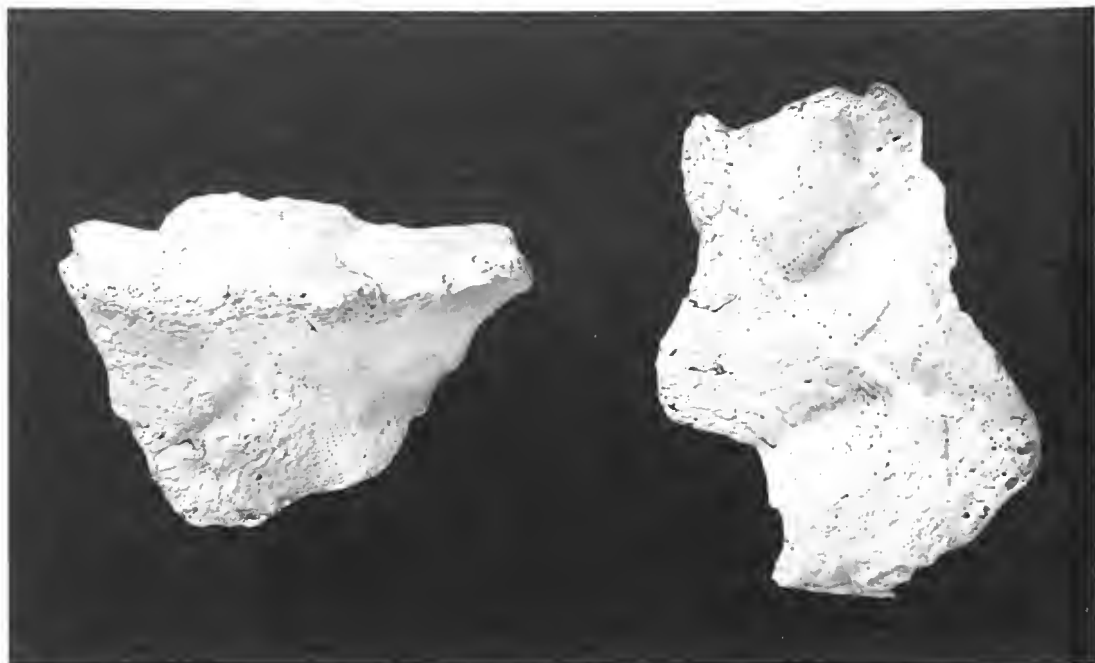


Fig 3. *Warkalania carinaminor* gen. et sp. nov. QMF 22650, left squamosal. **Left**, lateral view; **Right**, dorsal view.



Fig. 4. *Warkalania carinaminor* gen. et sp. nov. QMF 22654, left squamosal. **Left**, lateral view; **Right**, dorsal view.

are bordered by shallow grooves. *Warkalanía* has grooves rather than ridges and thus differs from *Meiolania platyceps*, and resembles *Ninjemys oweni* and *Niolamia* in this feature.

The midline area of the skull in *Warkalanía* is preserved in QMF 22651, a fragment that consists of scale X and surrounding portions of scales G and D. It probably represents the anterior part of both parietals and the posterior part of both frontals. On its dorsal surface there is a clear, oblong scale area in the midline, scale X, with a small, cone-shaped projection just left of the midline. Although not as well defined as in most *Meiolania platyceps* specimens, scale X in *Warkalanía* is similar in size and shape to the Lord Howe species. The small cone is also present in most *Meiolania*, but smaller. The dorsal surface is somewhat rugose in QMF 22651, and there are vague grooves that could be the sulci separating scales G and D from each other. However, if they are present, they are poorly differentiated from other surface irregularities.

In *Ninjemys oweni*, the X scale area is not well preserved, but it is smaller than in *Niolamia* and may be much as in *Meiolania platyceps*. The D scales of *Warkalanía* and *Meiolania platyceps* meet in the midline. In *Niolamia* they are separated by a large X scale. In *Ninjemys oweni* the X scale margins are not clear but the X scale area is definitely not as large as in *Niolamia*, and the D scales probably do meet in the midline in *Ninjemys oweni*.

The ventral surface of QMF 22651 preserves the dorsalmost portion of the cavum cranii. Most of this region is formed by the parietal but a small part of the anterior extension of the supraoccipital is preserved on the midline. The area of the cavum cranii preserved includes the space usually filled in life by the cartilaginous remnant of the synotic tectum (Gaffney 1979). This area is preserved in a number of specimens of *Meiolania platyceps* and in *Ninjemys oweni* but not in *Niolamia*. Although this region is similar in all turtles, there are differences between *Ninjemys oweni* and *Meiolania platyceps*. Unfortunately, not enough is preserved in QMF 22651 to determine to which one it is most similar. The processus inferior parietalis is broken on both sides, but anterolaterally on the outside of each process, is a concavity also seen in *Meiolania platyceps* but not in *Ninjemys oweni*. This concavity is apparently involved in the attachment area of the M. adductor mandibulae pseudotemporalis. The broken edge of the crista supraoccipitalis is preserved in QMF 22651. To

the extent that it is preserved, it agrees with *Meiolania platyceps*.

The fragment of cranial roof, QMF 22651, taken alone, could not be distinguished from *Meiolania platyceps*, except in the absence of raised scale edges. But even this feature varies in *Meiolania platyceps*; AMF 57984 also lacks raised scale edges.

Scute D is a large, paired scale covering much of the posterior portion of the skull, and consists mostly of parietal and squamosal. Parts of Scute D are preserved in QMF 22649, 22650, 22651 and 22654. Even when the fragments are combined, the D scale area is not completely preserved in *Warkalanía*. The D scale area is best preserved on the left posterolateral portion of QMF 22651 and the left anteromedial portion of QMF 22650. The two areas do not have a good contact but, when restored using QMF 22652 and 22653 (braincase elements) for control of the skull width, only a small amount of bone appears to be missing between the two cranial roof sections. Posteriorly and laterally, the D scale lies against the A, B, and C scales, as in other meiolaniids. An anterior sulcus with scale H is not discernible in QMF 22649, which has enough bone preserved to expect the presence of the sulcus. It is likely, however, that poor preservation is the cause of the absence of the sulcus, rather than the actual absence of this sulcus. The posteromedial limits of the D scale are not preserved on any of the fragments. The region of the D scale is a distinctive convexity in both *Ninjemys oweni* and *Niolamia*. *Warkalanía*, however, agrees with *Meiolania* in having the D scale area relatively low.

The three scale areas, A, B, and C, are the most useful skull regions within meiolaniids for taxonomic comparisons. Fortunately, nearly all of these scale areas are preserved in *Warkalanía*. Scute C is a paired scale area on the posterolateral part of the skull, and is formed mostly by the squamosal bone. In QMF 22649, 22650, and 22654 are preserved significant parts of the C scale area. In these specimens the C scale forms a laterally projecting ridge that is roughly horizontal but with a slight anterodorsal trend. This ridge projects laterally to a lesser extent than either of the other scale areas, A and B. In QMF 22649 and 22650, the C scale has a more acute edge than in QMF 22654 but the entire scale area projects laterally to a greater extent in QMF 22654. In *Meiolania platyceps*, *Ninjemys oweni*, and *Niolamia* the C scale is more rounded and cone-shaped than in *Warkalanía*. *Meiolania*

platyceps varies from nearly flat in AMF 43183 to a well developed cone in AMF 57984, but it is never a horizontal ridge as in *Warkalania*.

The B scale area is preserved completely in QMF 22650 and QMF 22654, and in QMF 22649 the anterior half is preserved. The B scale is larger and projects more than the A scale, and it is flattened in the same plane as the A scale. In QMF 22654 the B scale is thicker and has a blunter lateral edge than in QMF 22649 and 22650. The most striking differences in skull morphology of meiolaniids can be found in the shapes of scale B. In *Ninjemyss oweni* and *Niolania* the B scale areas are very large, laterally projecting processes that extend laterally beyond the rest of the skull. In *Meiolania platyceps* the B scale also forms a projection but in this case it is the cow-like horn core distinctive of this genus. *Warkalania*, with its relatively small B scale area, forms a projection that is much less extensive than in *Ninjemyss oweni* or *Niolania*. The B horn core of some individuals of *Meiolania*

platyceps (e.g. AMF 43183, and AMF 18368) approaches the size of the B scale in *Warkalania*, but in none of the *Meiolania platyceps* specimens is the B scale as small as in *Warkalania*. *Meiolania platyceps* also has a B horn core that is conical, usually recurved, and not flattened in any plane. In both *Niolania* and *Ninjemyss oweni* the B horn is flattened in the horizontal plane as in *Warkalania* but not to the degree seen in *Warkalania*.

The A scale area lies at the back of the skull in meiolaniids and in *Meiolania platyceps* is formed mostly by the squamosal, with a smaller contribution from the supraoccipital. The A scale area in *Warkalania* is preserved in QMF 22650 and QMF 22654 but it is incomplete. Both specimens lack the posteromedial parts of the scale area that would allow the complete limits to be seen. We have restored the A scale area by assuming that the tympanic opening in *Warkalania* parallels the midline as in all other meiolaniids (and almost all other turtles) and filling in the missing

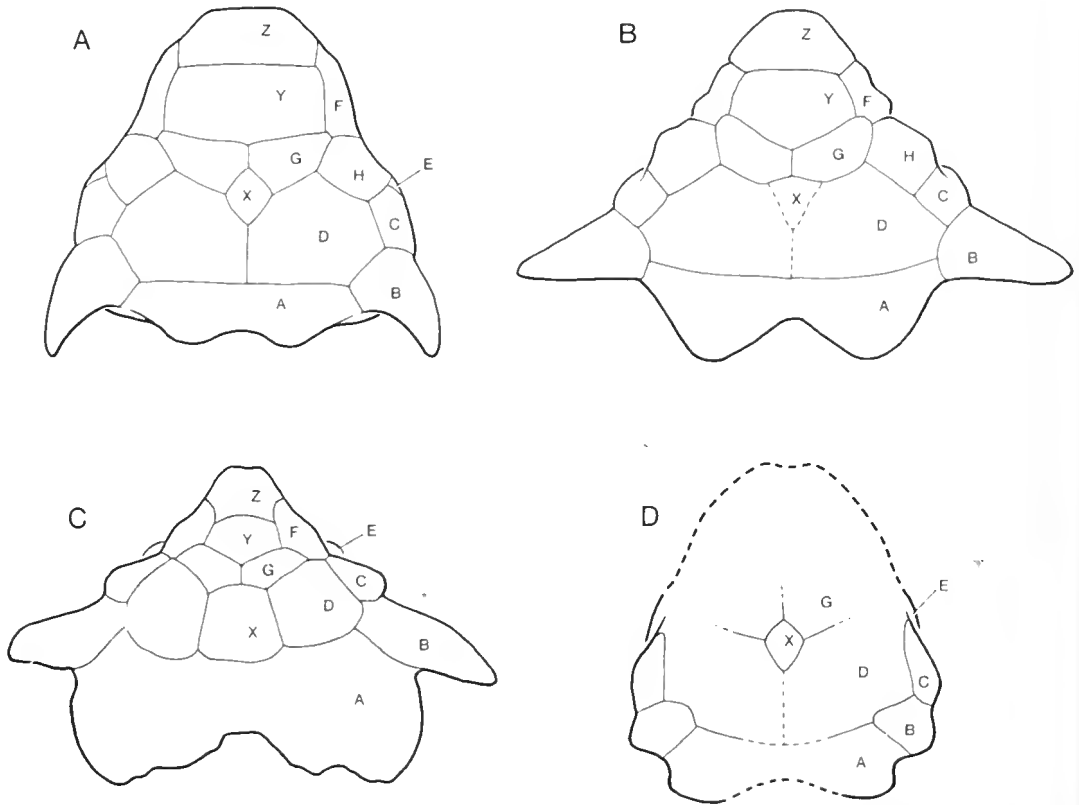


Fig 5. Meiolaniid skulls in dorsal view. **A**, *Meiolania platyceps* (after Gaffney 1983); **B**, *Ninjemyss oweni*, (after Owen 1881, and BMNH R391); **C**, *Niolania argentina* (after Woodward, 1901 and east); **D**, *Warkalania carinaminor* gen. et sp. nov. outline from *Meiolania platyceps*. Scale terminology from Gaffney (1983).

region as conservatively as possible. The A scale of *Warkalania* is very similar in size and shape to the B scale. In QMF 22650 it has an acute edge but in QMF 22654, the edge is blunter. The scale is flattened in a horizontal plane and extends posterolaterally from the main body of the skull. *Warkalania* has an A scale that is somewhat larger than in *Meiolania platyceps*, but it is much smaller than in *Ninjemys oweni* and *Niolamia*. In these latter taxa the A scale is the largest of the A, B, C series and forms a very prominent shelf at the back of the skull. In *Warkalania* the shelf still exists but it is relatively small, while in *Meiolania platyceps* the shelf is absent and the A scale is a flattened process smaller than the B scale horn core.

Portions of the ventral area of the squamosal, consisting mostly of the K scale area, are preserved in QMF 22649, 22650, and 22654. Of these, the most extensive and informative is QMF 22649. This specimen has the dorsal and ventral margins of the cavum tympani opening and a small part of the posterior edge. On the internal surface the attachment area of the pro-

essus articularis of the quadrate can be seen and, above it, the lateral wall of the antrum postoticum. The natural ventral margin of the squamosal is also preserved. It is clear from the specimens that *Warkalania* agrees with *Meiolania*, *Ninjemys oweni*, and *Niolamia* in having a completely closed ineisura eolumellae auris with a considerable section of squamosal below and behind the tympanic opening. Neither *Niolamia* nor *Ninjemys oweni* have the entire limits of the squamosal preserved; only *Ninjemys oweni* and *Meiolania platyceps* have the internal features of the squamosal visible. In *Warkalania* the squamosal (K scale area) posteroventral to the tympanic opening is more extensive than in *Meiolania platyceps*. This appears to be a similarity to *Niolamia*, the extent of the squamosal in *Ninjemys oweni* being indeterminate. The K/J suleus is preserved in QMF 22649 and it is more posterior to its position in *Meiolania platyceps*, but similar to the position in *Ninjemys oweni* in which the J scale extends more posteriorly than in *Meiolania platyceps*. The area is not preserved in *Niolamia*.

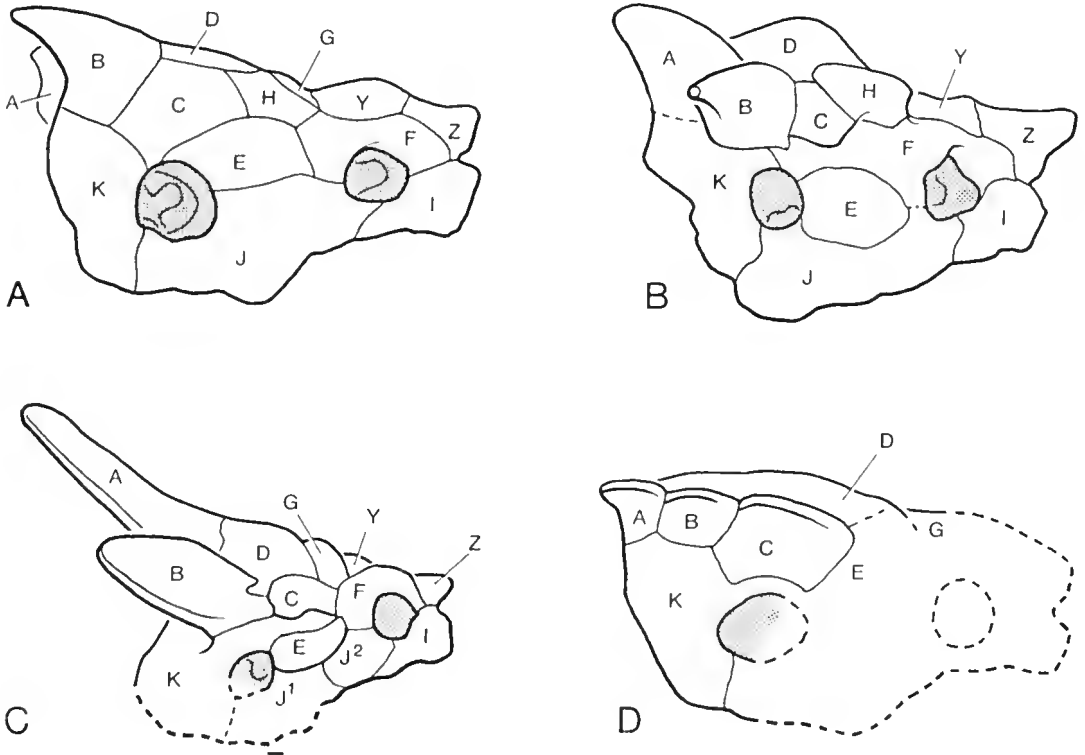


Fig 6. Meiolaniid skulls in right lateral view. Same as in Figure 2.

The three braincase fragments, QMF 22652, 22653, and 22682, all belong to the right side and probably are from the same individual. All three of these pieces very nearly come into contact when restored on the basis of *Meiolania platyceps* and are separated by relatively narrow areas of bone. Nonetheless, they do not have any contacts.

QMF 22682 is the part of the right supraoccipital that contains the semicircular canals, plus some small portions of the prootic and opisthotic. The fragment consists of the area of bone just anterior to the foramen magnum (the margin of that structure is not preserved) and posterior to the foramen nervi trigemini. The posterior margin of the foramen nervi trigemini is preserved. On the lateral surface of this piece of supraoccipital is the shallow groove that would lead to the foramen stapedio-temporale. Everything described so far is quite similar to *Meiolania platyceps* and does not vary a great deal from other generalized cryptodires.

The internal portion of QMF 22682 contains the dorsal impression of the canalis semicircularis horizontalis (see Gaffney 1979: Figs 49, 52, for terminology of the cavum labyrinthicum in turtles and Gaffney 1983: Figs 49-51, for the inner ear in *Meiolania platyceps*) with the ventral region missing. The recessus labyrinthicus prooticus and its connected canalis semicircularis anterior are present. The recessus labyrinthicus supraoccipitalis is intact but only the dorsal part of the canalis semicircularis posterior is present with a fragment of the bony strap defining this structure. The recessus labyrinthicus opisthoticus is missing also. The cavum labyrinthicum as preserved in *Warkalania* agrees with *Meiolania platyceps* except that the canals are smaller than in AMF 57984, presumably a function of the smaller skull in *Warkalania*.

QMF 22682 has two grooves preserved in the region of the dorsal edge of the hiatus acusticus. This opening is usually nearly closed in *Meiolania platyceps* and the edges are broken in QMF 22682. The grooves do not appear to be part of the fossa acustico-facialis but rather may be interpreted as the foramen aquaducti vestibuli and one of the foramen nervi acustici. Both grooves lead directly from the cavum cranii into the cavum labyrinthicum and their contents cannot be definitely determined. QMF 22652 is a right quadrate separated from the more medial part of the otic chamber at roughly the position of the quadrate-opisthotic/pterygoid suture, ex-

posing the canalis stapedio-temporalis and the canalis cavernosus. Laterally it preserves much of the cavum tympani and the incisura columellae auris. Although no sutures are present, the posterior part of the processus paroccipitalis of the opisthotic is preserved.

The medial surface of QMF 22652 shows the canalis stapedio-temporalis and the aditus canalis stapedio-temporalis (see Gaffney 1979: Fig 10) but not the foramen stapedio-temporale itself. The foramen would lie in the area broken off. The supraoccipital fragment, QMF 22682, has the more medial groove leading to the foramen which would lie in the missing contact area between pieces QMF 22682 and QMF 22652. The canalis cavernosus lies below the aditus canalis stapedio-temporalis and its posterior length is preserved in QMF 22652. The anterior part of the canalis and the foramen cavernosum are not preserved. These structures on the medial surface of the quadrate in *Warkalania* agree closely with *Meiolania platyceps*.

The anterior surface of the quadrate, probably with some of the prootic attached, bears the processus trochlearis oticum. The processus in *Warkalania* is slightly thicker than in *Meiolania platyceps*. The processus is not determinable in *Ninjemys oweni* or *Niolania*.

The incisura columellae auris of *Warkalania* is closely comparable to the incisura in *Meiolania platyceps*. The stapes and eustachian tube are contained within the elongated incisura that is closed posteriorly, probably by the squamosal. In QMF 22652 the incisura is incomplete posteroventrally but it was very probably closed as in *Meiolania*. The entire shape of the incisura is preserved only in *Meiolania platyceps* where there is some variability. The incisura of *Warkalania* is nearly identical to *Meiolania platyceps* except for the degree of development of the lobe of bone supporting the stapes about midway along the length of the incisura (Gaffney 1983: Fig. 45). In *Meiolania platyceps* this bony lobe is larger and more definitive than in *Warkalania*.

As in *Meiolania platyceps*, the cavum tympani of *Warkalania* is a large oblong spheroid, without a distinct antrum postoticum or preeolumellar fossa. The cavum tympani in *Warkalania*, however, is not as deep medially as in *Meiolania platyceps*. If the dorsomedial limit of the incisura columellae auris is used as a landmark when comparing both taxa, it is particularly apparent that the cavum extends medi-

ally to a greater degree in *Meiolania platyceps* than in *Warkalania*. Unfortunately, this area is not well enough preserved in other meiolaniid taxa for rigorous comparisons.

QMF 22653 consists of most of the basioccipital plus the right exoccipital. As in all the other *Warkalania* fragments, sutures are not distinguishable. The condylus basioccipitalis of *Warkalania* is similar in shape and proportions to *Meiolania platyceps*, the neck is relatively short and stout in both taxa, in contrast to most other turtles. The articular surface of the condylus is slightly concave in *Meiolania platyceps* and slightly convex in *Warkalania*. The degree to which the condylus occipitalis is made up of basioccipital versus exoccipitals is not determinable in *Warkalania*. The ventral surface of the basioccipital is broken off.

The foramen magnum of *Warkalania* slopes anterodorsally as in *Meiolania platyceps*, a relatively unusual chelonian condition but indeterminate in the other meiolaniids. There are two pairs of foramina nervi hypoglossi, one pair penetrating each exoccipital. In some *Meiolania platyceps* a very small, third foramen nervi hypoglossi is present (Gaffney 1983) but most specimens have two prominent foramina on each side as in *Warkalania*. The area of the exoccipital between the foramen magnum and the medial edge of the foramen jugulare posterius contains the two hypoglossal foramina, and in *Warkalania* this forms a relatively flat surface roughly parallel to a transverse plane. Both posterior foramina nervi hypoglossi open at an acute angle to this surface. In *Meiolania platyceps* this area between foramen magnum and foramen jugulare posterius is more curved, so that the more posterior of the foramina nervi hypoglossi opens at nearly right angles to the bone surface. In the absence of the rest of the cavum acustico-jugulare and fenestra postotica in *Warkalania*, and the absence of comparable regions in the other meiolaniids, the significance of this difference cannot as yet be determined.

In QMF 22653 the anterior and posterior openings of the foramina nervi hypoglossi can be seen on the right side, and on the left side some of the internal parts of the canals for these nerves can be seen in the broken surface. The anterior and lateral margins of QMF 22653 are mostly broken edges but the posterior margin of the foramen jugulare anterius and the posterior wall of the recessus scalae tympani (*vide* Gaffney, 1979) are identifiable.

Etymology. *Carina*, ridge, and *minor*, small, in reference to this species having scale areas A,B, and C as small ridges, a condition unique among meiolaniids.

Relationships of *Warkalania*. *Warkalania* is clearly a meiolaniid. It possesses two of the three synapomorphies proposed for the family by Gaffney (1983) and Gaffney and Meylan (1988):

1. Squamosal and supraoccipital produced into large posteriorly and posterolaterally directed processes that extend clear of skull.
2. Broad squamosal-quadratojugal contact ventral to quadrate.

The third character, the intrapterygoid slit, is indeterminate in *Warkalania*.

Relationships within the Meiolaniidae have only been briefly referred to by Gaffney and Meylan (1988:181 and Figs 5,8). They grouped *Ninjemys oweni* (now named *Ninjemys owni*, Gaffney 1992) and *Meiolania platyceps* as the sister group to *Niolania* on the basis of A scute area relatively small in comparison to the A scute area in *Niolania*. However, the squamosal-supraoccipital scale characters cannot be readily polarized by reference to a cryptodiran outgroup because the very presence of these elements is a meiolaniid synapomorphy unique to this group. The entire polarizing of the scales in meiolaniids rests on the argument that *Niolania* is the sister group of all other meiolaniids. This argument is based on a character that can be polarized by outgroup comparison, the structure of the intrapterygoid slit. Gaffney (1983:431-435, Fig. 60) argued that "*Crossochelys*" (Simpson 1938, congeneric with *Niolania*) has an intrapterygoid slit that is primitive with respect to the intrapterygoid slit of *Meiolania platyceps*. This is only one character, but, at present, it is the only character with any degree of complexity that can be used to resolve the polarity problem within the meiolaniids. It is then possible to hypothesize *Niolania* as the sister taxon to other meiolaniids and to use this hypothesis to resolve the various squamosal scale characters. In addition to the inherent weaknesses of this character, it should be noted that the intrapterygoid slit character is determinable only in *Niolania* (= "*Crossochelys*") and *Meiolania platyceps*, the region is absent in *Ninjemys oweni*, *Warkalania*, and other presumed species of *Meiolania*. Nonetheless, it seems reasonable to adopt the idea of *Niolania* as the sister taxon to all other meiolaniids (Fig. 7) as a working hypothesis and accept the limitations.

The genus *Meiolania* can be restricted to just those taxa with cylindrical, recurved, cow-like B horns, following Gaffney (1983) and Megirian (1989, 1992). The species *oweni* named by Woodward (1901) and placed in *Meiolania* by him should be removed to its own genus, *Ninjemys*, characterized by small, cone shaped C scales, laterally projecting B horns, and A scales intermediate in size between *Niolamia* and *Meiolania* (see also Table 1). Given these taxa and *Niolania* being a senior synonym of *Crossochelys*, there are three generic level taxa of meiolaniids to compare with *Warkalania* (Table 1).

The small size of the B scales is unique to *Warkalania* but the small size of the A scales may be interpreted as a synapomorphy in common with *Meiolania* and not found in *Ninjemys oweni* and *Niolania*. The absence of a laterally projecting B scale, found in *Ninjemys oweni* and *Niolania*, and presumably a primitive meiolaniid feature, could also be argued as a synapomorphy uniting *Meiolania* and *Warkalania*. However, the B scales of *Meiolania* and *Warkalania* are very different from each other. A better character is the low D scale of *Warkalania* and *Meiolania*, produced into a raised tubercle in *Ninjemys oweni* and *Niolania*. This analysis of the few characters available at present is reflected in the cladogram in Figure 7.

Other meiolaniid specimens from Riversleigh sites. *Skull fragment.* QMF 22655 appears to be the left A scale area of a species very similar to *Meiolania platyceps*. The specimen is unfortunately very limited in useful features, and a break in the middle of the scale area makes other interpretations possible. As preserved, the fragment is a triangular piece of bone with the apex divided by breakage. It looks as if the broken area was originally filled with bone forming a single, large projection. However, the presence in the Miocene of northern Australia of

at least two meiolaniid taxa makes a less likely alternative possible, namely that this is a B plus C scale area with the gutter between the two represented by the broken area. However, on the dorsal surface there is no sign of a trough or depression as in *Warkalania*, and, most importantly, on the internal surface there is one continuous sheet of finished bone with no indications of a depression for each scale area as in *Warkalania*. QMF 22655 does differ from *Meiolania platyceps* in having more acute posterior edges, which are rounded in *Meiolania platyceps*. The A horn of the Bullock Creek *Meiolania brevicollis* (Megirian 1989, 1992) is lower than in either *Meiolania platyceps* or QMF 22655 and does not have acute edges either. At present, however, the best interpretation of this specimen is that of *Meiolania* in the strict sense, species indet.

Lower jaws. A lower jaw of a meiolaniid from Riversleigh is QMF 22656 (Camel Sputum Site). The specimen consists of most of the fused dentaries, the right side being more broken posteriorly. The jaws are very deep, much deeper than any chelid, but relatively narrow. In addition to *Meiolania platyceps* (Gaffney, 1983), partial lower jaws are known for *Niolania* (Woodward 1901) and for an unnamed meiolaniid known from very fragmentary material from Gulgong, NSW (Mining Museum of Sydney 13898). All the jaws are relatively deep, have fused mandibular symphyses, and parallel labial and lingual ridges separated by a trough. In *Niolania* and the Gulgong fragment, the ridges are low and the trough shallow (probably exaggerated by breakage) and there is no symphyseal or median cusp. In *Meiolania platyceps* and QMF 22656, the ridges are sharp and well defined and a median cusp is present (Gaffney 1983:449). The lingual (inner) ridge is distinctly higher than the labial (outer) ridge in *Meiolania*

Table 1. Comparison of the cranial morphology meiolaniid genera.

	<i>Warkalania</i>	<i>Meiolania</i>	<i>Ninjemys oweni</i>	<i>Niolania</i>
D scales meet in midline	yes	yes	probably intermediate	no
X scale large	no	no	high	yes
D scale	low	low	yes	high
A, B, and C scales forming a continuous shelf	yes	no	yes	yes
C scale cone-shaped	no	yes (when present)	yes	yes
C scale a horizontal ridge	yes	no	no	no
B scale projecting laterally	no	no	yes	yes
B scale flattened	yes	no	yes	yes
A scale very large and forming shelf at back of skull	no	no	yes	yes
Y scale relatively large	indet	yes	yes	no

platyceps and QMF 22656 in contrast to the ridges being even in *Niolamia* and the Gulgong fragment. The Riversleigh jaws, however, do differ significantly from *Meiolania platyceps*. The lingual ridge in *Meiolania platyceps* is accompanied by an equally well developed accessory ridge, absent in QMF 22656. This accessory ridge (Gaffney 1983:Fig 62) is matched by an accessory ridge in the skull (Gaffney 1983: Fig. 32), also present in *Ninjemys oweni* and the Bullock Creek *Meiolania s brevicollis* (both of which lack lower jaws but presumably would have accessory ridges on them). It is unlikely that QMF 22656 belongs to the genus *Meiolania*. It is possible that it belongs to *Warkalania*, although there is no real evidence for this.

Caudal vertebra. QMF 22657 (Camel Sputum Site) is a caudal vertebra split horizontally through

the centrum with the lower part lost. The preserved section, consisting of neural spine, zygapophyses, and dorsal part of the centrum, is very similar to described caudals of *Meiolania platyceps*. QMF 22657 is similar to AMF 18715, figured in Gaffney (1985: Fig. 15C). The neural spine is a bit shorter and more like AMF 57984 (Gaffney 1985: Fig. 15B) which is a more anterior caudal vertebra.

Tail Rings. Three meiolaniid tail ring pieces have been recovered from Riversleigh sites. Despite the relatively large number of specimens of meiolaniids found on Lord Howe Island, an articulated caudal series of vertebrae or dermal ossifications is still unknown for any meiolaniid. It is possible to determine roughly relative positions of tail rings and to categorize serial differentiation (Gaffney, 1985:26). Using criteria de-

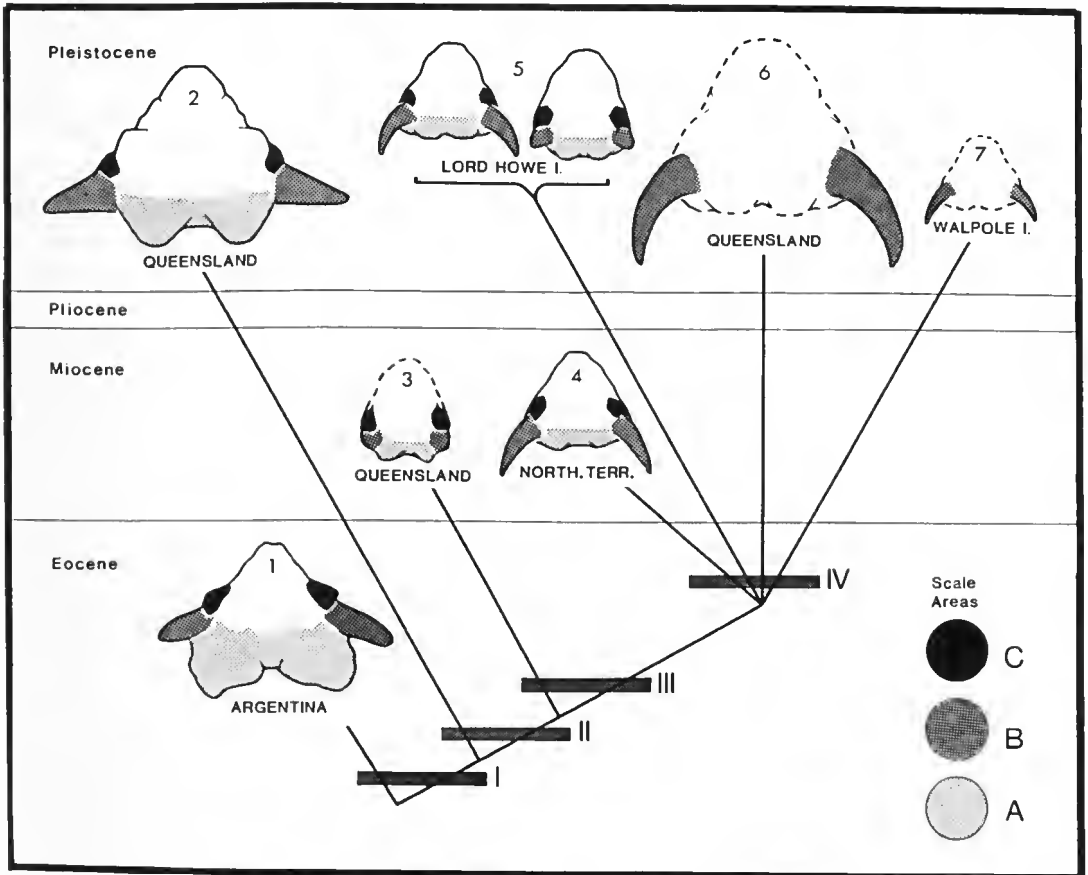


Fig 7. Cladogram of meiolaniid turtles showing skulls in dorsal view with three scale areas (A,B,C) indicated for comparison. Temporal range not to scale. Synapomorphies for the following groups: **I**, Meiolaniidae, see diagnosis; **II**, D scales meet in midline, X scale small; A scale equal to or smaller than B scale; apertura narium externa divided; Y scale relatively large; two accessory ridges on triturating surfaces; **III**, D scale low, A scale relatively small and not forming shelf at back of skull; **IV**, B scale forming recurved horn; A,B, and C scales do not form continuous shelf. The taxa illustrated are: (1) *Niolamia argentina*; (2) *Ninjemys oweni*; (3) *Warkalania carinaminor* gen. et sp. nov.; (4) *Meiolania brevicollis*; (5) *Meiolania platyceps*, showing two extremes of horn variations; (6) *Meiolania* sp., Wyandotte; (7) *Meiolania mackayi*.

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veloped from *Meiolania platyceps*, the most anterior tail ring is QMF 22660 (Camel Sputum Site), with more posterior rings being QMF 22658 (Ringtail Site), and QMF 22659 (Sticky Beak Site). The anterior ring, QMF 22660, has two projections, probably the two on the right side, and is similar to the fragment figured by Owen (1888: Pl. 36, Figs 7-9). The projections in QMF 22660 are more acute than in the figured specimen, but this is probably due to the Riversleigh specimen being from a more posterior position.

A more posterior tail ring is QMF 22658 (the specimen originally identified by A. Ritchie), which is the only Riversleigh tail ring to be essentially complete. It is similar to AMF 50635, figured in Gaffney (1985: Fig. 21), but the projections are lower in QMF 22658. Again, however, this is probably due to QMF 22658 being more anterior than AMF 50635. In *Meiolania platyceps*, it is likely that the paired projections of the tail rings become more pointed posteriorly, and that the anteroposterior width of the ring increases posteriorly but the diameter decreases posteriorly. QMF 22659 is similar to but less complete than QMF 22658. Both seem to be from the posterior part of the tail although QMF 22659 has a smaller diameter and may be more posterior than QMF 22658.

Both *Niolania* (Woodward 1901: Pl 18, Fig. 2) and *Niujemys oweni* (Owen 1881: Pl 65, Figs 1-4) have posterior tail rings preserved. As noted by Gaffney (1985:27), the only apparent systematic difference among the tail rings of meiolaniids is that the posterior rings of *Niolania* and *Niujemys oweni* are complete circles, while in *Meiolania platyceps* the posterior rings are incomplete ventrally. QMF 22658 is well enough preserved to show that it is incomplete ventrally and nearly indistinguishable from *Meiolania platyceps*.

Tibia. A partial right tibia, QMF 22661, (Camel Sputum Site) consists of the distal two thirds of this limb bone. The bone is indistinguishable from *Meiolania platyceps* (see Owen 1888: Pl 36, Fig. 2), except in being worn around the edges. The size is also within the middle range of *Meiolania platyceps* tibiae.

Osteoderm. QMF 22662 (Camel Sputum Site) is an asymmetrical, tear-drop shaped osteoderm, typical of meiolaniids and nearly identical to ones found on Lord Howe Island belonging to *Meiolania platyceps*. A figure of a *Meiolania platyceps* osteoderm that is very similar to this Riversleigh specimen can be found in Owen (1888: Pl. 36, Fig. 10).

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A NEW LARGE MADTSOIID SNAKE FROM THE MIOCENE OF THE NORTHERN TERRITORY.

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ABSTRACT

Eighteen large snake vertebrae from a single locality within the Camfield Beds (middle Miocene) at Bullock Creek, Northern Territory, Australia, represent a single individual of *Yurlunggur camfieldensis* new genus and species. The family Madtsoiidae is correctly referred to the Alethinophidia, but distinguished from all other Alethinophidian taxa by combinations of vertebral and cranial characters most fully represented in *Wonambi naracoortensis*.

KEYWORDS: Serpentes, Alethinophidia, Madtsoiidae, *Yurlunggur camfieldensis*, Miocene, Northern Territory.

INTRODUCTION

Apparently primitive snakes similar to the South American *Madtsoia bai* Simpson, 1933, have been described from Upper Cretaceous to Eocene deposits in Madagascar, South America and Africa (Andrews 1901, 1906, Simpson 1933, Hoffstetter 1961, Albino 1986). The subfamily Madtsoiinae was recognised as an assemblage of primitive boids by Hoffstetter (1961) and raised to family status by McDowell (1987). The group was defined on the basis of vertebral morphology (Hoffstetter 1961, and see below), as diagnostic cranial material had not been described. Fossil snake vertebrae possessing the same distinctive features shared by *Madtsoia* and *Gigantophis* are also known in Australia, from Quaternary and (now) Tertiary deposits. *Wonambi naracoortensis* Smith, 1976 is similar in vertebral morphology to *Madtsoia bai* (Barrie 1990), and is the only madtsoiid yet described from Australia. It was widespread but apparently uncommon in southern and eastern Australia during the Late Pleistocene (Molnar 1982, Barrie 1990, McNamara 1990). The Madtsoiidae is thus completely Gondwanan in known distribution, and has the longest known fossil record of any group of snakes.

A long Australian history for the madtsoiids is implied by the presence of *Wonambi naracoortensis* in the Pleistocene, but Tertiary specimens

have not been described previously. A representative is here reported from Bullock Creek, and remains are also known from the Riversleigh deposits (Oligo-Miocene; Scanlon 1988, Archer *et al.* 1989, Scanlon in prep.) and Murgon (Eocene; Godthelp *et al.* 1992, Scanlon in press.) in Queensland. Vertebrae from the Oligo-Miocene Etadunna Formation of South Australia have been identified as snake (Estes 1984) and could also be madtsoiid, but insufficient descriptions are available.

MATERIALS AND METHODS

The Bullock Creek snake fossils were found and prepared by P. Murray, D. Megirian and K. Roth, scattered among the remains of other vertebrates in a large mass of arenaceous limestone at the "Blast Site" locality of probable middle Miocene age (Woodburne *et al.* 1985). A pythonid, *Morelia antiqua* Smith and Planc, 1985 (emended here from *Morelia antiquus* to agree in gender), has already been described from the Camfield Beds based on a well-preserved dentary. Pythonid vertebrae, presumably representing the same taxon, and an elapid vertebra have also been obtained and are under study. Earlier collections made at the Blast Site locality at Bullock Creek, now held at the Na-

tional Museum of Victoria, included large snake vertebrae which may belong to the same skeleton as the material described here (T.H. Rich, pers. comm.), but they have not yet been examined.

Eighteen madtsoiid vertebrae from this site have been studied, all apparently representing a single large individual described as *Yurlunggur camfieldensis* n. gen. and sp. Its vertebrae are distinguished from those of previously named genera by morphology of articulating surfaces, neural spine and hypapophysis, and the sample of separated vertebrae allows a description of aspects of intracolumnar variation in the precaudal region. Terminology for vertebrae follows Auffenberg (1963) and Hoffstetter and Gase (1969).

Comparisons are based on figures and descriptions in the literature, articulated skeletons of pythonids (*Morelia spilota*, *Liasis olivaceus*, *L. fuscus*, *L. stimsoni*, *Aspidites melanocephalus*, *Python molurus*; Queensland Museum, Australian Museum) and fossil material representing *Wonambi naracoortensis* (South Australian Museum, Australian Museum, and private collection of D.J. Barric) and undescribed madtsoiid species from Riversleigh and Murgon, Queensland (Queensland Museum collections, under study in Sydney).

SYSTEMATICS

Order Squamata Oppel, 1811

Suborder Serpentes Linnaeus, 1758

Infraorder Alethinophidia Nopcsa, 1923

Snakes with anterior dentigerous process of palatine, and trigeminal foramen divided. These characters are unknown for most madtsoiids, but the palatine and prootic have been described in *Wonambi naracoortensis* (Barric 1990), which possesses the apomorphic states of the Alethinophidia.

Family Madtsoiidae Hoffstetter, 1961

Diagnosis. (Modified from Hoffstetter 1961; vertebral features only). Accessory (prezygapophyseal) processes absent; zygapophyses strongly inclined above horizontal; width across paradiapophyses nearly as great or greater than width across prezygapophyses; paracotylar foramina present on most vertebrae; parazygantral foramina present on most vertebrae; neural spine usually step-like in profile, narrow anteriorly, thicker and higher posteriorly.

Yurlunggur n. gen.

Type species. *Yurlunggur camfieldensis* n. sp.

Diagnosis. Large snakes (estimated to exceed 5m in length) differing from other madtsoiid genera in the following combination of vertebral characters: neural spine low but posteriorly overhanging zygantrum; zygapophyses inclined at less than 22° from horizontal, and approximately equal to diapophyses in width; condyle and cotyle moderately depressed and wider than high.

Comparable in size to species of *Madtsoia*, *Gigantophis* and *Wonambi*, and considerably larger than species of *Alamitophis*, *Patagoniophis* and *Rionegrophis*. Neural spine considerably lower and less steep than in species of *Wonambi*, *Madtsoia*, *Alamitophis* and *Rionegrophis*, but somewhat higher (at similar positions in the column) than in *Gigantophis garstini* and much more developed than in *Patagoniophis parvus*. Neural canal trifoliate in section, not triangular as in species of *Rionegrophis* and *Patagoniophis*, and somewhat wider than deep. Condyle and cotyle more oblique and depressed than in *Gigantophis garstini* and zygosphenic relatively higher and narrower. Postzygapophyses aligned more obliquely posteriad than in species of *Madtsoia* and *Wonambi*, and less distinct in dorsal view from interzygapophyseal ridge (thus more similar to species of *Gigantophis* and the smaller Patagonian genera).

Etymology. *Yurlunggur* is the name of the mythic Rainbow Serpent in the language of the Ngolju (Dua and Jiritja) people of north-eastern Arnhem Land, Northern Territory (Mountford 1978). Gender is masculine.

Yurlunggur camfieldensis n. sp.

Type Locality. 'Blast Site', Bullock Creek Local Fauna, Camfield Beds, north central Northern Territory.

Age. Middle Miocene, approx. 12 MYBP (Woodburne *et al.* 1985).

Specific diagnosis. As for the genus, until additional species are described.

Material. HOLOTYPE: A partial skeleton presently represented by 18 precaudal vertebrae and 11 rib fragments, separately registered in the Northern Territory Museum (NTM) vertebrate fossil collection. These are listed below in order from anterior to posterior, as interpreted here (number in brackets), giving the specimen numbers, and a brief description of the condition of the fossils:

- (1) P895-5, missing zygosphene and right prezygapophysis;
- (2) P895-3, right anterior portion sheared off with damage to zygosphene, cotyle and postzygapophysal facet, prezygapophysis absent; hypapophysis broken below condyle;
- (3) P894-5, left parapophysis damaged, otherwise complete;
- (4) P87115-1, complete except for distal part of hypapophysis;
- (5) P8695-128, with damage to right parapophysis, posterior part of hypapophysis and neural arch, missing right postzygapophysis;
- (6) P8695-169, missing zygosphene, left pre- and postzygapophyses, and postero-ventral part of centrum including condyle;
- (7) P87103-23, complete;
- (8) P8695-243, crack through left neural arch, slight damage to left prezygapophysis and diapophysis;
- (9) P8695-244, neural spine damaged, and with a single shear fracture extending from ventral midline to *margo lateralis* so that the left paradiapophysis is missing, and pre- and postzygapophyses, hypapophysis and cotylar rim are incomplete;
- (10) P8695-25, slight breakage to paradiapophyses and right prezygapophysis;
- (11) P8695-245, missing anterolateral corner of left prezygapophysis;
- (12) P8695-246, missing right prezygapophysis, paradiapophysis, part of zygosphene and cotylar rim;
- (13) P8695-127, complete but cracked through right side of cotyle, paradiapophysis and neural arch, slightly distorted;
- (14) P87103-22, right side complete except for breakage to cotylar rim, left side mostly missing (zygosphene and neural canal almost complete);
- (15) P8695-23, left side of zygosphene broken, cotylar rim damaged, vertebra broken across horizontally and rejoined with slight distortion;
- (16) P87103-24, posterior part of neural spine and narrow section of zygantral roof missing;
- (17) P8692-28, postero-ventral part of centrum (from just behind cotyle) sheared away, particularly on right where postzygapophysis and part of paradiapophysis are also missing; crack through left side of neural arch with slight distortion;

(18) P8695-247, complete; neural canal remains filled with matrix.

No cranial or caudal remains have yet been obtained, but some partial ribs have been collected and are held at the NTM: 4 rib-heads (P87108-21, P8792-24, P8792-23, P8695-261) and 7 rib shafts (P8695-260, -262, -263, -264, P87108-17, -18-19(fit together) and -20).

Description. *Body regions.* The 18 vertebrae are of three general types corresponding to anterior, middle and posterior regions of the trunk. Number 1 is from a position close behind the head (as indicated by the possession of processes on the posterior margin of the neural arch, which occur up to the seventh vertebra in the pythons examined), but vertebrae 1 to 10 (Fig. 1, A-C) form a relatively smooth series which increase in overall size while hypapophysis depth reduces, anterior to posterior, as in the anterior region of modern snakes. Number 10 is the largest vertebra in the sample, but larger elements may have occurred in the unrepresented mid-thoracic region. Also in this missing region, the transitions from single to double hypapophysis, and from flat to concave zygosphene would have occurred. Vertebrae 11 to 17 (Fig. 1, D-E) have low hypapophyses which are double, lateral structures at the posterior end of a flattened haemal keel rather than a single median process. These vertebrae also have the zygosphene and zygantrum strongly concave dorsally, a regional feature not seen to the same extent in other snakes. Number 18 (Fig. 1, F) is of similar size to no. 1. It is typical of posterior trunk vertebrae of snakes in being long and wide relative to depth and in having deep grooves separating the haemal keel and cotyle from the *margo ventralis* and parapophysis on each side. In the region represented by no. 18 the zygosphene is once again relatively flat, not "eurlled up" as in 11-17, and the paired hypapophyses are located further from the condyle.

Morphology. The centrum is short and wide, in ventral view approximating an equilateral triangle truncated posteriorly (but relatively longer in no.18). The cotyle is about as wide as the zygosphene in anterior trunk and cloacal regions, but wider than the zygosphene in the intermediate region. The condyle is moderately oblique. The underside of the centrum is slightly to strongly concave on either side of the haemal keel.

The hypapophysis of each anterior vertebra extends from a low ridge immediately below the cotyle, to a deep keel ending just anterior to the

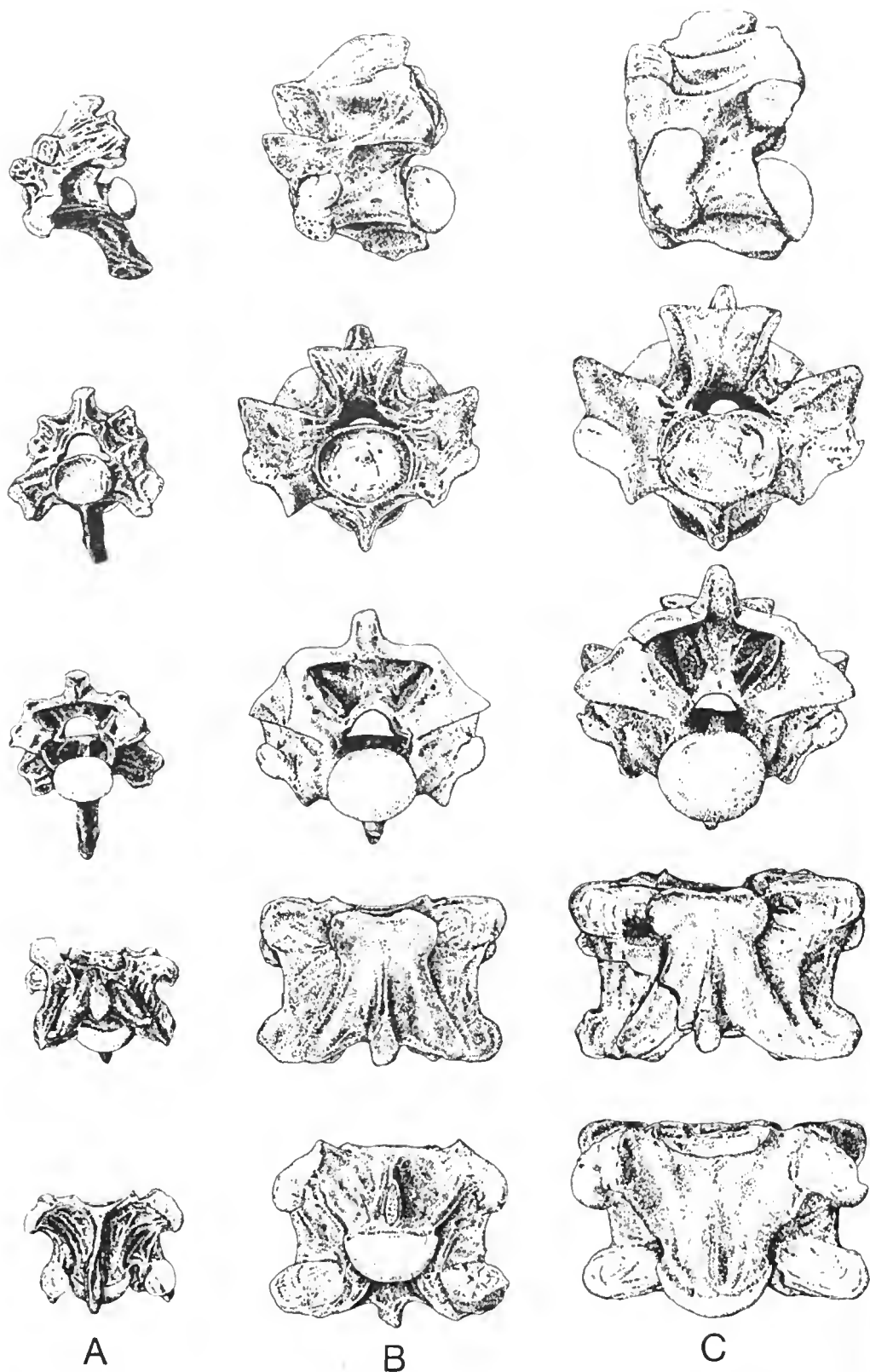
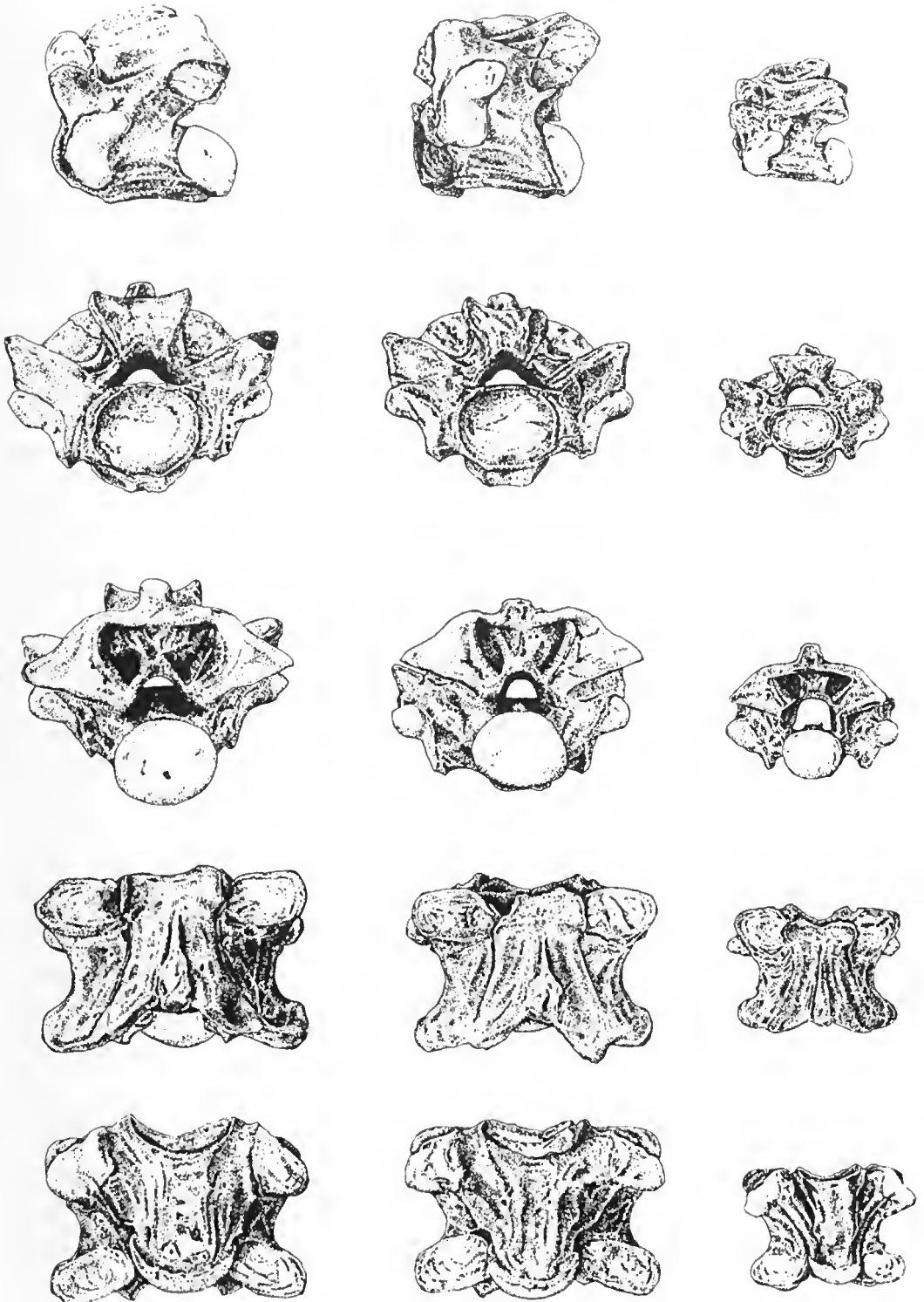


Fig. 1. Vertebrae of holotype *Yurlunggur camfieldensis* in (top to bottom) lateral, anterior, posterior, dorsal and ventral views. A (1), P895-5; B (4), P87115-1; C (8), P8695-243. Scale bar equals 2 cm.



D

E

F

Fig. 1. (cont.): D (11), P8695-245; E (15), P8695-23; F (18), P8695-247. Scale bar equals 2 cm.

condyle. This keel is rounded in section anteriorly (approx. 2/5 of centrum length) and at the deepest, most posterior part (approx. last 1/5), while the middle part is more blade-like. In lateral view, the anterior part is concave ventrally, set off by a more or less distinct step-like inflexion from the straighter middle section (more or less strongly oblique, steepest in no.4), while the posterior part of the ventral margin is convexly rounded and continuous with the near-vertical posterior edge below the condyle (more oblique in 1 and 2). Between anterior and posterior edges of the hypapophysis, the lines of inflexion between the lateral concavity and wedge-like keel form low but distinct longitudinal ridges.

The hypapophyses of more posterior vertebrae are represented by more extensive paired, low parallel ridges extending from the cotylar rim to just anterior to the condyle, defining a flattened, rectangular haemal keel which is somewhat concave ventrally in transverse and longitudinal section. The ridges end posteriorly in dorsoventrally compressed, diverging nipple-like processes extending below (but anterior to) the condylar rim, some of which have a rough, pitted surface and/or conical tips free of the ventral face of the centrum. In the most posterior vertebra, possibly very close to the cloacal region, these processes are in a more anterior position (approx. 2/3 centrum length from cotylar rim). They face directly laterad, are elongated anteroposteriorly, and their surfaces are quite smooth.

The zygapophyses are inclined at 17-21° above the horizontal (steepest in no. 10-14), defining planes which intersect the neural canal near the middle of its height, corresponding to the position of the internal lateral ridges. The articular facets are roughly rectangular through most of the trunk. The long axes of prezygapophyses are nearly directly transverse, while those of postzygapophyses are more oblique (extending posterolaterad) and without the angular distinction from interzygapophyseal ridges seen in species of *Wonambi* and *Madtsoia*. In no. 1 the zygapophyses are narrower, and hence their axes diverge less from the sagittal plane. The anterior edge of the prezygapophyseal facet is slightly concave on anterior vertebrae, becoming straight and then convex posteriorly. In no. 18, all facets are more rounded in outline. Growth rings are clearly visible on all articular facets excluding the condyle and paradiapophyses. Prezygapophyseal (accessory) processes are absent as such, but the surface of the prezygapophyseal buttress is convex and forms a low horizontal

ridge for muscle attachment parallel with, and extending slightly lateral to extremity of facet.

The zygosphenes are thick, mostly deeper than the neural canal (shallower in no. 1, about equal in no. 18), and its facets diverge at 30-34° from the vertical, defining planes which intersect at or below the floor of the neural canal. Zygosphenal facets are roughly semicircular in anterior vertebrae, having a straight leading edge which becomes convex posteriorly. The anterior face of the zygosphenes has a median concavity below, passing smoothly (or with vertical striations, but no transverse ridge) into the roof of the neural canal, between lateral ridges formed by the zygosphenal facets. The upper part of the anterior face is near vertical in most anterior vertebrae, and limited above by a strong transverse ridge, which is weaker at the midline forming a median concavity seen from above, as in species of *Madtsoia*. More posteriorly (no. 11-17) this ridge lies below and behind the upper edge of the lateral facets so that the anterior and dorsal faces of the zygosphenes are strongly concave across the midline. The facets, which in anterior vertebrae are slightly concave laterad near their upper extremities, are in the posterior region strongly convex, and visible from above. In no. 18, the zygosphenes are of similar form to no. 3-10, though much less deep. Number 3 has the zygosphenes concave above, but not as strongly as in the posterior trunk, and the facets face ventrolaterad.

The neural arch and zygantrum closely follow the form of the zygosphenes in their variation along the column; the zygantral roof is of approximately uniform thickness across the width of each vertebra, its posterior edge facing somewhat dorsad medially but vertical or inclined slightly ventrad at the lateral extremities or "shoulders". In no. 1 there are distinct dorsolateral protuberances at these points, increasing leverage for short-span dorsal flexors which attach in this region; these are in a similar position to the 'pterapophyses' occurring in trunk vertebrae of the genera *Palaeophis* and *Pterosphenus* (Palaeopheidae), but they seem more comparable to features of anterior neck vertebrae in pythons. Number 15 also has an asymmetric posterior extension from the same point, which is the only clear case of irregular bone growth in the sample.

The *margolateralis* is smoothly concave, without a sharp angle anterior to the postzygapophysis. The neural spine is low, composed of two portions: a narrow lamina anteriorly, rising from just anterior to the constriction behind the

zygosphene; and a higher columnar part posteriorly, sloping back to overhang the zygantrium, and bearing an irregular expansion (elliptical, triangular or roughly pear-shaped) of its dorsal surface for tendinous attachments. The dorsal edge of laminar portion varies from a nearly straight oblique edge (no. 2 and 4) through leveling off for a short section near its upper extremity (no. 10), to having only a short steep anterior section and much longer shallowly oblique 'step' (no. 11-18).

The paradiapophyses are similar in most respects to species of *Madtsoia* and *Wonambi*, varying somewhat in relative size and position along the column, but in this sample not greatly exceeding the zygapophyses in maximum width (in contrast to those genera).

Paracotylar and parazygantral foramina are present on all vertebrae, as well as subcentral, zygantral and several groups of lateral foramina. Paracotylar, ventrolateral (posterior to diapophysis), midlateral (posterior to zygosphene) and dorsolateral foramina (at base of neural spine, sometimes extending posterolaterally near edge of neural arch) occur as clusters of small apertures, mostly in distinct bowl-like depressions within larger concave areas, and numbering 2-5 (or more numerous where dorsolateral foramina occur over a larger area). Parazygantral and zygantral foramina are larger, and occur individually as deep pits directed anteroventrad and mediad from the posterior surface of the vertebra. There are frequently two or more pairs in each case, the more ventral being largest and most symmetrical in occurrence and position. A single pair of subcentral foramina is present, usually small but one member enlarged in a few cases, and in no. 9 both foramina are on the same side of the midline.

Ribs. The ribs of *Yurlunggur camfieldensis* are similar to those of *Wonambi naracoortensis* (see Barrie 1990) in shape of head and shaft, and presence of only small foramina in the dorsal groove. Both these forms differ from *Madtsoia bai* (Simpson 1933) in the virtual absence of an anterodorsal process adjacent to the head, and thus resemble more typical alethinophidians.

Etymology. The specific epithet refers to the type locality.

DISCUSSION

The type specimen of *Yurlunggur camfieldensis*. The recognition of individuals is

a necessary step in the description of taxa, but may be problematic in the case of disarticulated material. The interpretation that the material described here represents a single individual is supported by two kinds of evidence. First, all the vertebrae and identifiable ribs are from a single quarry site and horizon, whereas madtsoiid remains are unknown from other sites in the area. Thus madtsoiids appear to be a rarely preserved element of the local fauna, and the likelihood of two or more skeletons being intermingled is correspondingly low. Second, vertebral measurements are interpreted as consistent with normal variation dependent on position within the column, where position is indicated by hypapophysis type and proportions (e.g. Hoffstetter & Gasc 1969). Neural canal height, in particular, varies little within the sample, while other linear dimensions differ considerably between mid-trunk and extreme vertebrae. Similar morphoclines are seen in skeletons of extant pythonids (unpublished data).

Estimates of the size of snakes based on vertebral dimensions can only be imprecise because, even if the relative position of the vertebrae within the column can be inferred accurately, the total number cannot be known unless the whole skeleton is found. Simpson (1933) was fortunate enough to have an articulated sequence of 40 vertebrae from which to describe *Madtsoia bai*, but admitted that his estimate of around ten metres could only be a rough guess because of the uncertain vertebra number. Other estimates of the size of madtsoiids have been based on comparison with pythons; Andrews (1901) derived a length estimate of approximately 30 feet (9m) for *Gigantophis garstini* by assuming an equal proportion between the width of the largest vertebra and total length, in the fossil species and a specimen of the modern *Python molurus*. Barrie (1990) made measurements of vertebrae from two partial skeletons of *Wonambi naracoortensis*, and assuming a similar 'shape' (dependence of size and proportions on position in the column) to a modern python *Morelia spilota variegata*, used an analog technique to estimate a total vertebra number of 350 to 400, and arrived at length estimates for the larger *Wonambi* of 5.39 to 6.13m. The present specimen appears to have been considerably larger than the Henschke's Cave *Wonambi*, for the largest vertebrae are about the same size in each case, but the middle region of the body is unrepresented in the Bullock Creek material. It can therefore be suggested conservatively, assuming similar verte-

bral numbers in both madtsoiid genera, and similar body proportions to the python, that this specimen of *Yurlunggur camfieldensis* was greater than 5m in length.

The classification of the Madtsoiidae. The monophyly of the Madtsoiinae, and its systematic position within the Serpentes, have been subject to doubt in the absence of cranial remains. Their retention within Boidae by Hoffstetter (1961), Smith (1976) and Albino (1986), among others, was appropriate given the traditional palaeontological diagnoses in which Boidae was clearly paraphyletic or polyphyletic. Madtsoiid vertebrae possess a number of plesiomorphic character states for alethinophidian snakes. McDowell's (1987) classification of the Madtsoiidae within an explicitly paraphyletic group, the Cholophidia, reflects a view that madtsoiids were "more primitive than *Dinilysia*", but the differences cited in support, such as shape and lateral projection of the paradiapophyses, position and slope of the zygapophyses, and absence of a prezygapophysal process, are not as clear as was supposed (see Rage and Albino 1989).

When comparisons are made with *Dinilysia patagonica* as an outgroup to the Alethinophidia (the vertebrae are described by Hecht 1982, and Rage and Albino 1989), the following plesiomorphic characters of the Madtsoiidae can be noted: paracotylar foramina are present (variable in *Dinilysia*); zygapophyses are inclined well above the horizontal (but less so than in lizards or *Lapparentophis defrennei* Hoffstetter, 1959); the anterior edge of the zygosphenon is indented (lacking a median prominence or transverse ridge); the neural spine consists of a thin anterior lamina and posterior column; the hypapophysis is prominent on anterior vertebrae but reduced or absent in the middle and posterior trunk; the diapophyses are prominent laterally, and in posterior vertebrae they project beyond the prezygapophyses. Taken together, these plesiomorphic characters exclude the madtsoiids from membership of any extant families: indeed, reduction of diapophysis width could be seen as a synapomorphy of the Alethinophidia. However, there remains a considerable phenetic similarity between madtsoiids and some members of the Boidae, which includes forms with relatively plesiomorphic vertebrae and has therefore been very broadly defined in the palaeontological literature (e.g. Hoffstetter 1961).

Several vertebral characters can be regarded as synapomorphies defining the Madtsoiidae:

they possess large and distinct parazygantral foramina on all but rare vertebrae (exceptions noted in *Wonambi* by Smith 1976, and in *Madtsoia* by Albino 1986); posterior trunk vertebrae have laterally paired swellings of the flattened haemal keel, here referred to as paired hypapophyses, at least in *Madtsoia* (Simpson 1933), *Wonambi* (Smith 1976) and *Yurlunggur* n. gen.; and prezygapophysal accessory processes are absent, though they may be represented by a low horizontal ridge ventral and slightly lateral to the facet. Of these, the madtsoiid condition is matched only by the absence of a prezygapophysal process in some Boinae which, if the monophyly of Boidae is accepted, must be convergent.

Thus the Boidae (comprising Boinae and Eryeinae, as in McDowell 1987) is difficult to separate clearly from the Madtsoiidae in terms of easily observed apomorphies of the vertebrae alone (Underwood 1976), although in practice madtsoiid vertebrae are readily identified. Analysis of isolated vertebrae seems unable to resolve the phylogeny of snakes at this level. Evidence from the skull must decide whether madtsoiids are derived among the Boinae (Underwood 1976), "more primitive than *Dinilysia*" (McDowell 1987) or represent a distinct lineage close to the origin of the Alethinophidia.

Barrie (1990) describes cranial material of *Wonambi naracoortensis*, regarded as a probable relative of *Madtsoia* spp. (Smith 1976), and finds characters indicating a position within the Alethinophidia (presence of a palatine dentigerous process and divided trigeminal foramen) but distinct from pythons and boas, and plesiomorphically similar to arochordids and, particularly, to tropidopheids (in palatine morphology, number and relative size of teeth, symmetrical vidian canals and a persistent cerebral foramen). This contrasts with both of the previous phylogenetic hypotheses, and is the basis for the classification adopted in this paper.

The multiplication of genera in the Madtsoiidae might be seen as undesirable, but in such a long-lived and geographically widespread lineage diversity is to be expected. It is useful at this stage to name fossil forms pending better resolution of systematics within the group. The alternative to erecting new genera is to lump together forms as different in vertebral morphology as distinct living families, or which lived on separate continents tens of millions of years apart; or to describe remains without naming them; or to fail to describe them altogether. A thorough

phylogenetic analysis of the included taxa will use evidence from the vertebrae (including intracolumnar variation), ribs, and from jaw and braincase elements, and the evolutionary polarities of characters may be determined from outgroup comparisons with Dinilysiidae and numerous families of alethinophidians. Such a rigorous phylogenetic analysis of the Madtsoiidae is beyond the scope of this paper.

Nevertheless, a number of dichotomies or morphoclines have been indicated in the diagnosis above which are potentially useful for such an analysis, such as: maximum known size, neural spine height and steepness, shape of neural canal (trifoliate except in *Rionegrophis* and *Patagoniophis*, where it is distinctly triangular - but this is possibly a feature of the anterior body region as suggested for palaeopheids by Rage 1983), angle of inclination of zygapophyses, width and depth of zygosphenes, width of diapophyses relative to prezygapophyses, shape and inclination of condyle, inclination of postzygapophyses from the transverse plane, and angulation of interzygapophyseal ridge (*margo lateralis*). *Madtsoia*, *Alamitophis*, *Rionegrophis* and *Wonambi* have a high neural spine, long axis of postzygapophyses transverse, and angulate *margo lateralis*. *Gigantophis* and *Yurlunggur*, in contrast, have a moderate neural spine, postzygapophyses inclined posteriad and *margo lateralis* smooth. *Patagoniophis parvus* is distinguished from other described forms by its very low neural spine, but a low spine is also seen in specimens from the Australian Eocene (Scanlon in press). Whether these groupings represent phylogenetic units, or adaptive complexes related to body form, locomotion or dietary specialisation, can not be determined until more evidence is available on phylogenetic relationships between at least some of the genera. It seems likely, by analogy with living forms, that the madtsoiids with low neural spines were terrestrial, while those with high neural spines may have had some combination of aquatic, arboreal and saxicoline habits.

Further remains of *Y. canfieldensis* are likely to be discovered in future, as the type locality continues to be worked by the NTM. In addition, material referable to *Yurlunggur*, *Wonambi* and possibly new madtsoiid taxa is known from Oligo-Miocene and Eocene deposits in Queensland, and will be described in forthcoming publications. Madtsoiids appear to have formed a major component of Australian snake faunas

throughout the Tertiary, the extent and pattern of whose radiation remains to be seen.

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NOTE ADDED IN PROOF

Since this paper was accepted for publication, eleven more madtsoiid vertebrae from the Blast Site, Bullock Creek, have been examined, and all are considered to be derived from the *Y. camfieldensis* holotype skeleton. These newly prepared elements can be interpolated into the series of eighteen described in the text above, on the basis of both qualitative features of the various regions of the skeleton, and dimensions to be published later.

P908-4 is the axis, missing the anterior hypapophysis (which, as in most snakes, is sutured rather than fused to the centrum) and the left side of the neural arch. There is a good fit between the condyle of the axis and the cotyle of P895-5 (no. 1 in the series described above), showing that no. 1 is actually the third cervical vertebra, and the most anterior vertebra to bear ribs.

P895-28 and P895-22 are complete vertebrae bearing single hypapophyses, are very similar to each other in size and morphology, and come from the region between no. 4 and no. 5.

P908-1, P895-27, P895-25 and P895-23 are nearly complete vertebrae from between no. 10 and no. 11. All are larger than no. 11, but have the hypapophyses flat or double, and the zygosphenes somewhat concave above, so all must be posterior to no. 10. P908-1 is the largest vertebra yet known from this snake, with a width across the prezygapophyses of 46.4 mm.

P895-245, P908-2 and P895-24 are intermediate between no.13 and no.14. In P908-2 the zygapophyses, neural arch and zygosphenes are mostly broken away, but the other two speci-

mens are complete. P895-21 is a complete vertebra from between No. 16 and no.17.

Three significant segments of this skeleton remain unknown, namely the skull, the posterior trunk between no. 17 and no. 18, and the cloacal and caudal region. Hopefully the processing of more Blast Site material will produce the re-

quired specimens. The recovery of the additional Blast Site material listed here, also representing the holotype skeleton, and the absence of any other madtsoiid specimens from the Camfield Beds, confirms the interpretation of *Yurlunggur camfieldensis* as a rarely preserved element of the Bullock Creek Local Fauna.

ORIGINS OF THE AUSTRALIAN SCINCID LIZARDS: A PRELIMINARY REPORT ON THE SKINKS OF RIVERSLEIGH.

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ABSTRACT

The fossil skinks from the Oligo-Miocene to Pliocene limestone deposits at Riversleigh, Queensland, include eight or more taxa representing the *Sphenomorphus*, *Egernia* and *Eugongylus* Groups of the subfamily Lygosominae. Some of these are practically indistinguishable from living taxa, while others appear to have left no descendants. This is the richest fossil skink fauna yet recorded in Australia and probably the world. The presence in the early Miocene of all three of the major lygosomine lineages present in the modern Australian fauna means that these lineages arose no later than the early Tertiary.

Keywords: Lizards, Scincidae, fossils, Miocene, Australian fauna.

INTRODUCTION

The fossil deposits of the Carl Creek Limestone, Riversleigh, northwestern Queensland, are becoming well known for their preservation of the Miocene to Pleistocene record of mammalian evolution in Australia (Archer *et al.* 1989). Other vertebrate groups have also been recovered from these deposits: these include the lizards, a group which is numerically very important in the modern Australian fauna (over 500 species) but is all but unknown in the Australian fossil record. Covacevich *et al.* (1990) reported on the agamid lizards from Riversleigh, showing that this family was present at many of the fossil sites, with both modern and extinct taxa represented. This deals with the skinks (family Scincidae), the largest family of lizards and the largest family of terrestrial vertebrates in Australia (about 325 extant species in about 32 genera).

All Australian skinks belong to the subfamily Lygosominae, one of four scincid subfamilies defined by Greer (1970). In Australia there are three suprageneric groups, each apparently a monophyletic unit (Greer 1979, 1989): the *Sphenomorphus* Group (13 genera), the *Egernia* Group (3 genera) and the *Eugongylus* Group (16 genera). The *Egernia* Group is used here in the restricted sense of Greer (1979) rather than his later use of an expanded unit, the *Mabuya* Group (Greer 1989, Hutchinson 1981), as this latter unit may be paraphyletic.

This is a preliminary report on the scincid taxa identified to date at Riversleigh. Individual specimens will be described in detail and final taxonomic decisions made in future publications. Even at this preliminary stage of identification, it is apparent that the specimens recovered include some which strongly resemble modern taxa, some which are similar to, but can be differentiated from, modern taxa, and some which do not seem to have any close living relatives. On this basis, it is possible to summarise the composition of the Miocene skink fauna at Riversleigh and to arrive at some fairly firm conclusions regarding the origins and age of the Australian skink radiation.

Prefixes to specimen numbers are as follows: SAMA, South Australian Museum, Adelaide; UNSW AR, temporary University of New South Wales registration numbers for material collected by Dr Michael Archer and associates (all to be lodged eventually with the Queensland Museum).

DESCRIPTIONS

Lizard skulls, like those of most non-mammalian vertebrates, disarticulate *post-mortem*, so that specimens recovered from fossil deposits are most often isolated bones rather than partial crania or mandibles. This creates difficulties in identification since the literature on scincid os-

teology emphasises relationships between bones of intact skulls. The great majority of the fossil skink specimens recovered are lower jaw elements, mostly isolated dentaries, sometimes with one or more of the postdentary bones still in articulation. Characters of the scineid mandible which vary in taxonomically meaningful ways are indicated in Figure 1. The presence or absence of Meckel's groove, sutural relationships and degree of fusion of bones, positions of foramina and the shape of the retroarticular process have all been found to be useful in identifying skinks to varying degrees of precision.

Sphenomorphus Group

Most jaw fragments found have an open Meckel's groove, a primitive feature retained in the *Sphenomorphus* Group and in the subfamily Scineinae. Skinks of the latter taxon are not found in the modern Australian fauna, the closest occurrence of the group being the genus *Brachyneles* Duméril and Bibron from the Philippines (Greer 1970). Evidence for the Riversleigh specimens belonging to the *Sphenomorphus* Group comes from several nearly complete mandibles which preserve the articular region of the lower jaw. In these, the retroarticular

process is almost parallel-sided, as is the case in living Australian members of the *Sphenomorphus* Group, with only a poorly developed, or no medially-directed expansion, as is the case in the Scineines examined by the author (the "inflated" condition described by Estes *et al.* 1988). Thus there is no reason as yet to think that the Scineinae has ever been present in Australia, and for now all dentaries with an open Meckel's groove are regarded as *Sphenomorphus* Group lygosomines.

"*Sphenomorphus*" spp. The genus *Sphenomorphus* Fitzinger is a grade group of generalised skinks at the base of the *Sphenomorphus* Group. In Australia, there are broadly two groups of species in this genus: a robust, long-legged and deep-bodied morphotype (treated by some recent workers as the genus *Eulamprus* Fitzinger: Cogger 1986; Greer 1989), and an attenuate morphotype with reduced limbs to which the same workers have applied the name *Glaphyromorphus* Wells and Wellington. Fossils attributable to both groups have been identified, representing very probably more than one species of each morphotype.

Two nearly complete mandibular rami (e.g. Fig. 2) represent a large member of the "robust *Sphenomorphus*" morphotype, and are structurally similar to the modern *S. murrayi* (Boulenger)

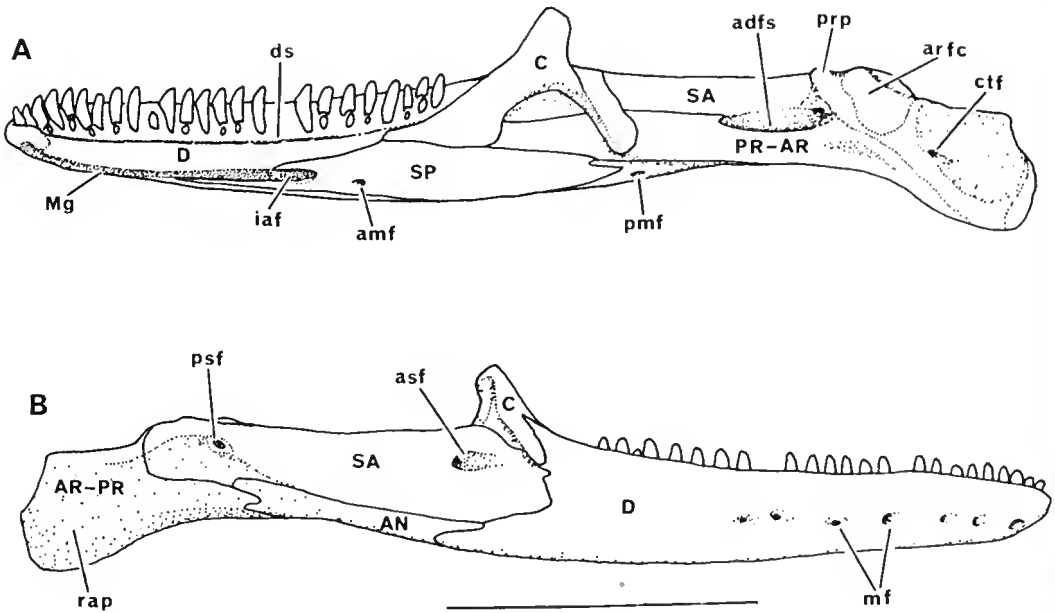


Fig. 1. Mandible of a primitive skink, the North American scineine *Eumeces fasciatus*, (SAMA R35701), in (a) lingual and (b) labial views. Scale bar equals 5 mm. Abbreviations: **adfs**, adductor fossa; **amf**, anterior mylohyoid foramen; **AN**, angular; **arfc**, articular facet; **AR-PR**, fused articular and prearticular; **asf**, anterior surangular foramen; **C**, coronoid; **ctf**, chorda tympanica foramen; **D**, dentary; **ds**, dental sulcus; **iaf**, inferior alveolar foramen; **mf**, mental foramina; **Mg**, groove for Meckel's cartilage; **pmf**, posterior mylohyoid foramen; **prp**, prearticular process; **psf**, posterior surangular foramen; **rap**, retroarticular process; **SA**, surangular; **SP**, splenial.

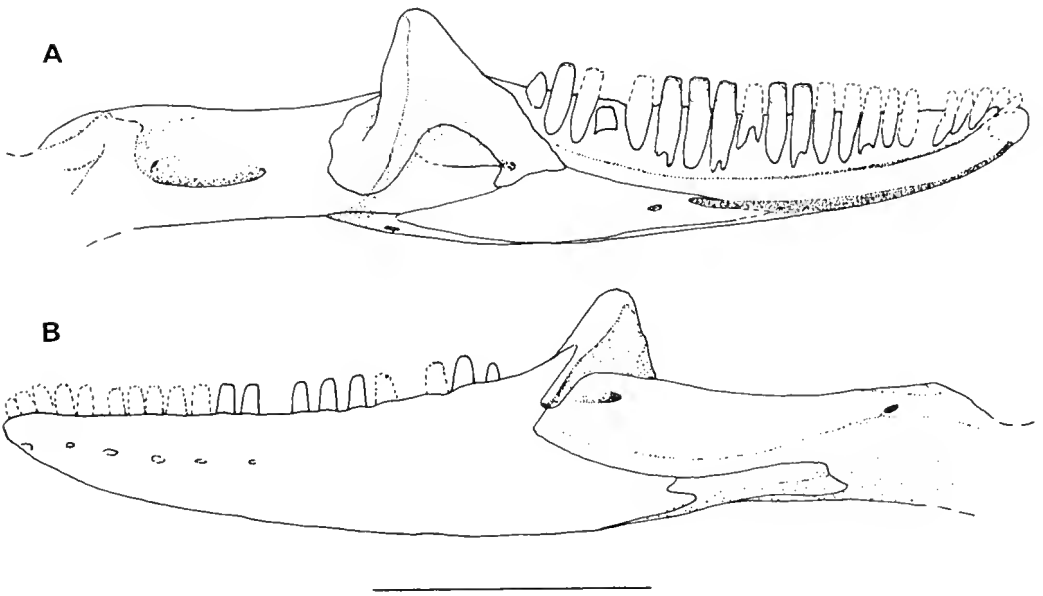


Fig. 2. Nearly complete left mandibular ramus of a robust member of the genus *Sphenomorphus* (*sens. lat.*), (UNSW AR 17309, Camel Sputum Site), in (a) lingual and (b) labial views. Scale bar equals 5mm.

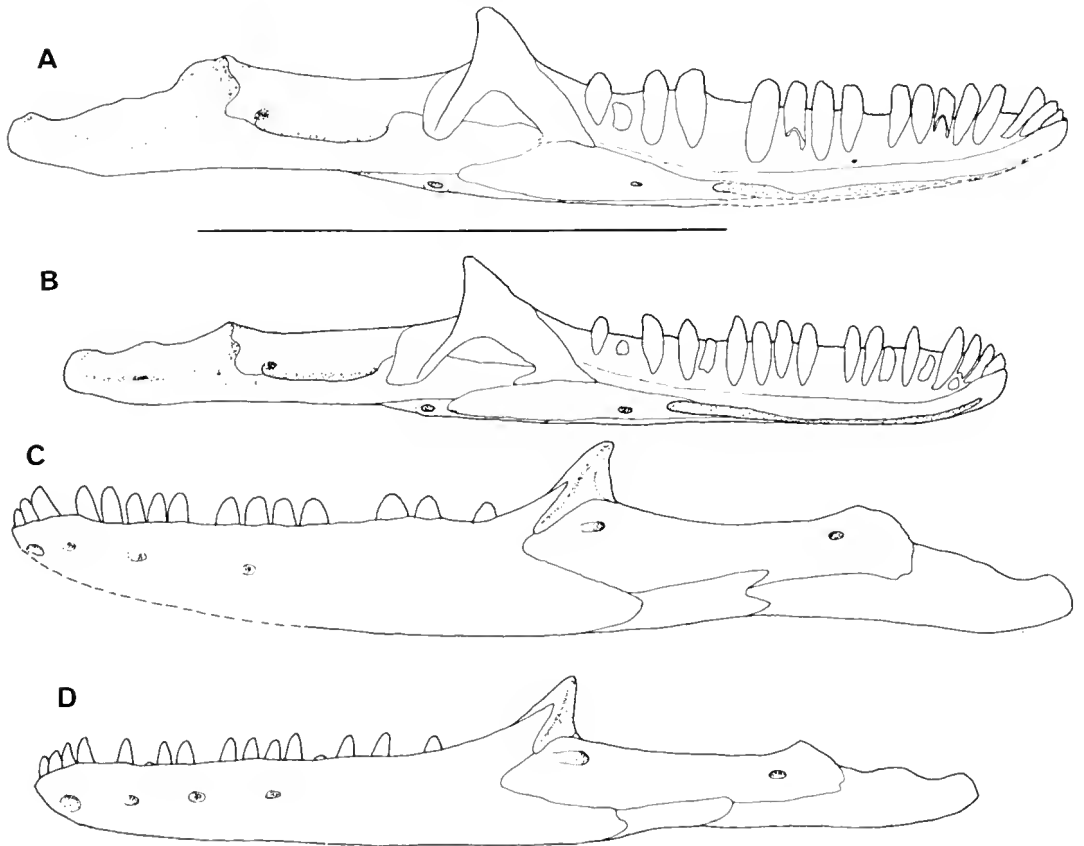


Fig. 3. Slightly restored left mandibular ramus of (a and c) an attenuate member of the genus *Sphenomorphus* (*sens. lat.*) (UNSW AR4550, Gag Site) compared with (b and d) a very similar living species, *Sphenomorphus mjobergi* (SAMA R35674). (a) and (b), lingual views; (c) and (d), labial views. Scale bar equals 5mm.

or *S. luteilateralis* Covacevich and McDonald. Small differences in the architecture of the coronoid and in the relative depth of the mandible suggest specific differentiation of the fossil. Other more fragmentary dentary remains may belong to a skink of this type, but might also belong to a water skink (*S. quoyii* complex). Isolated frontals, parietals and a quadrate are also attributable to this morphotypic group.

The "attenuate *Sphenomorphus*" morphotype is represented by a nearly complete mandibular ramus and is distinguishable from modern species such as *S. njobergi* (Lönnerberg and Anderson) or *S. punctulatus* (Peters) only by its slightly larger size and more robust teeth (Fig. 3). Additionally, isolated frontals have been found representing two taxa which have relatively broad interorbital regions and indications of narrow separation of pre- and postfrontals, and which might be attributable to skinks of this group (Fig. 4). In extant species, these modifications of the frontal are associated with fossorial habits and limb reductions.

Sphenomorphus Group, new genus and species. One of the best preserved skink finds is an almost complete mandibular ramus of a *Sphenomorphus* Group lizard not attributable to any living genus (Fig. 5). The teeth are relatively large and apparently durophagous. The mandible is relatively short and deep with high and deep insertions for adductor muscles. These proportions are not matched by any living species examined. The closest similarity is to *Lerista* Bell which may also have enlarged, durophagous teeth (Estes and Williams 1984), the larger species of which have a relatively short, bowed mandible with an unusually well-developed retroarticular process. However, the specimen lacks several derived features characteristic of *Lerista* and the similarities are probably analogous, suggesting similar modes of life rather than relationship. Several specimens referable to this taxon have been found at the Gag Site, including an isolated postdentary portion and other dentaries of possibly earlier ontogenetic stages.

Genus and species indeterminate - small insectivores. Numerous, but mostly fragmentary remains of quite small skinks (estimated skull length less than 12 mm) have an open Meckel's groove and tapering, pointed teeth such as those present in small insectivorous species of several genera (e.g. small *Ctenotus* Storr; Asian *S. sanctus* species-group). The fossils do not ex-

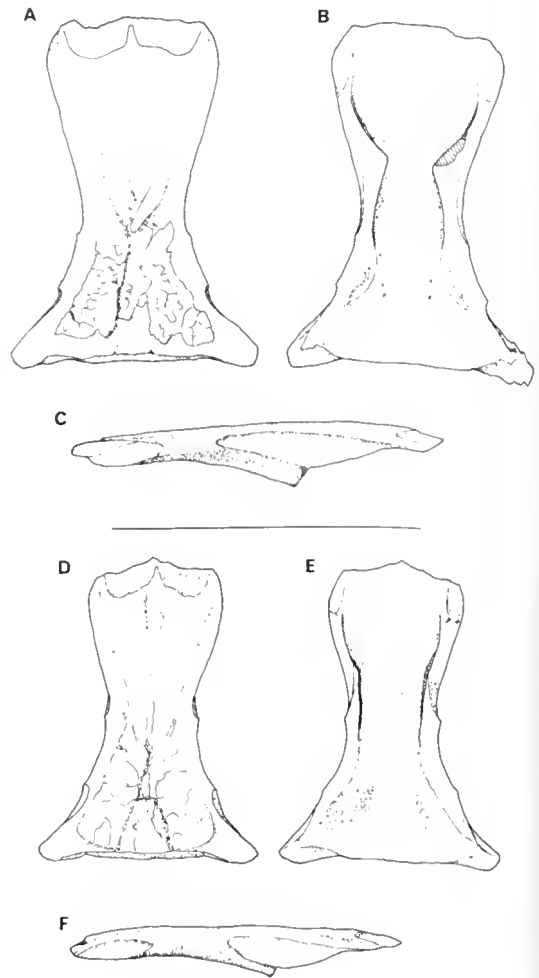


Fig. 4. Scincid frontal bones from the Gag Site (a-c, UNSW AR4419; d-f, UNSW AR 5340) in (a, d) dorsal, (b, e) ventral and (c, f) right lateral views. Both show a reduced gap between the prefrontal and postfrontal facets; UNSW AR4419 shows enhancement of the descending processes of the frontals. Scale bar equals 5mm.

actly match any extant member of the *Sphenomorphus* Group examined, and modern tropical Queensland skinks filling the insectivore niche are mainly members of the *Eugongylus* Group. The high frequency of dentaries of this morphotype suggests that one or more small skink taxa, now extinct, were an important part of the Riversleigh ecology.

Egernia Group

Several skink mandibles from Riversleigh have a closed Meckel's groove and a large, elongate inferior alveolar foramen positioned

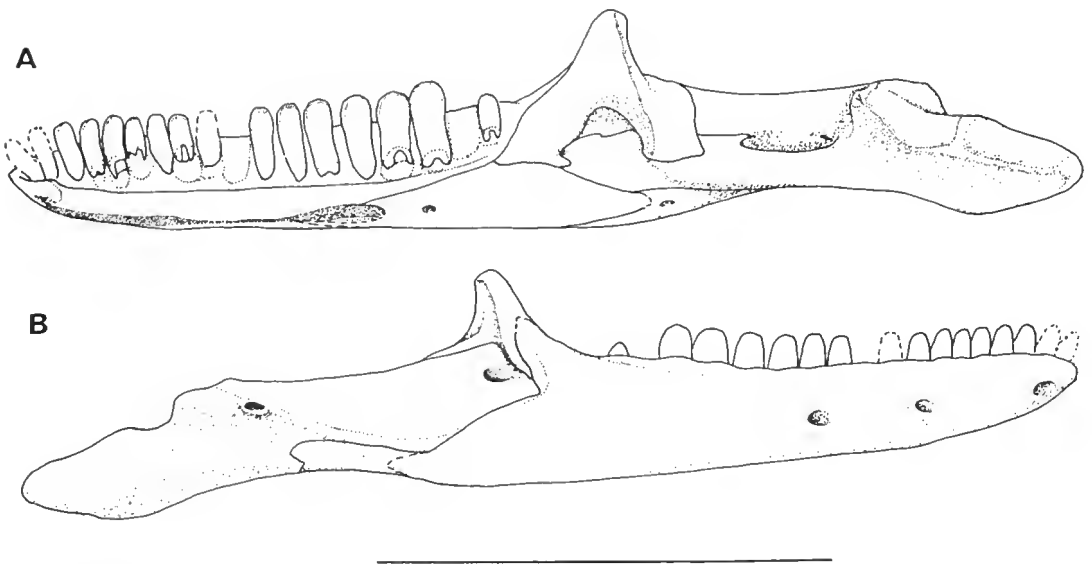


Fig. 5. Right mandibular ramus (restored; based mainly on UNSW AR5218, with details from UNSW AR4355 and UNSW AR4323, all Gag Site) of an undescribed member of the *Sphenomorphus* Group in (a) labial and (b) lingual views. Scale bar equals 5mm.

relatively low and anteriorly. This morphology is characteristic, in the modern Australian fauna, of the *Egernia* Group. Generic allocation in this group is based on tooth morphology; durophagous in *Tiliqua* Gray and *Cyclodomorphus* Fitzinger, slender in *Egernia* Gray.

Egernia frerei species-group. Tooth morphology does not vary much within the species groups defined by Horton (1972) and Storr (1978), but differs between them. Several fragments from Riversleigh have slender, chisel-crowned teeth which are identical to those found in large skinks of the *E. frerei* species-group (*E. frerei* Günther and *E. major* Gray; those of *E. rugosa* De Vis are similar, but not identical).

Egernia striolata species-group. A nearly complete anterior half of a mandible, plus several fragments, have teeth with crowns which are slightly labio-lingually compressed anteriorly, and expanded and rounded posteriorly. An identical morphology is seen in living members of the *Egernia striolata* species-group (Storr 1978), in which the differential pattern develops ontogenetically from a more homodont condition, in which all teeth are like the anterior teeth described above. The best preserved specimen is more robust than any living *E. striolata* Group jaws examined, but not extremely so (Fig. 6).

Tiliqua sp. nov. Shea and Hutchinson (1992) have identified two fragmentary dentary specimens from the Gag locality (System C, Middle

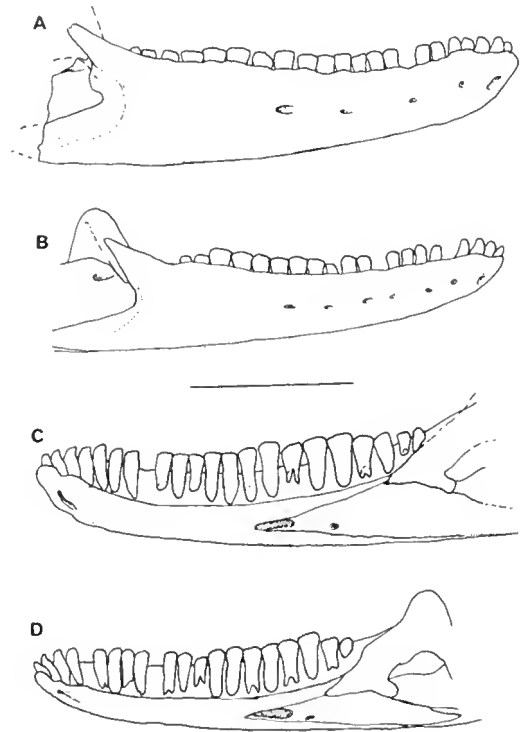


Fig. 6. Partly restored mandible of a species of (a and c) *Egernia* (UNSW AR 5212, Gag locality) compared with (b and d) a very similar living species, *Egernia striolata* (SAMA R24877). (a) and (b), labial views; (c) and (d), lingual views. Scale bar equals 5mm.

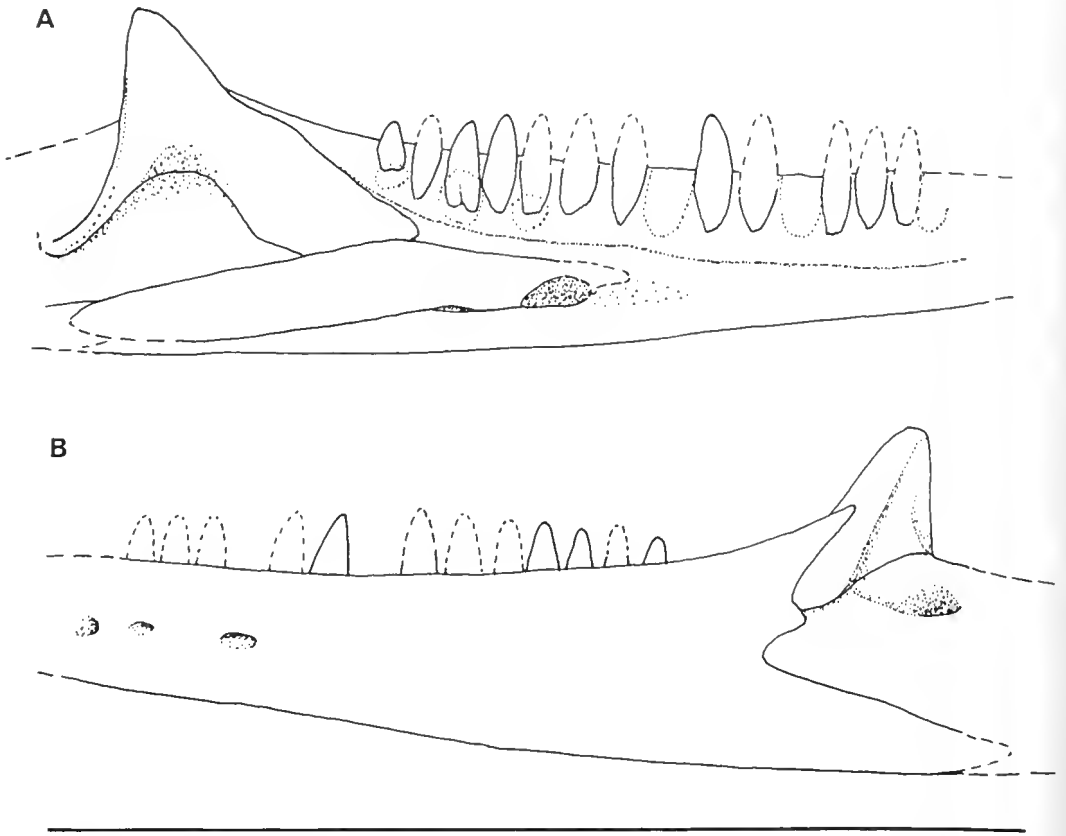


Fig. 7. Partial right mandible of a *Eugongylus* Group skink (UNSW AR17371, Ringtail Site) in (a) lingual and (b) labial views. Scale bar equals 5mm.

Miocene: Archer *et al.*, 1989) as a new species of this genus (in the restricted sense of Shea (1990)). It is much smaller than any living species of the genus, with the exception of *T. adelaidensis* (Peters), and although fragmentary, its distinctive teeth have allowed not only recognition of its generic relationship, but also permit its diagnosis as a new species. It is not obviously allied to any particular extant member of the genus.

Eugongylus Group

The rarest skink lineage at Riversleigh is the *Eugongylus* Group. Two well-preserved, informative specimens, plus several other fragmentary dentaries, have been recovered. Although rare, representatives of this lineage are stratigraphically widespread. A dentary and a partial mandible represent two different taxa, probably distinguishable at the generic level. The dentary is, in size and proportions, most like modern *Niveoscincus* Hutchinson *et al.* but differs in having more robust, pointed teeth, com-

pared with the blunt-crowned teeth of *Niveoscincus*. The partial mandible is most like modern *Carlina* Gray in the shape of the coronoid and the dentary-surangular contact, and in having a dorsally-oriented opening for the anterior surangular foramen. However, in proportions the jaw appears to be shorter than in modern *Carlina*. This estimation is based on the position of the inferior alveolar foramen (Fig. 7) which is separated from the most posterior mental foramen by a distance equal to eight to eleven tooth loci in *Carlina*, but only five tooth loci in the fossil.

COMPARISON OF MODERN AND MIOCENE FAUNAS AND THE ORIGINS OF THE AUSTRALIAN SKINKS

The stratigraphic distribution of provisionally identified skink taxa is summarised in Table 1. This is likely to give an underestimate of the true diversity, since several species or even genera

TABLE 1. Distribution of fossil skink taxa at Riversleigh sites; + = present. 1, robust *Sphenomorphus* (more than one taxon); 2, attenuate *Sphenomorphus* (more than one taxon); 3, durophagous taxon ("erusher"); 4, small insectivore; 5, *Egernia* cf. *frerei*; 6, *Egernia* cf. *striolata*; 7, *Tiliqua* sp. nov.; 8, indeterminate genus (more than one taxon).

Site	<i>Sphenomorphus</i> Group				<i>Egernia</i> Group			<i>Eugongylus</i> Group
	1	2	3	4	5	6	7	8
Early to mid Miocene								
"System C"								
Henk's Hollow	+	+		+				
Two Trees	+		+	+				+
Ringtail		+		+				+
Wang		+						
Gag	+	+	+	+	+	+	+	
Early Miocene								
"System B"								
Neville's Garden	+	+	+	+	+			+
Boid Site East	+					+		+
Camel Sputum	+	+	+	+	+			+
Helicopter		+	+		+			
Inabeyanee								+
Mike's Menagerie	+	+		+				
Upper		+	+	+	+	+		+
VDU	+							
Outasite		+						
RSO		+						
Wayne's Wok		+		+			+	
Wayne's Wok 2		+		+				

may well be lumped in some of the column categories. Table 2 compares the early to mid Miocene Riversleigh skink fauna to the modern faunas of southeastern and northeastern Queensland forests.

The faunas are similar in being dominated by the *Sphenomorphus* Group, with the *Egernia* Group present, but, as a minor faunal component. They differ in apparent generic composition, with seemingly fewer specialised taxa being present during the Miocene. The *Eugongylus* Group appears to be relatively rare at Riversleigh, compared to its moderate frequency in modern Queensland forests. Living members of this group are predominantly small, but their rarity at Riversleigh cannot be simply attributed to physical taphonomic factors. The relative abundance of *Sphenomorphus* Group remains, which are just as small, indicates that hydrodynamic sorting, for example, has not influenced the frequency of occurrence of the *Engongylus* Group in this deposit. It is possible that the Riversleigh Miocene ecosystem was depauperate in *Eugongylus* Group skinks, and that their role as small insectivores was filled by small members of the *Sphenomorphus* Group.

Prior to the acceptance of continental drift, and to the modern studies of scincid phylogeny, the family was viewed as a relatively recent

arrival in Australia, with a relatively low level of endemism at the genus level (Keast 1959; Storr 1964). Subsequent to this, it has become clear that skinks show a higher degree of generic endemism than previously thought (e.g. *Leiolopisma*, Hutchinson *et al.* 1990). Discovery of the oldest "skinks" on a Laurasian landmass implied a northern origin (Cracraft 1974; Estes 1983b), and the wide gap thought to have separated Australia and Southeast Asia during the Palaeogene (Smith and Bryden 1977) seemed consistent with a recent arrival of the family in Australia (no earlier than Miocene). Recent advances in the understanding skink phylogeny identify centres of endemism in Australia, tropical Asia and Africa-Madagascar, suggesting a Gondwanan, rather than Laurasian, origin for skinks.

Fossil data on the past distribution of skink lineages would clearly contribute greatly to resolving both the geography and timing of their origins. In spite of its size and global distribution, the family Scincidae has a very poor fossil record both in Australia and elsewhere (Estes 1983a, 1983b). Indisputable skinks first appear in the Oligocene of North America, with specimens allocated to the still living (although archaic) *Eumeces* Wiegman. North American scincoid remains from the Eocene, Paleocene

TABLE 2. Comparison of the Riversleigh skink fauna with skink faunas of modern northeastern, and southeastern Queensland. "+" denotes the presence of a taxon, "-" its absence.

Genus	Northeastern Queensland	Southeastern Queensland	Riversleigh
Sphenomorphus Group			
<i>Anomalopus</i>	+	-	-
<i>A. reticulatus</i> sp. group	+	+	-
<i>Calyptotis</i>	+	+	-
<i>Ophioscincus</i>	-	+	-
<i>Saiphos</i>	-	+	-
robust <i>Sphenomorphus</i>	+	+	+
slender <i>Sphenomorphus</i>	+	-	+
" <i>Tropidophorus</i> "	+	-	-
Riversleigh "insectivore"	?	?	+
Riversleigh "crusher"	-	-	+
Egernia Group			
<i>Cyclodomorphus</i>	+	+	-
<i>Egernia</i>	+	+	+
<i>Tiliqua</i>	-	-	+
Eugongylus Group			
<i>Carlia</i>	+	+	-
<i>Lampropholis</i>	+	+	-
<i>Lygisaurus</i>	+	+	-
Genus indet.	?	?	+
TOTAL	11	10	7

and Late Cretaceous are too incomplete to be identified with confidence as skinks. There is a wider geographic representation from the Miocene onwards, with records from several North American sites, Morocco and Australia, but diversity is still very low. Just two genera are recorded from the Miocene: *Eumeces* in America and North Africa and *Egernia* in Australia (Estes 1984). Only in Plio-Pleistocene sediments do skinks become relatively diverse, but these faunas are not significantly different from living skinks in the same geographic areas.

The Riversleigh Tertiary skink fauna is the richest yet recorded and the first from a land mass rich in living skinks. These finds show that the mid-Tertiary skink fauna was already completely Australian in character. Not only were all three lygosomine generic groups present, but they were also diverse, and both extant and extinct genera seem to have been present. These fossils support the idea that the modern Australian skink fauna is largely the product of *in situ* evolutionary radiation, rather than waves of invaders which differentiated elsewhere. The presence of the three lygosomine groups in the Riversleigh Miocene indicates that their origins must pre-date the Oligo-Miocene boundary. The suggestion of an earliest Tertiary date for their phylogenetic divergence, based on immunologi-

cal data on albumin evolution (Baverstock and Donnellan 1990), is compatible with the estimated age of the Riversleigh fossil fauna.

The ultimate origin of Australia's skinks is not clarified by these finds. Recent reviews of data on continental drift (Audley-Charles 1987; 1991) concluded that Australia's isolation from Asia during the Tertiary was less complete than previously believed and also that it separated from Antarctica earlier than previously thought: i.e. prior to the Eocene. If lygosomines evolved outside Australia and first arrived around the K-T boundary, they had to cross via an archipelagic sweepstakes route, whether they came via the Indo-Malayan archipelago or East Antarctica. As Greer (1979) suggested, the number of "sweepstakes winners" necessary to establish the Australian fauna was probably no more than one to three.

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THINHEADS, THICKHEADS AND AIRHEADS - FUNCTIONAL CRANIOLOGY OF SOME DIPROTODONTIAN MARSUPIALS.

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ABSTRACT

The development of complex air cells surrounding the internal brain capsule in diprotodontid, palorchestid and thylacoleonid marsupials is related to a pronounced allometric differential between brain volume to body size resulting in independent growth programs for the inner and outer table of the neurocranium. The dimension of the inner table is directly determined by brain volume and the outer table dimension is determined by jaw adductor mass which increases in relation to overall body size. In large diprotodontids, the presumptive ectocranial area provided by expansion of the neural capsule due to brain growth would provide insufficient external surface for the attachment of the adductor muscles. Diprotodontid marsupials circumvent this potential limitation to the attainment of large body size by independent expansion of the outer table of the neurocranium in proportion to the surface area required by the musculature. The majority of large placental herbivores have responded to the same constraint by a reorganization of the adductor muscle configuration.

KEYWORDS: endocranial sinuses, Thylacoleonidae, Diprotodontidae, Vombatidae, Palorchestidae, allometry, functional craniology, jaw musculature.

INTRODUCTION

Owen (1877) was first to draw attention to the presence of large endocranial air sinuses surrounding the lateral and posterior portions of the neural capsule in certain marsupials. Van der Klaauw (1931) described the relationship of some of these sinuses within the squamosal, occipital and alisphenoid in relation to the anatomy of structures surrounding the middle ear of marsupials and other mammals. Klaauw's (1931, 1946, 1948-52) observations form the anatomical basis of numerous subsequent studies of mammalian cranial form.

It seems, however, that the truly remarkable extent to which certain large marsupial crania are composed of little more than air cells has eluded anatomical investigation. Rather similar developments had been noted in the frontoparietal region of elephants (Osborne 1942) and in suids. Gregory (1903) related the development of the frontal dome in the elephant to the separation of the inner and outer table of the braincase in order to support the trunk musculature

anteriorly and the nuchal musculature posteriorly (see Gregory 1974: Figs 21-32, 21-33).

As well as being relatively more extensive than in elephants and pigs, the neurocranial sinuses of *Palorchestes* Owen, *Kolopsis* Woodburne, *Neohelos* Stirton, *Zygomaturus* Meleay, *Diprotodon* Owen and *Thylacoleo* Owen originate from different regions of the cranium. Thus, while it is likely that a general explanation of the sinuses applies to both marsupials and placentals, the reasons for the developments differ for each group. The more specific details of sinus development in the diprotodontians are sought in this investigation.

The particular manifestation of these endocranial sinuses in the Thylacoleonidae, Diprotodontidae and Palorchestidae are considered to have systematic importance (Klaauw 1931, Ride 1964, Aplin 1987). Their presence moreover, constitutes an anatomical curiosity deserving, at least, a description sufficiently detailed and accurate to attract the attention of other craniometrists and functional anatomists better equipped to make broader and more pertinent

observations than the preliminary study presented here.

In this investigation I describe the endocranial sinuses in a representative sample of diprotodontian genera. Several variables that appear to be related to the development of the condition are considered and a hypothesis explaining the manifestation in terms of these variables is presented.

METHODS AND MATERIALS

The investigation uses proportional comparisons of cranial components in a series of living and extinct diprotodontians. A hypothetical growth series of the extinct genus *Kolopsis* was reconstructed from late Miocene Alcoota Local Fauna (LF) material for comparison with a placental series of *Bos taurus* Linnaeus, the domestic cow.

The observations to follow are based on fossil crania with natural breaks exposing the sinuses to view, thus allowing an occasional accurate measurement. While such information is adequate for the formulation of a hypothesis, the data may not be deemed suitable for verification. I envision that such a study might require sophisticated techniques such as radiographic serial reconstruction, tomography or sonographic probing combined with computerized data points for accurate computations. Although such an investigation is beyond the means of my current situation, the observations from this cruder data set indicate that more technical applications are feasible and that the results might prove interesting.

Crania of the following living marsupial genera were employed in the investigation: *Didelphis* Linnaeus, *Marmosa* Gray, *Cercartetus* Burmeister, *Pseudocheirus* Ogilby, *Trichosurus* Lesson, *Phascolarctos* Blainville, *Phalanger* Storr, *Lasiorchinus* Gray, *Vombatus* Geoffroy and *Macropus* Shaw. The fossil material includes: Palorchestidae: *Propalorchestes* Murray (NTM P895-1, P8552-10); Diprotodontidae: *Neohelos* (NTM P8695-38, P8551-13, CPC F23038), *Kolopsis* (NTMP1007, P8893, P92185, P92186, P92187), *Zygomaturus* (unregistered specimen, Victoria Fossil Cave) and *Thylacoleo* (SAM P16730). Abbreviations: NTM, Northern Territory Museum; CPC, Commonwealth Palaeontological Collection; SAM, South Australian Museum. Marsupial systematics follows Aplin and Archer (1987).

ANATOMICAL DESCRIPTION

Endocranial sinuses enveloping all but the ventral surface of the internal capsule of the brain appear to be found among only the larger palorchestid, diprotodontid and thylacoleonid marsupials of the Infraorder Vombatomorpha. Other diprotodontians show various degrees of sinus development, particularly within the squamosal and sometimes within the frontals, but not within the posterodorsal components of the neurocranium, e.g. the parietals, interparietal and supraoccipital. The primary sinus development of the squamosal region is termed the Epitympanic Sinus (Klaauw 1931). An anterior epitympanic sinus is present in nearly all Australidelphian marsupials (Ride 1964). A posterior component of the epitympanic sinus is largely confined to the diprotodontians, among which, in living forms, its greatest degree of development is found in vombatids (Figs 1, 2).

Even in *Lasiorchinus*, in which the anterior and posterior epitympanic sinuses are greatly enlarged, only the squamosal portion of the internal capsule is separated from its outer table (Fig. 2). In the extinct palorchestids and diprotodontids the sinuses continue around the dorsal surface of the brain capsule resulting in its virtual suspension by thin bony septa within a series of large airspaces.

These aircells are interconnected by small openings and contain emissary venous channels that anastomose with venous intracranial sinuses (greater petrosal and sigmoid). Diploic emissaries associated with the postglenoid canals may have passed through the epitympanic fenestra, a large opening in the superficial meatus that leads directly into the epitympanic sinuses.

It can be seen that there are three basic states of sinus development in diprotodontians; these are characterized in the title as "thinheads, thickheads and airheads". In the species with thin cranial bones, for example phalangerids, macropodids and *Phascolarctos*, sinus development is confined to a small group of coalesced diploe in the squamosal lamina (Fig. 3). In thick-headed forms (*Lasiorchinus*, *Vombatus*), large epitympanic sinuses are present but are entirely confined to the squamosal. However, the parietal bones are greatly thickened, with the inner and outer tables being widely separated by intervening diploe. In the airheads (zygomaturines, palorchestines) the region corresponding to the parietal diploe in vombatids is entirely pneumaticized into larger cells with the septa

corresponding to the sutural contacts of the parietal and squamosal (Fig. 2).

In terms of body weight, the diprotodontian species with thin cranial walls are small to medium-sized animals with relatively large brain volumes (Moeller 1973). *Lasiorhinus* and *Vombatus*, which possess thick-walled crania, are among the heaviest living marsupials and

also have relatively large brain weights. The forms with greatly enlarged intracranial air cells are all extinct and cannot be directly compared by weight with the others. However, all of them were from about twice to over 10 times more massive than any living marsupial.

About a half or slightly more of the total coronally sectioned width of a thin-walled cra-

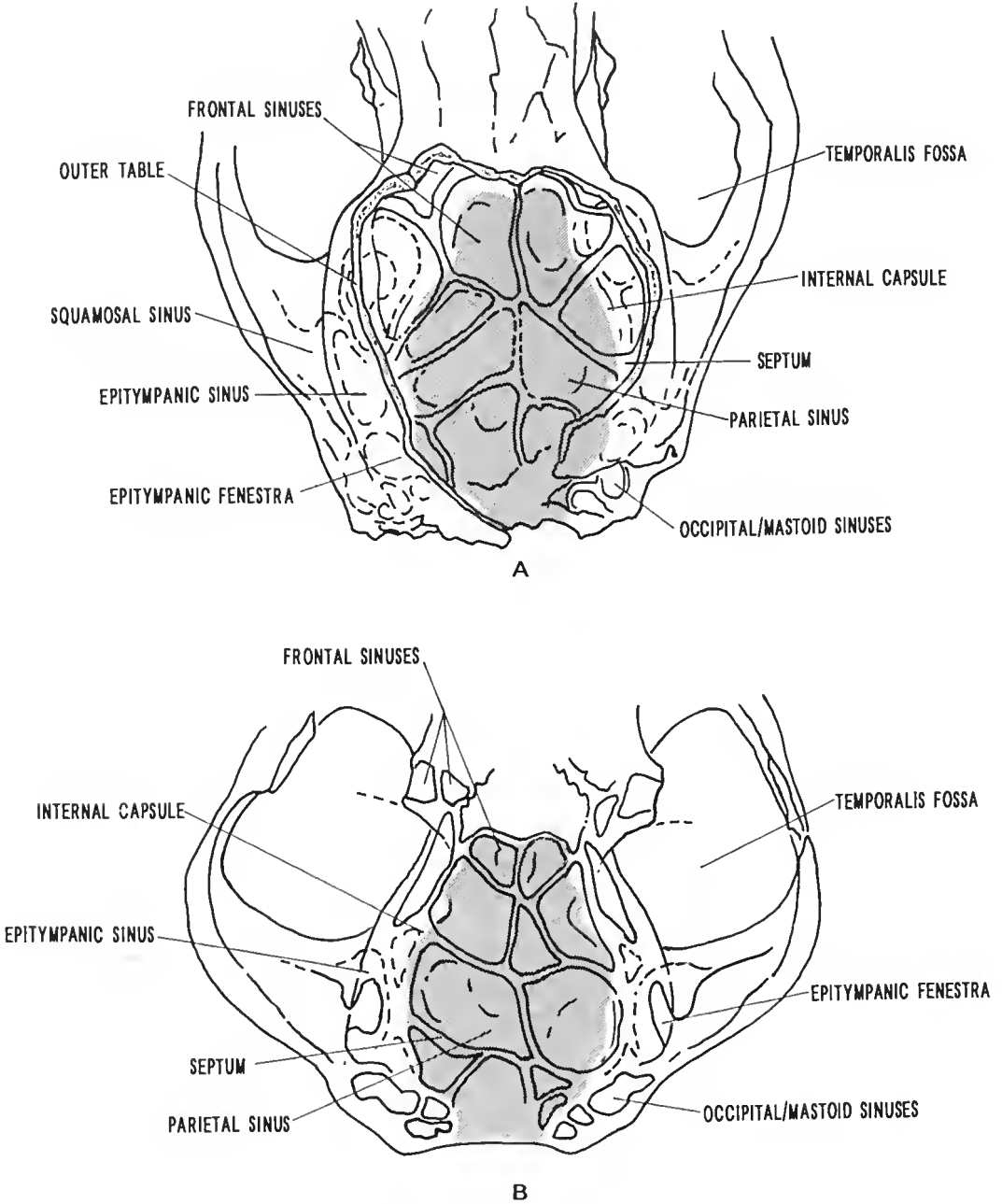


Fig. 1. Line drawing of dorsal aspect of pneumaticized diprotodontian crania showing form and extent of air cells surrounding the neural capsule; A, Miocene diprotodontid *Kolopsis torus* 0.5X; B, Late Pleistocene thylacoleonid *Thylacoleo carnifex* 0.5X.

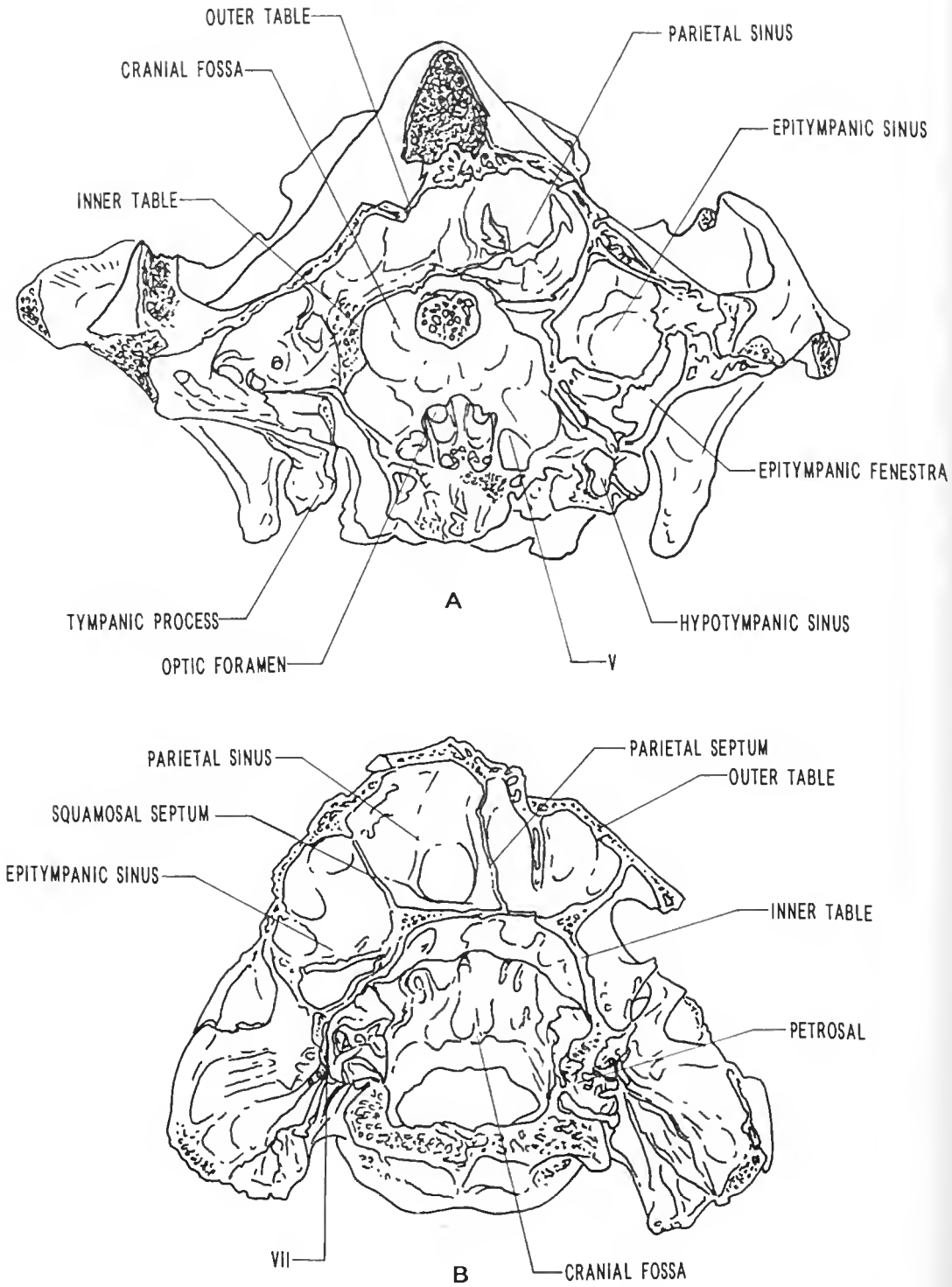
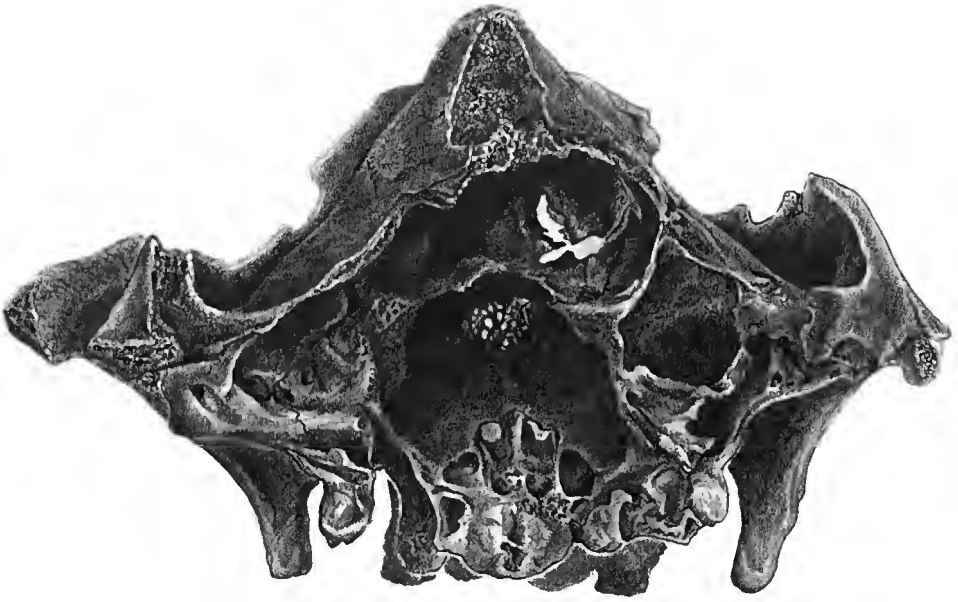
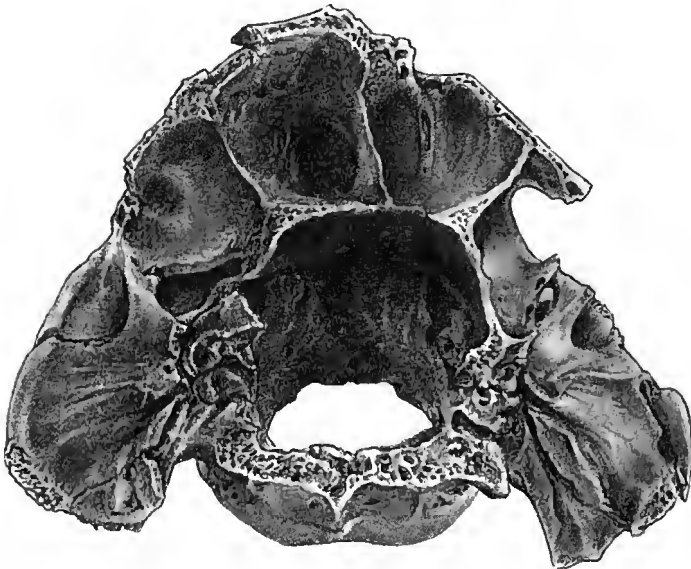


Fig. 2. A-B, drawings of A, naturally broken coronal section through the highly pneumaticized cranium of Miocene palorchestid *Propalorchestes novaculacephalus* Murray, looking into anterior portion 0.5X; B, *P. novaculacephalus*, looking into the posterior portion 0.5X.



a



b

Fig. 2. A-B, (cont.): In A-B the large air cells dorsal and lateral to the internal capsule of *Propalorchestes* correspond to the thickened diploic region dorsally (the former being fusions of the many cells of the latter) and large epitympanic sinuses laterally in *Lasiorhinus* (C-D).

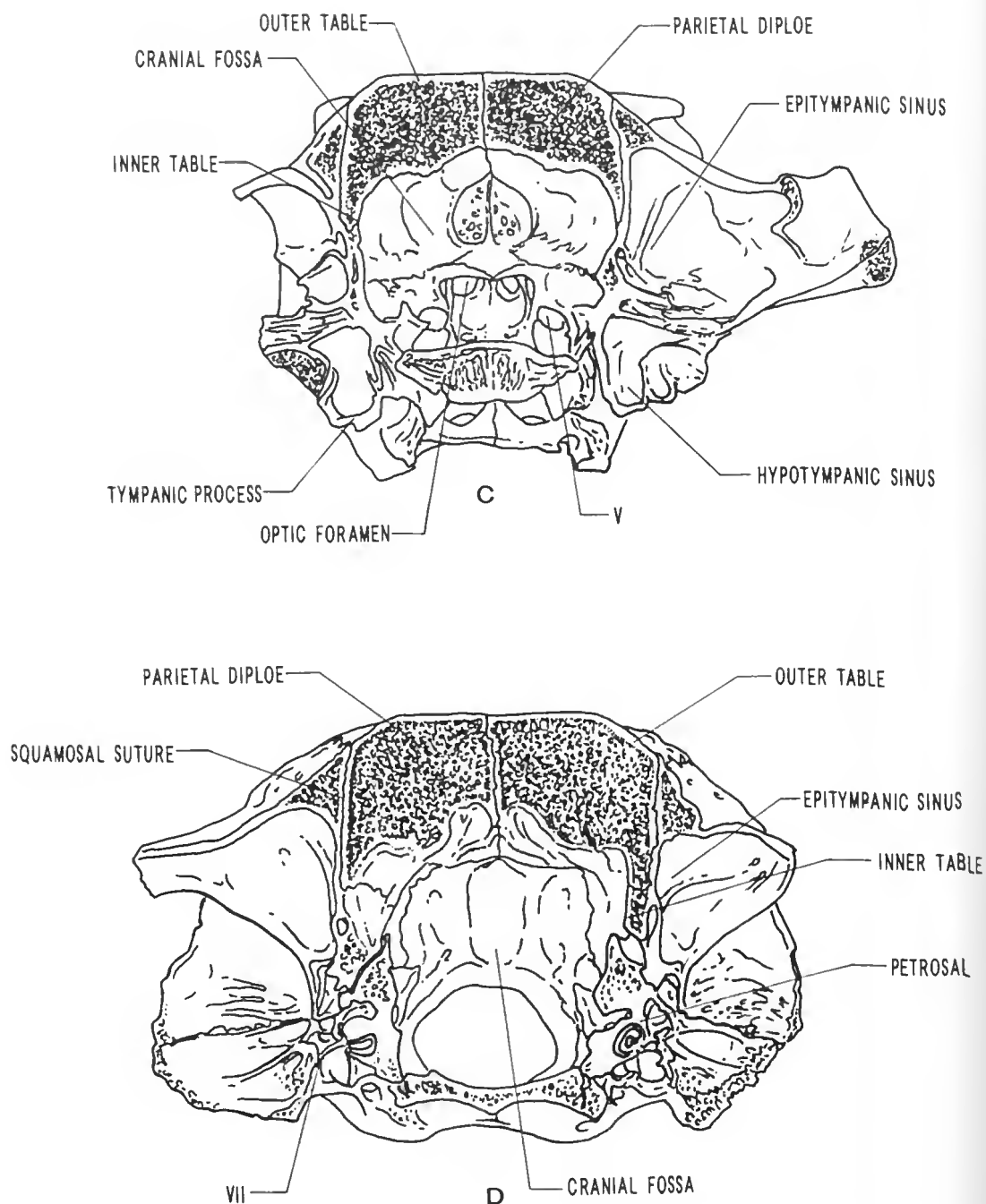
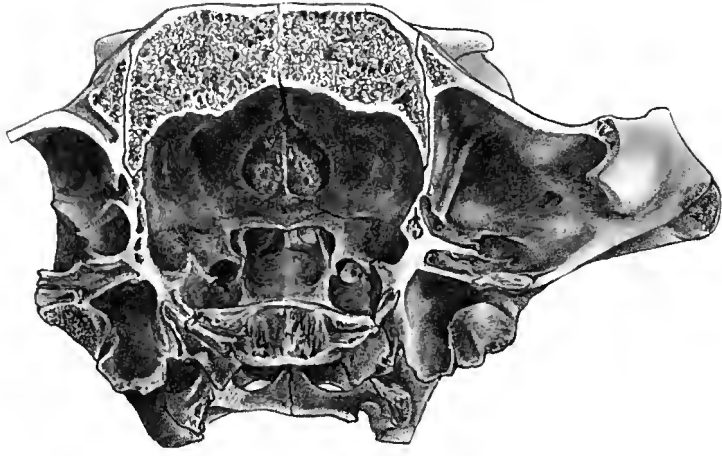
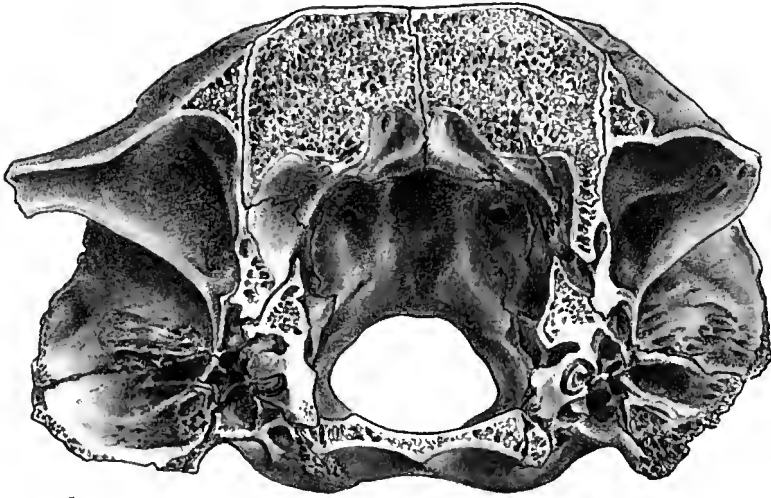


Fig.2. C-D, drawings of C, coronally sectioned cranium of living vombatid *Lasiorhinus latifrons* (Owen), looking into the anterior portion 1.0X; D, *Lasiorhinus latifrons*, looking into the posterior portion 1.0X.



c



d

Fig. 2. C-D (cont.): In A-B the large air cells dorsal and lateral to the internal capsule of *Propalorchestes* correspond to the thickened diploeic region dorsally (the former being fusions of the many cells of the latter) and large epitympanic sinuses laterally in *Lasiorhinus* (C-D).

nium is represented by the endocranial space occupied in life by the brain and its associated tissues. In the thick-walled crania, about a third of the total width of the cranium is endocranial space, and in the pneumaticized cranium less than a fourth of its total width is represented by endocranial space (Figs 4, 5). Plots of the width of the endocranial space to the width of the temporalis fossa yields a coefficient of about 0.45, whereas the trend of outer braincase dimensions to width of the temporalis fossa is much steeper, with a coefficient of about 0.80 (Fig. 6).

A divergence in the trends, indicating a transition to allometric growth of the outer table in relation to the internal capsule, becomes apparent at the point at which the internal cranial dimension of the large extinct diprotodontians approximates the external braincase dimension of the largest living representatives. This transition, which is simply a manifestation of the surface to volume functions of the inner and outer tables, is not at all apparent from the external aspect of the crania, which retain very similar adductor mass to braincase proportions among species ranging from mouse-sized *Cercartetus* to rhino-sized *Zygomaturus*.

The linear proportional relationships observed in a phyletic series of diprotodontian marsupials is similarly reflected in the ontogeny of the diprotodontid species *Kolopsis torus* (Fig. 7) which is considered typical of the family. In the cranium of the placental herbivore *Bos taurus*, there is a marked change in the proportions of the splanchnocranium relative to the neurocranium during the later stages of maturation. The conspicuous proportional sliding between the neural and facial components of the cranium is characteristic of the majority of large placental herbivores (Klaauw 1942).

The anatomical observations suggest the following: 1) the endocranial sinuses are associated with large-bodied diprotodontian marsupial species, in which the external surface of the braincase remains co-linear in relation to increased body size (the ectocranial surface remains proportional to the square of any of its linear dimensions), whereas the internal capsule of the braincase increases proportionally to the cube of any of its linear dimensions; 2) a tendency toward expansion of the outer table away from the inner table of the brain case is incipiently present in the larger, thin-skulled forms (e.g. *Phascolarctos*) and definitely manifested in the thick-skulled vombatid species; and 3) externally, the

diprotodontians retain a linear proportional relationship between the neural and facial components of the cranium, both phyletically and ontogenetically, in contrast to placental herbivores of equivalent size. Internally, the volume of the neural capsule of large vombatiforms is somewhat smaller than in an equivalent-sized placental herbivore.

SINUS DEVELOPMENT

Two lines of evidence show the process of sinus development in the large marsupial herbivores. The evolutionary process is suggested by the presence of a thickened diploic layer in the larger living diprotodontian species, *Phascolarctos*, *Lasiorhinus* and *Vombatus*, an exception being the large living *Macropus* species. The ontogenetic development is shown in a series of immature *Kolopsis torus* Woodburne specimens.

The formation of intracranial sinuses is thoroughly documented (Moss and Young 1960). Their development relates primarily to the progressive separation of the inner and outer tables of the braincase. As these separate, the bone thickens through the formation of a diploic layer. The small airspaces within the diploic layer then coalesce into increasingly larger spaces until the region is fully pneumaticized.

In *Lasiorhinus*, the cranial vault has attained a pre-pneumatic stage of inner and outer table separation similar to that of an immature *Kolopsis torus*. In *Kolopsis*, the process of pneumaticization of the parietals becomes apparent when the M^5 has begun to emerge from its crypt. As the animal matures, the inner and outer table become increasingly separated; the inner capsule remains in intimate contact with the brain and the outer table continues to expand in proportion to the enlargement of the splanchnocranium and zygomatic arches.

FUNCTIONAL CRANIOLOGY

Moss and Young (1960) outlined the principles of differential growth of the mammalian cranium, emphasizing the influences of soft tissue growth and function on various cranial components. Primary among these are the outer table, diploe and inner table components of the neurocranial plate that grow independently of one another, functionally dissociating in response to their respective soft tissue demands. The inner

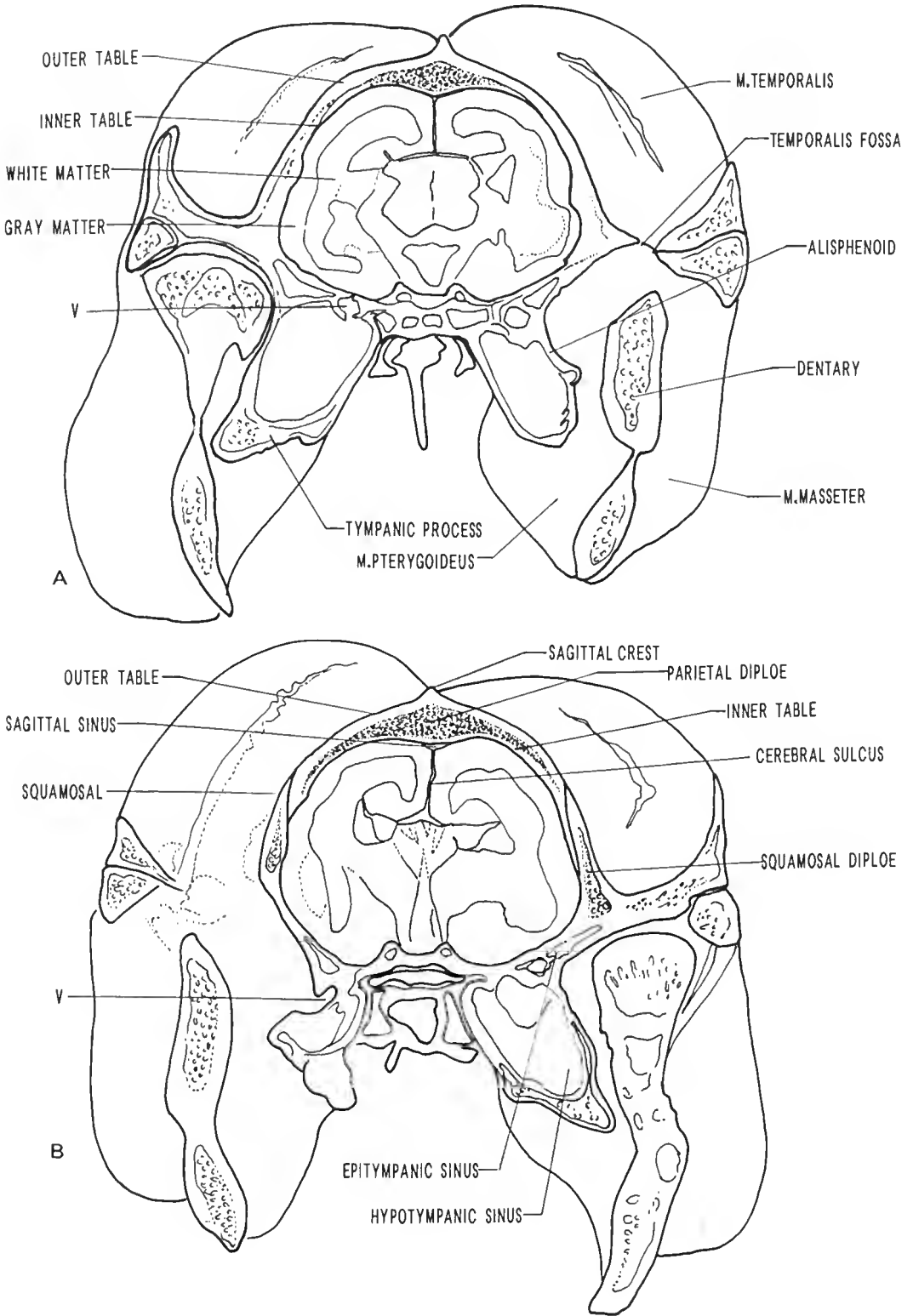


Fig. 3. Coronal section through the comparatively thin-vaulted neurocranium of the Koala, *Phascolarctos cinereus* (Goldfuss), showing soft tissue relations of the braincase; **A**, looking anteriorly; **B**, looking posteriorly; note the development of a thin diploic layer, presence of small squamosal epitympanic sinuses and the approximately equal-sized masses of the m. temporalis and m. masseter.

table grows in reponse to brain growth and is highly sensitive to changes in brain size and shape throughout the lifetime of the animal. The outer table responds to the increasing demands of scalp tissues in general and specifically to the requirements of the jaw adductor muscles. The diploe intervene in proportion to the extent of functional dissociation between the inner and outer table. If the dissociation is extensive, large sinuses develop within the diploe layer as a result.

Consequently, the presence of large neurocranial sinuses in gigantic marsupial herbivores are readily explained by differential growth between the inner table which forms the neural capsule and is under the direct influence of brain growth, and the outer table which is under the direct influence of ectoeranian tissue demands. In the earliest stage of maturation in the fossil sample (*Kolopsis torus*), the inner and outer braincase are separated by a thin diploic

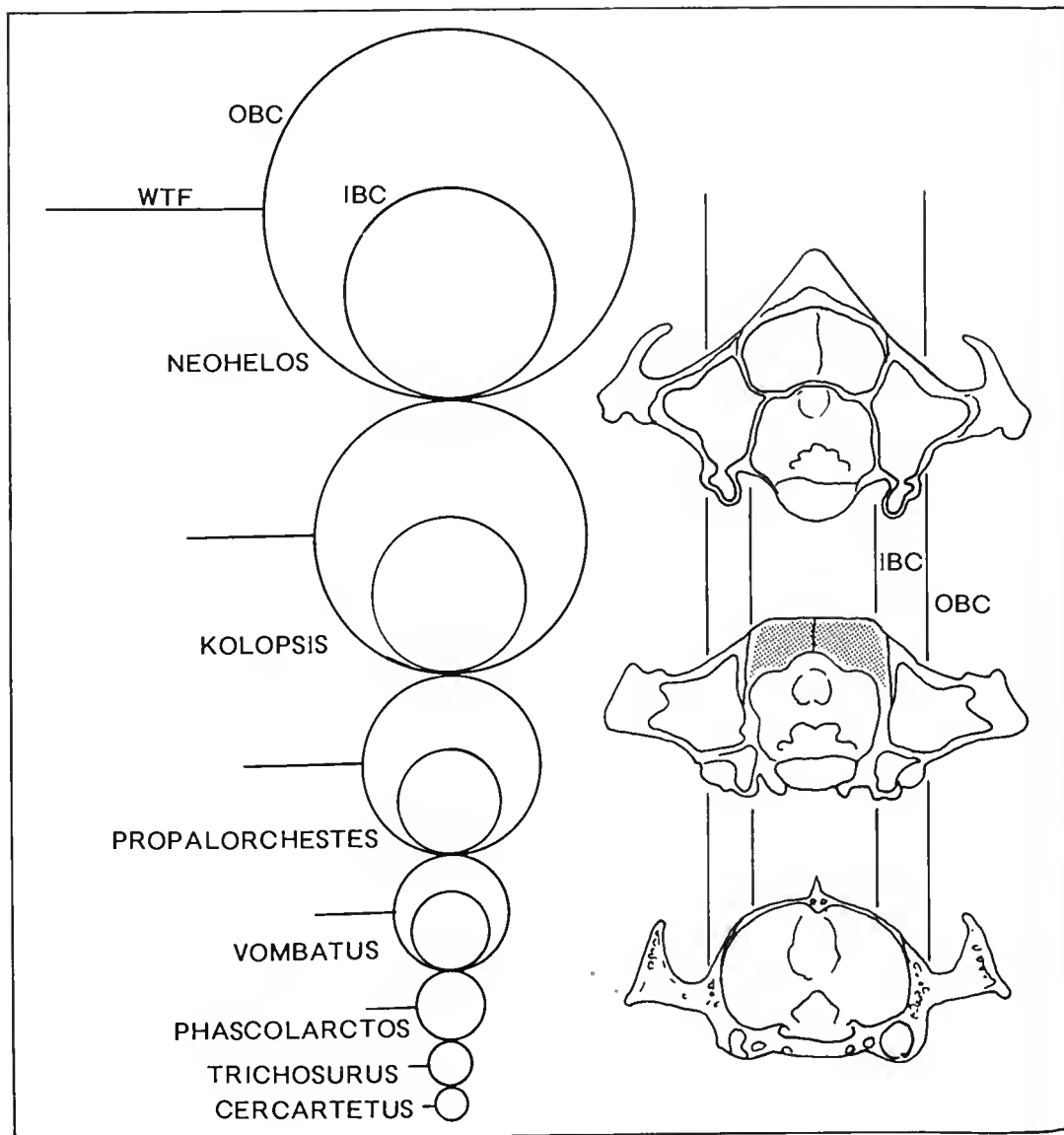


Fig. 4. Illustration of the relative extent of separation of the outer table (OBC) from the inner brain capsule (IBC) in a series of diprotodontian marsupials; line labelled WTF represents the width of the temporalis fossa in each genus. Note the differential in brain size (inner circle) relative to outer braincase size increases dramatically with the size of the animal, indicating a marked allometry in growth. Figures to the right are scaled to equivalent bitygomatic width: below, brushtailed possum, *Trichosurus*; middle, hairy-nosed wombat, *Lasiorhinus*; above, marsupial tapir, *Propalorchestes*. Abbreviations: OBC: outer table; IBC, inner brain capsule; WTF, width of temporalis fossa.

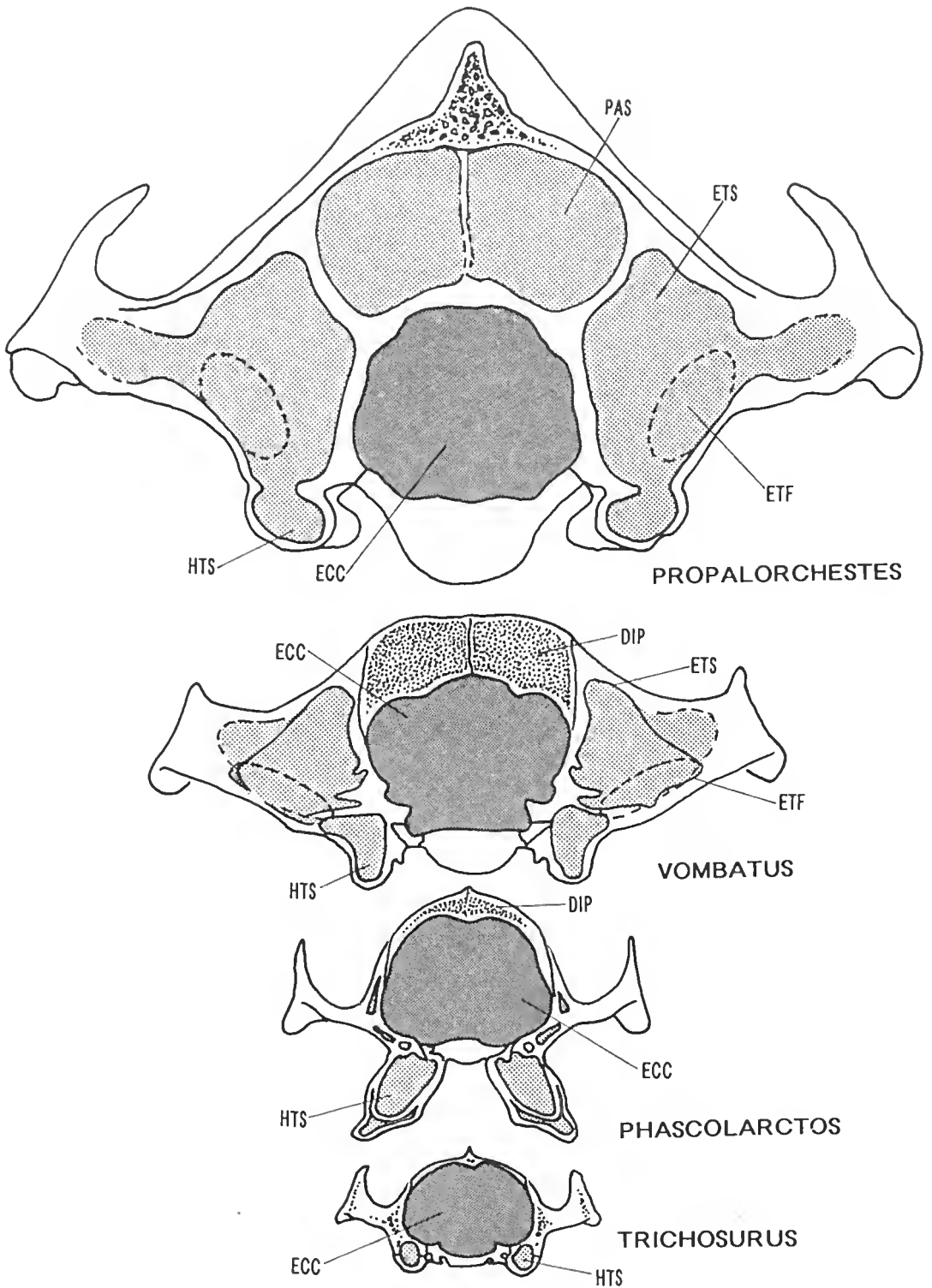


Fig. 5. Scale representation of size of neural capsule to size of the external braincase in a representative series of diprotodontian marsupials; note thin diploic layer in *Trichosurus*; Abbreviations: ECC, endocranial cavity; DIP, diploe; ETF, epitympanic fenestra; ETS, epitympanic sinus; HTS, hypotympanic sinus; PAS, parietal sinus.

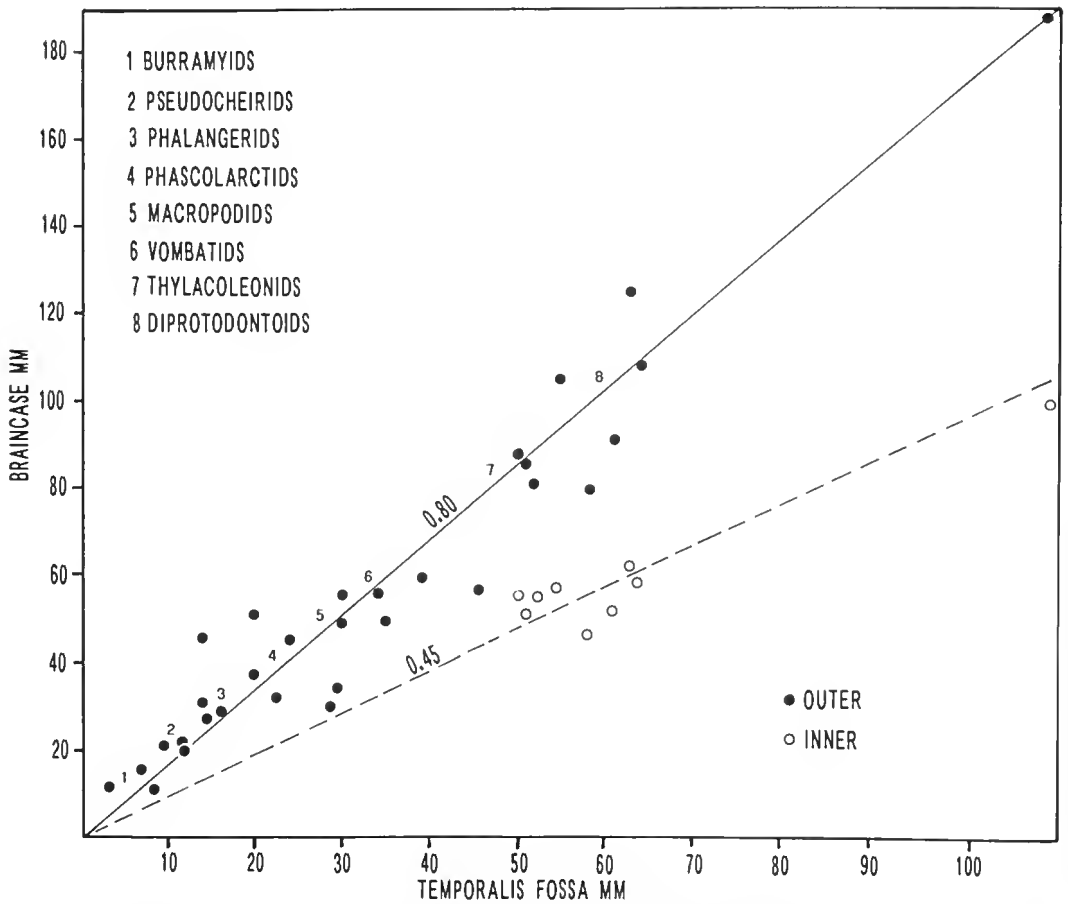


Fig. 6. Scatter diagram depicting differential growth between the outer braincase and neural capsule in a representative series of diprotodontian marsupial genera. The open circles represent the inner braincase width in genera in which there is a significant difference between the inner and outer table diameter. The difference in coefficients between the solid trend line (0.80) and the dashed trend line (0.45) indicate that brain growth is a primary factor in the separation of the inner and outer tables of the brain case.

layer and both surfaces correspond to the contour of the brain. By this encrypted M^4 stage, the brain had reached $4/5$ of its maximum volume, establishing the basic extent and form of the inner table of the cranial vault for the remainder of the animal's life. However, the external surface of the cranium of this species will have nearly doubled as the outer table of the neurocranium continues to grow in a linear proportion to the rest of the skull.

The most obvious advantage of the positive allometric growth of the outer table in giant marsupial herbivores is for the support of large adductor muscle masses. An external cranial surface determined by the volume of the relatively small neural capsule in diprotodontids would offer a very reduced surface area for their attachment, which would in any case have re-

quired the development of enormous sagittal and lambdoid crests. The development of a sinus-expanded extracranial surface has the additional advantage of being lighter than solid bony flanges, the air spaces insulate the brain from intramuscular temperature changes (overheating) and could even protect the brain from external trauma.

COMPARISON OF MARSUPIAL AND PLACENTAL HERBIVORES

The question remains as to why similar conditions are rare in large placental mammals, many of which show a high degree of proportional sliding between the splanchnocranium and the neurocranium. In the horse and domestic cow for

example, the facial skeleton becomes greatly enlarged in proportion to the neurocranium at maturity, yet there is no apparent equivalent compensatory increase in the surface area for adductor muscle attachment. Factors that seem relevant to this question are: 1) in placentals, the brain volume is generally greater, and the brain continues to expand until later in maturity; 2) the pattern of deciduous tooth replacement is markedly different and the tooth emplacement is relatively farther forward; and 3) the adductor muscle complex emphasizes a contrasting biomechanical pattern.

Brain size and growth. Investigations of marsupial brain size (endocranial volumes or mass) indicate that the diprotodontians (phalangeridans and vombatiformes) have attained brain sizes equivalent to the lower category of middle-ranked placentals (Moeller 1973, Jerison 1973) which consists primarily of large rodents (*Hystrix* Linnaeus, *Castor* Linnaeus, *Marmota* Blumenbach) in Moeller's (1973) sample. The brain mass to body mass ratios in the larger marsupial species are therefore not especially low. However, direct comparison among

very large marsupial and placental species shows the endocranial volume of the marsupial *Zygomaturus trilobus* Melcay to be approximately 400ml for an estimated body weight of 600kg, whereas the volume of the brain of a 763kg rhinoceros is 655ml (Crile and Quiring 1940). Thus while the differences are probably not great, absolute brain mass may account for some of the tendency for sinus formation in the cranium of large marsupial herbivores.

The factor of continued brain growth during later stages of maturation is difficult to compare because the growth stages of *Kolopsis torus* are not actually known and therefore cannot be directly compared with that of a cow. The endocrania of the cow and horse continue to show a small amount of expansion until they attain full size. Measurements of *Kolopsis* indicate that the endocranium ceases to expand by the time it reaches approximately half its mature cranial dimensions. It is possible, therefore, that the growth of the endocranium in placentals is able to maintain closer proportional growth to the splanchnocranium than its marsupial equivalents.

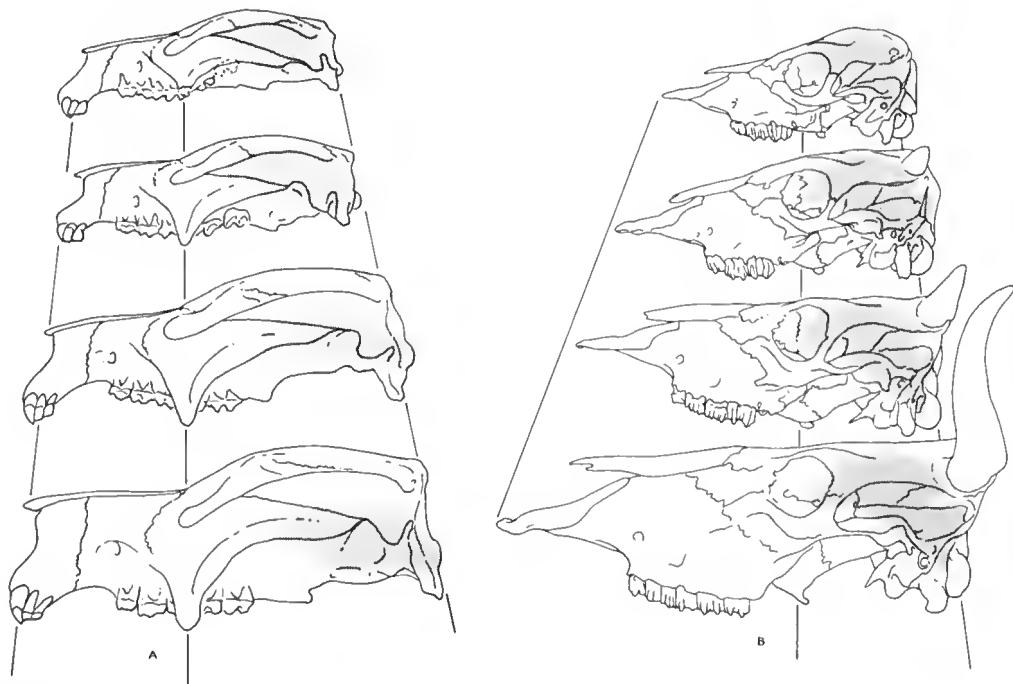


Fig. 7. Comparison of diprotodontid marsupial and placental herbivore cranial proportions during growth; **A**, a "growth series" of Miocene diprotodontid marsupial *Kolopsis torus* specimens from an encrypted M^1 stage to maturity; **B**, a growth series of the domestic cow, *Bos taurus*. Drawn to approximately equivalent cranial lengths for comparison, cow is actually about 25% larger than *Kolopsis*. Stipple represents the approximate size and shape of the neural capsule; lines compare extent of differential growth. The marsupial outer table growth shows a positive allometry over the splanchnocranium in contrast to the cow in which the splanchnocranium eventually dominates the neurocranium.

Tooth replacement. A primary difference in the development of the splanchnocranium relative to the neurocranium in marsupial and placental herbivores appears to be related to changes in the tooth row. In diprotodontid marsupials the length of the cheek tooth row is practically constant from the "active joey" stage to maturity. In the approximately equivalent postnatal to mature stages of the cow, the cheek tooth row, and consequently the entire facial component of the cranium, changes markedly in relation to the neurocranium. These modifications occur chiefly in relation to the cheek tooth replacement system in placentals, which by contrast to the marsupials is much more complex. Consequently the marsupial splanchnocranium undergoes relatively little proportional change in relation to either its cheek tooth row or its neurocranial component.

Adductor muscle complex. The form of the adductor muscle complex is the most important factor in the differences between large marsupial herbivore and large placental herbivore cranial form. Diprotodontid, palorchestid and even the large carnivorous thylacoleonid *Thylacoleo carnifex* Owen differ substantially from their placental eomorphic counterparts in retaining a relatively unspecialized adductor complex, classified by Turnbull (1970) as belonging to the Generalized Group.

Turnbull's classification pertains to the extent to which the temporalis, masseter and pterygoideus muscles contribute to jaw closure. In diprotodontids, palorchestids and thylacoleonids the temporalis fossa and surface attachment areas are very large, accounting for 50% or more of the total adductor mass. Felids, the placental equivalents to thylacoleonid marsupials, have Specialized Group I ("carnivore-shear") muscle complexes, and ungulates, the placental equivalents to the diprotodontids, have Specialized Group II ("ungulate-grinding" or "mill" type complexes (Fig. 8).

In the Specialized Group I complex, the temporalis muscle group is decidedly dominant. The muscle complex is characteristic of carnivores with shearing carnassial sets. In Specialized Group II species, the masseter is by far the dominant adductor accompanied by a relatively large pterygoideus contribution. The muscle mass classification of Turnbull (1970) is clearly paralleled by the schematization of jaw mechanics presented by Smith and Savage (1959).

Applied to the forms belonging to Turnbull's specialized groups, the Smith and Savage model closely corresponds. When applied to differenti-

ating the shearing-toothed carnivore *Thylacoleo* from the mill type herbivorous jaws of diprotodontids, the Smith and Savage model produces an ambiguous resolution due to the retention of a generalized adductor muscle complex in the two functional extremes found in the Diprotodontia (Wells *et al.* 1982).

It therefore follows that if the Generalized Group musculature is retained in diprotodontian marsupials, the underlying bony architecture must also be retained, despite the potentially constraining effect of a relatively small internal capsule of the braincase. A relatively small braincase does not constitute a limitation in the Specialized Group II placentals in which the role of the temporalis muscle is significantly reduced.

MACROPODID "EXCEPTIONS"

Large, living macropodid species have nearly the same brain mass to body mass proportions as the vombatids. Moreover, there were some very large extinct macropodids of the genera *Sthenurus* Owen and *Procoptodon* Owen that attained body masses at least two or three times as great as those of the largest living *Macropus* species. If the allometric principle for outer table expansion applies to the Vombatidae, Diprotodontidae and Thylacoleonidae, should it not apply equally to the large macropodids? Obviously it does not, as none of the macropodids, even *Procoptodon goliath* (Owen), the largest species known, had developed large intracranial sinuses surrounding the internal brain capsule.

Measurement of the proportional areas of jaw musculature attachment in large macropodid crania reveals the apparent reason for the lack of conformity in *Macropus*. The temporalis fossa is unusually small and the surface for attachment of the temporalis is reduced compared to diprotodontids (Fig. 8F). Conversely, the m. masseter is large in relation to the m. temporalis and as might be anticipated, the proportions of the jaws conform to the Smith and Savage model of placental herbivore jaw mechanics.

Macropus, *Sthenurus* and *Procoptodon* are practically unique among marsupials in having a jaw adductor complex corresponding to Turnbull's Specialized group II (Turnbull 1970). Consequently, the absence of an expanded outer table of the neurocranium of large macropodids is anticipated and as such, provides additional evidence in support of the explanation of sinus development in vombatomorphs.

DISCUSSION

Current understanding of these growth and proportional phenomena does not indicate whether the development of the Specialized Group II jaw muscle complex represents an evolutionary alternative to positive allometry of the neurocranium in association with increased body size, or invariably, a naturally-selected functional refinement from a generalized pattern involving a reorganization of the muscle complexes in relation to trophic specializations. Turnbull (1970) concludes that mammals, in their course of evolution, tended to utilize the Generalized Group proportions long after other specializations had become established (i.e. specialized dentitions) until that configuration no

longer sufficed, at which point there was a shift over to the appropriate Specialized Group pattern.

Among the giant Australian marsupials, selection for development of compensatory scaling adjustments in the neurocranium, in order to retain a Generalized muscular plan has been favoured over a reorganization of the adductor muscle complex, irrespective of the considerable dental specializations found in vombatids, thylacoleonids and diprotodontids. This observation seems to beg the question as to the degree of trophic specialization necessary to induce selective pressures that would result in a Specialized muscular configuration. The retention of a Generalized adductor complex in the majority of marsupials may be related to less stringent competition among browsers and carnivores than

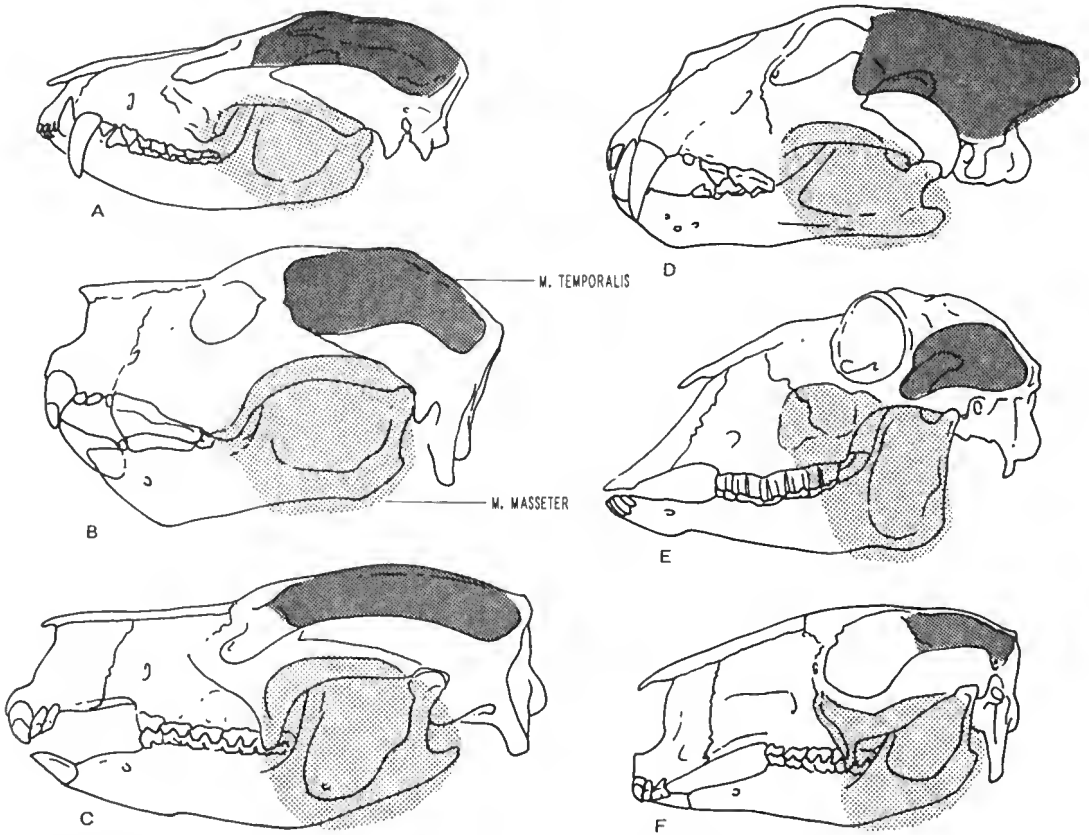


Fig. 8. Drawings of the lateral aspect of marsupial and placental skulls comparing the relative sizes of jaw adductor muscles in each species; the dark stipple represents the m. temporalis; the light stipple represents the m. masseter; **A**, living Virginia opossum *Didelphis virginianus* Kerr; **B**, Pleistocene marsupial lion *Thylacoleo carnifex*; **C**, miocene diprotodontid *Neohelos tirarensis* Stirton; **D**, living placental lion *Panthera leo* Linnaeus; **E**, living sheep *Ovis aires* Linnaeus (after Turnbull 1970); **F**, living red kangaroo (Macropodidae) *Macropus rufus* Desmarest. The large m. temporalis and almost equally large m. masseter contributions in A-C places these forms in Turnbull's (1970) Generalized Group; **D**, the lion, a placental carnivore, is an example of the Specialized Group I muscle complex in which the m. temporalis is clearly dominant over the m. masseter; **E**, *Ovis* the placental herbivore, is an example of the Specialized Group II muscle complex in which the m. masseter is dominant; **F**, the red kangaroo is decidedly a Specialized Group II marsupial. The small temporalis muscle in Specialized Group II herbivores does not require expansion of the neurocranial surface for its attachment.

among their placental counterparts, or it may reflect other conditions or restraints of which I am not aware.

The principal modifications of the specialized group adductor musculature pertain to changes in the cross-sectional areas of the muscle masses relative to their points of attachment. In the Generalized Groups, the muscular complexes are predominately broad, oval sections, whereas in the specialized group II muscle complexes, the musculature assumes a more rounded cross-sectional area. However, these gross observations do not provide an adequate explanation of the complexity of the functional modifications involved (Gans and Vree 1987, Gans 1988).

That the Specialized Group II muscle complex has evolved in macropodids but not in diprotodontids, palorchestids or thylacoleonids raises a potentially interesting line of investigation that may be ultimately related to dental evolution in these forms. More detailed studies of some of the parallels between macropodids and Group II placental herbivores may provide new insights into the functional evolution of jaw adductor complexes. Sanson (1989) points out, for example, that the grazing macropodines require very precise occlusion, a feature that might underly the development of specialized adductor systems in all mammals with similar requirements.

SUMMARY AND CONCLUSIONS

Large extinct marsupials of the families Diprotodontidae, Palorchestidae and Thylacoleonidae have highly pneumaticized braincases. The internal capsule of the braincase in these forms is suspended within the outer table by thin septa that correspond to the original parietosquamosal and parietal to parietal contacts. A phylogenetic trend towards this condition is seen in the living wombats in which the cranial vault is greatly thickened, but retains the intervening diploe. It is suggested that vombatids are sufficiently large to reflect a positive allometric relationship of the outer table of the neurocranium to the inner table surrounding the neural cavity. However, large kangaroos, which have about the same brain mass to body mass proportion as vombatids, do not develop a thickened cranial vault.

Previous studies (Gregory 1903, Moss and Young 1960) have demonstrated that the inner

and outer tables of the braincase develop independently of one another in accordance with the demands of their associated soft tissue relations. The inner table responds to brain growth and the outer table responds to the supportive requirements of the jaw musculature.

Because the large diprotodontians express an allometry of inner table surface area relative to body size increase, due to brain growth proportional to the cube of its linear dimensions, the neural capsule itself offers inadequate surface area for the attachment of the large jaw adductor musculature, especially the temporalis. The outer table of the braincase responds to the surface area requirements of the temporalis muscle by growing outwards, proportional to the square of its linear dimensions, independently of the inner table. This process of separation of the inner and outer tables of the neurocranium results in the creation of large air spaces or sinuses between the two laminations of bone.

A similar degree of sinus formation is rare in equivalent-sized placental mammals. The placental herbivores also show a marked difference in the proportioning of their jaw muscle complex, in which the temporalis muscle is greatly reduced, thus eliminating the requirement of a large surface for its attachment. Diprotodontids, palorchestids and thylacoleonids however, retain a generalized or primitive adductor muscle complex in which the temporalis remains as large, or larger than, the masseter, thus necessitating a correspondingly large surface for its attachment.

The large kangaroos represent an exception to the diprotodontian allometric principle. They are unique among diprotodontian marsupials in having developed a specialized jaw adductor complex very similar to that of placental herbivores in which the masseter muscle is dominant to the *m. temporalis*. The absence of cranial thickening or intracranial sinuses in kangaroos is therefore consistent with the present model.

ACKNOWLEDGEMENTS

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THE SMALLEST NEW GUINEA ZYGOMATURINES- DERIVED DWARFS OR RELICT PLESIOMORPHS?

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ABSTRACT

Three Pleistocene species of zygomaturine diprotodontids are presently known from New Guinea. Two of these distinctive marsupials are much smaller than any of the late Tertiary zygomaturines that occurred in Australia, but are more similar in size to certain mid to late Mioene genera. Stirton *et al.* (1967), Flannery and Plane (1986) and Flannery (1988) have suggested that the late Tertiary New Guinea assemblages represent relict species with closest affinities to the mid to late Mioene faunas of Australia. A broad comparison of the morphology of late Pleistocene New Guinea zygomaturines indicates that they are derived species of the Australian Plio-Pleistocene *Zygomaturus* clade. As the relict fauna hypothesis appears to stem primarily from a "stage of evolution" interpretation of the New Guinea diprotodontids, this conclusion has significant implications for the palaeozoogeographic interpretation of New Guinea.

KEYWORDS: Diprotodontidae, *Zygomaturus*, New Guinea, Tertiary biochronology, palaeozoogeography, marsupial systematics and morphology.

INTRODUCTION

Stirton (1967) and Plane (1967) originally observed that the New Guinea zygomaturine diprotodontids *Kolopsis rotundus* Plane and *Kolopsoides cultridens* Plane expressed closer affinities with the Australian Miocene species *Kolopsis torus* Woodburne than to any of the Plio-Pleistocene species of *Zygomaturus* Mcleay. At the time it was thought that the Awe Loal Fauna (LF) was an early Pliocene-aged fauna. Moreover, it was generally held that the smaller diprotodontids were more primitive and therefore older than the larger species. In the next decade, Flannery and Plane (1986) described a small zygomaturine marsupial from the Pleistocene of New Guinea as *Hulitherium tomasettii* Flannery and Plane. They conclude that the monotypic *Hulitherium* also represents a relict species, reminiscent of certain Mioene genera known from the mainland of Australia. Shortly after their 1986 publication, another New Guinea Pleistocene zygomaturine was discovered in Irian Jaya. Though significantly smaller and apparently more specialized, this

new diprotodontid shows some close resemblances to *Hulitherium*. This paper provides an alternative hypothesis of New Guinea zygomaturine phylogeny in which the available evidence is found to agree with revised radiometric dates and our current understanding of diprotodontid stage of evolution biochronology. I intend to establish the following points in the discussion: 1) that with the exception of *Kolopsoides cultridens*, all known Pleistocene New Guinea zygomaturines are members of the *Zygomaturus* clade; 2) the character states of all three New Guinea Pleistocene forms are derived relative to early to mid Pliocene *Zygomaturus* species known from mainland Australia; 3) there is sufficient biochronological and phylogenetic information to establish the most likely ancestor for the New Guinea Pleistocene species; 4) consequently, it is possible to give an estimation of the time the genus *Zygomaturus* entered New Guinea; 5) that the size and morphology of the two smallest species is best explained as habitat related size-reduction or insular dwarfing; and finally 6) that the estimated time of arrival of zygomaturines in New Guinea does not support

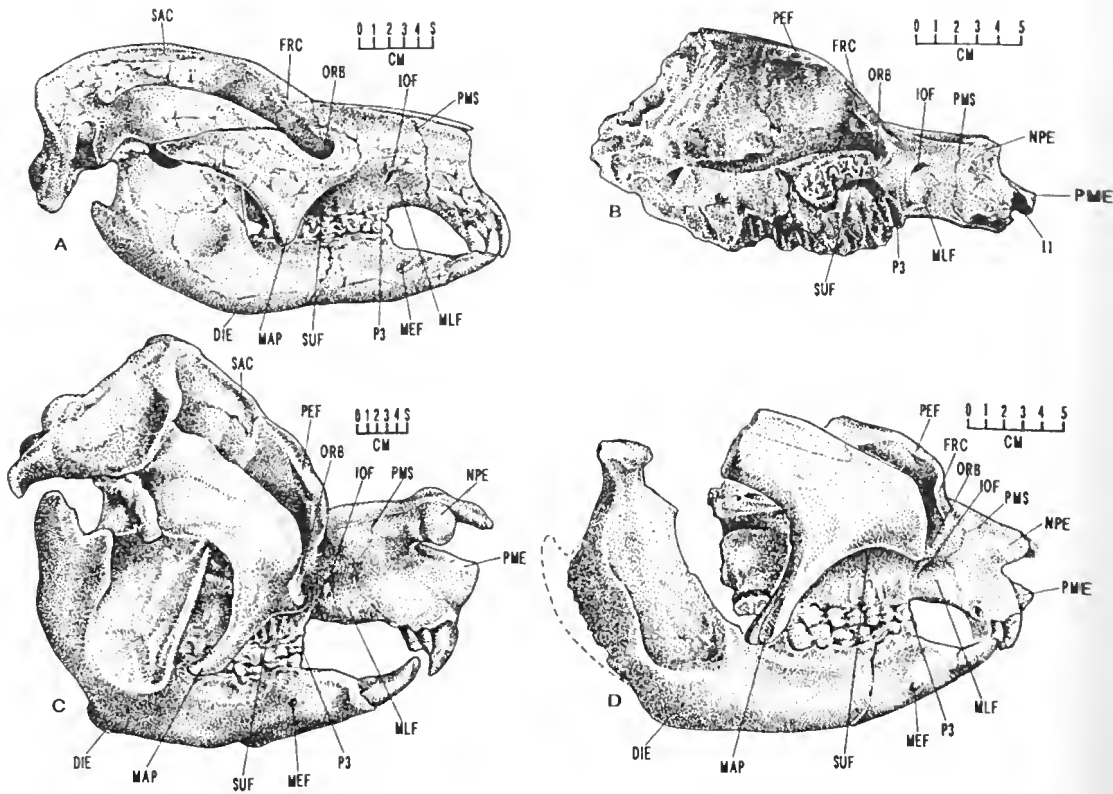


Fig. 1. Lateral aspects of representative zygomaturine crania, A, *Kolopsis torus*, Alcoota LF, Late Miocene, an advanced zygomaturine genus and likely structural precursor of *Zygomaturus*; B, *Hulitherium tomasetti*, Pureni LF, Late Pleistocene (drawn from photograph in Flannery and Plane 1986); C, *Zygomaturus trilobus*, Mowbray Swamp LF, Late Pleistocene (drawn from a cast prepared by Queen Victoria Museum, Launceston); D, N.G. Gen. nov. NTM P8660-1, P8660-2, P8668-3, Balliarn LF, Late Pleistocene. Labels are defined in the key to anatomical abbreviations. Note deflected cranial bases, steep frontal profiles, deep suborbital fossae, short, deep zygomatic arches with and strap-like zygomatic processes (missing on B), low narial apertures and anteriorly situated orbits in B-D.

the hypothesis of an early Miocene faunal disjunction (Flannery 1988) from Australia.

Three Late Pleistocene New Guinea zygomaturines have each been assigned to different genera: *Hulitherium* (Flannery and Plane 1986), *Zygomaturus* (Hardjasasmita 1985); and a new genus, as yet undescribed (Flannery, pers. comm.) (Figs 1-2). I refer to T. Flannery's proposed new genus as "N.G. Gen. nov." in order to avoid a nomen nudum. My observations on this new New Guinea species are based on another specimen (NTM P8660-1, P8660-2, P8660-3) that may differ somewhat from Flannery's proposed type, which I have not had the opportunity to examine first hand. However, the points I made at the CAVEPS symposium (Murray and Walker 1991) did not entail a formal description of the species, and it was only after I received a prepublication copy of Flannery's manuscript that I realized that there might be a potential problem.

At present, the majority of Australian Tertiary age estimations of Local Faunas are based on faunal correlations, primarily involving a succession of diprotodontid marsupials (Stirton *et al.* 1967, Archer *et al.* 1989). In light of recent revisions of the age of the Awe Fauna (Hoch and Holm 1986, Page and McDougal 1972), the systematic conclusions in Stirton *et al.* (1967) and Flannery and Plane (1986) imply that biostratigraphic age determinations for New Guinea are inherently unreliable. In re-examining some of the morphological evidence relating to the apparent discrepancy in stage of evolution correlations with radiometric age determinations for New Guinea, I found that a relatively minor re-interpretation of the data places the biochronological evidence in accordance with the radiometric dates.

The genus *Zygomaturus*, which first appeared in the late Miocene Sandringham Sands at Beaumaris, Victoria, had differentiated into three

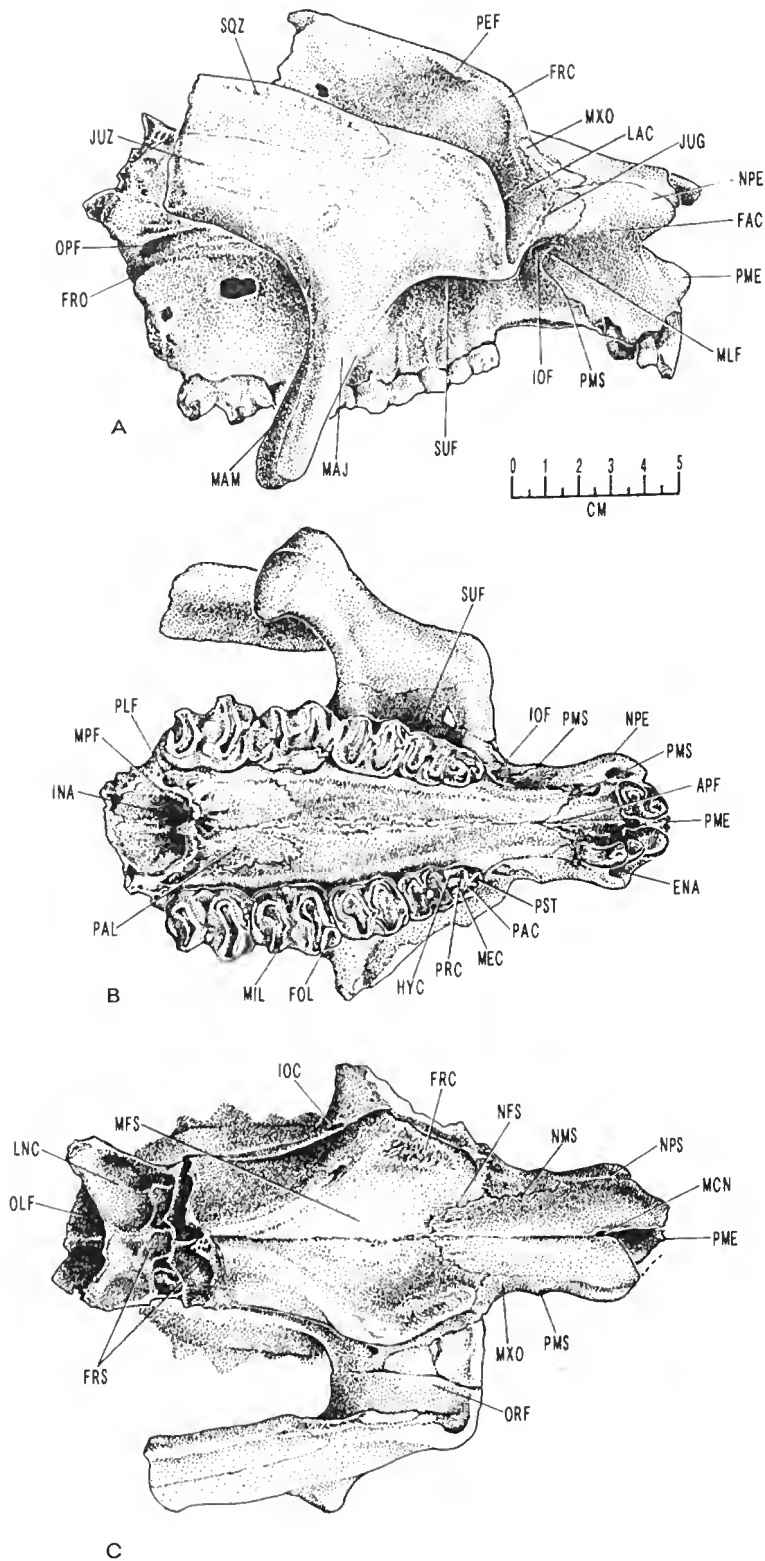


Fig. 2. Cranium of Baliem LF zygomaticurine NTM P8660-1 (N.G. *Gen. nov.*), A, lateral aspect; B, ventral aspect; C, dorsal aspect; showing many similarities to the Australian Pleistocene species *Zygomaturus trilobus*. Labels are defined in key to abbreviations.

or perhaps four Australian species by the late Pleistocene (Stirton *et al.* 1967, Woodburne *et al.* 1985). There is no evidence for the existence of the genus before the late Miocene or early Pliocene (Woodburne *et al.* 1985).

The morphological succession toward *Zygomaturus* is based upon the addition of cusps and proportional changes in the permanent upper premolar crown; initially, the hypocone becomes a consistent feature in the mid Miocene genus *Neohelos* Stirton, followed by the division of the para-metacone into two distinct cusps in the late Miocene genus *Kolopsis* Woodburne (Stirton *et al.* (1967) (Fig. 3). Present in the mid to late Miocene were two basic zygomaturine clades: 1) plesiomorphic 3-and 4-cusped forms retaining an elongated, undifferentiated para-metaconal crest (*Neohelos*, *Plaisiodon* Woodburne, *Alkwertatherium* Murray) and 2) apomorphic 5-cusped forms with fully differentiated paracone and metacone (*Kolopsis* and *Zygomaturus*) (Murray 1990) (Figs 3-4).

A species of *Kolopsis* (Figs 1, 3-4) is the most likely structural precursor for *Zygomaturus* (Stirton *et al.* 1967, Woodburne *et al.* 1985, Murray 1990). Accordingly, the genus *Kolopsis* is the designated sister taxon of the genus *Zygomaturus*, constituting the plesiomorphic outgroup for phylogenetic analysis below the generic level. The genus *Kolopsis*, which apparently became extinct in Australia in the late Miocene, was thought to have persisted in New Guinea until the late Pliocene (Planc 1967,

Woodburne *et al.* 1985). Evidence presented in this paper indicates that *Kolopsis rotundus* is a member of the *Zygomaturus* clade. The New Guinea zygomaturine genus *Kolopsoides* Plane, 1967, is considered here to represent a distinct derived lineage external to the *Kolopsis-Zygomaturus* ingroup.

ANATOMICAL ABBREVIATIONS

APF	Anterior palatal fenestra/incisive foramen
BC	Buccal cingulum
DIF	Digastric fossa
DIE	Digastric eminence
ENA	External nares
FAC	Facial crest
FOL	Forelink
FRC	Frontal crest
FRO	Foramen rotundum
HYC	Hypocone
I ⁿ	Upper incisor
INA	Internal nares
IOF	Infraorbital foramen
JUG	Jugal
JUZ	Jugal portion of zygomatic arch
LAC	Lacrimal
LC	Lingual cingulum
LNC	Lamina of neurocranium
MAJ	Jugal portion of masseteric or zygomatic process
MAM	Maxillary portion of masseteric

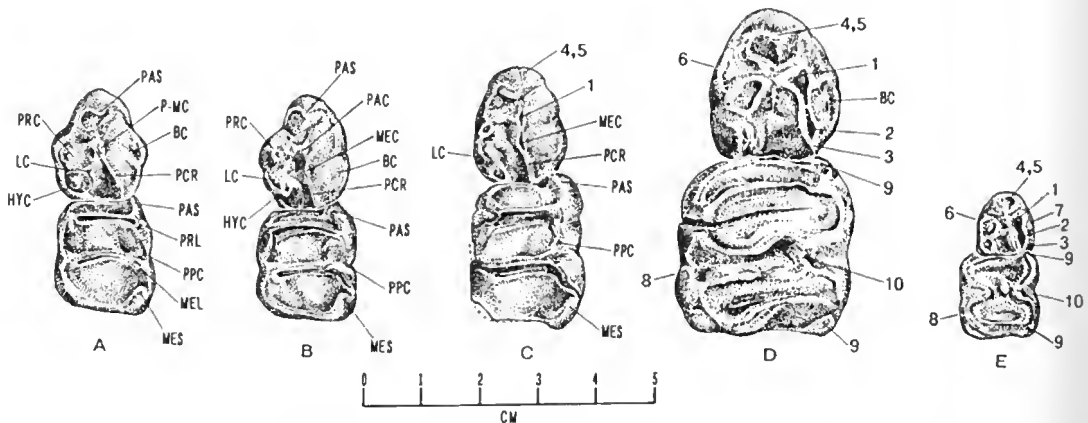


Fig. 3. Occlusal aspects of P¹ and M² of A, *Neohelos* sp. Bullock Creek LF, mid Miocene; B, *Kolopsis torus*, Alcoota LF, late Miocene; C, *Kolopsis* sp. nov. Ongeva LF, late Miocene; *Zygomaturus trilobus*, Victoria Cave LF, Late Pleistocene; E, N.G. Gen. nov. NTM P8660-1., Balicim LF, Late Pleistocene. The morphological succession in dentition from *Neohelos* to *Zygomaturus* is gradual and continuous. *Zygomaturus* P¹ morphology is distinguished by a trend towards molarization, broadening of the crown and reduction of crown length relative to M². The four principle cusps become arranged in a square and the parastyle becomes more confluent with the outline of the crown. Large numerals refer to *Zygomaturus* synapomorphies given in Tables 1-2; labels on structures are defined in the key to abbreviations.

MAP	or zygomatic process	PAC	Paracone
MCN	Masseteric/zygomatic process	PAL	Palatine
MEC	Median cleft between nasals	PCR	Postpara-metacrista
MEC	Metacone	PEF	Postorbital eminence of frontal crest
MEL	Metoloph	PLF	Posterolateral palatine foramen
MES	Mctastyle	P-MC	Para-metacone
MFS	Median frontal sulcus	PME	Premaxillary eminence
MIL	Midlink	PMS	Premaxillary-maxillary suture
MLF	Maxillo-labial fossa	PMX	Premaxilla
MPF	Posteromedian palatine foramen	PPC	Postparacrista
MX	Maxilla	PRC	Protocone
MXO	Ossicle of maxilla	PRL	Protoloph
NPE	Naso-premaxillary eminence	PST/PAS	Parastyle
NMS	Naso-maxillary suture	PTF	Pterygoid fossa
OLF	Internal cavity of olfactory bulb	SAC	Sagittal crest
OPF	Optic foramen	SQZ	Squamosal process of zygomatic arch
ORB/ORF	Orbit/orbital fossa	SUF	Suborbital fossa
P ³	Permanent upper premolar		

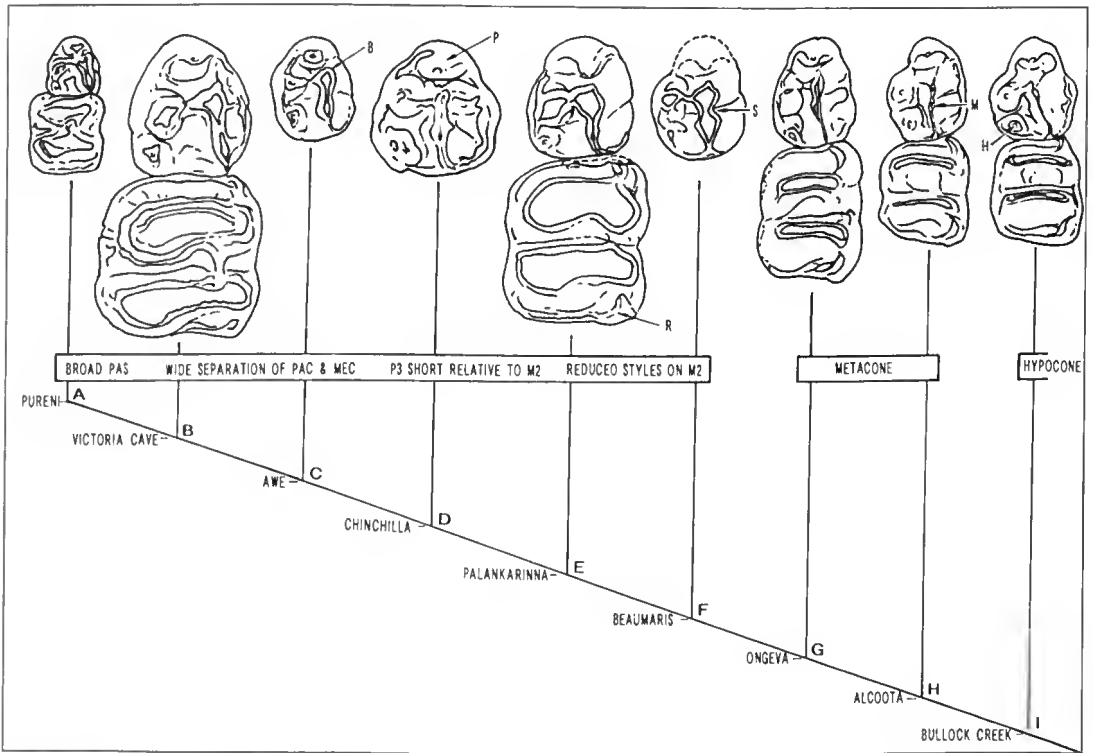


Fig. 4. Diagram depicting the broader eladistic units of the Zygomaturinae based on upper third premolar and second molar morphology; species are ordered stratigraphically according to the estimated age of respective local faunas; **A**, N.G. *Gen. nov.* Baliem LF, New Guinea, late Pleistocene; **B**, *Zygomaturus trilobus*, Victoria Cave LF, Naracoorte, S.A., late Pleistocene; **C**, *Kolopsis rotundus*, Awe LF, New Guinea, late Pliocene; **D**, *Z. cf. trilobus*, Chinchilla LF, QLD., late Pliocene; **E**, *Z. keanei*, Woodward Quarry, Palankarinna LF, S.A., late Pliocene; **F**, *Z. gilli*, Beaumaris LF, Vic., late Miocene-early Pliocene; **G**, *Kolopsis* sp., Ongeva LF, N.T., late Miocene; **H**, *Kolopsis torus* Alcoota LF, N.T., late Miocene; **I**, *Neohelos* sp., Bullock Creek LF, N.T., mid Miocene; drawn to scale. Abbreviations: H=addition of hypocone; M=differentiation of metacone from unitary para-metacanal cusp; S=increased separation of paracone and metacone accompanied by broadening of cusps; R=reduction of styles on M²; P=closer approximation and broadening of parastyle; B=paracone and metacone situated closer to the buccal margin of the crown.

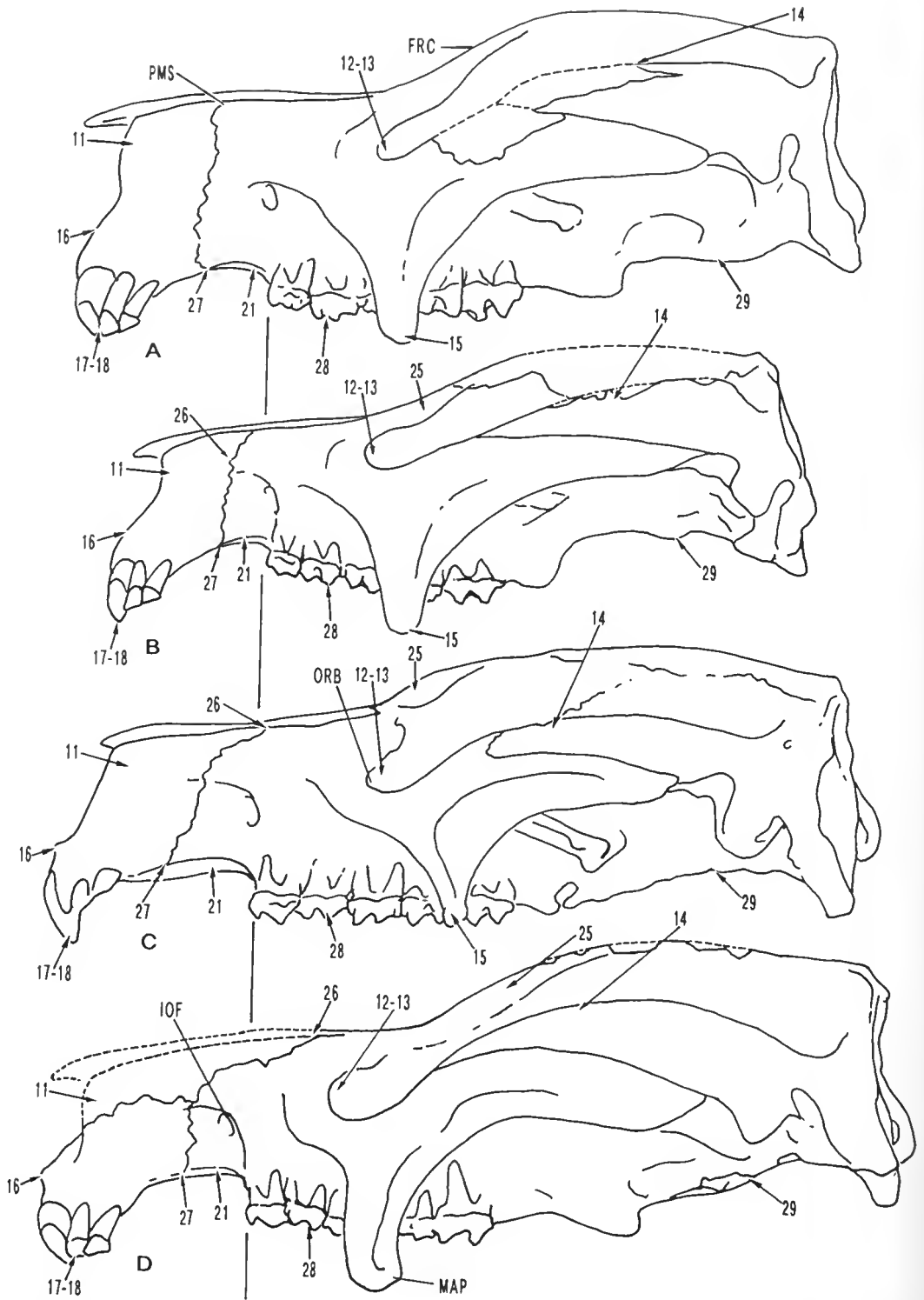


Fig. 5. Outlines of skulls of Australian Miocene zygomaturine genera representing plesiomorphic sister taxa of the genus *Zygomaturus*, scaled to equivalent cheek tooth row length for comparison; **A**, *Kolopsis torus*, Alcoota LF, late Miocene (X1/3); **B**, *K. torus*, Alcoota LF (showing typical size variation, possibly dimorphic), (X1/3); **C**, *Neohelos* sp., Bullock Creek LF, mid Miocene, (X1/3); **D**, *Plaisiodon centralis*, Alcoota LF (compare with type, Woodburne 1967: Fig. 32), late Miocene (X1/4). Small, narrow numerals depict symplesiomorphic states described in Table 1.

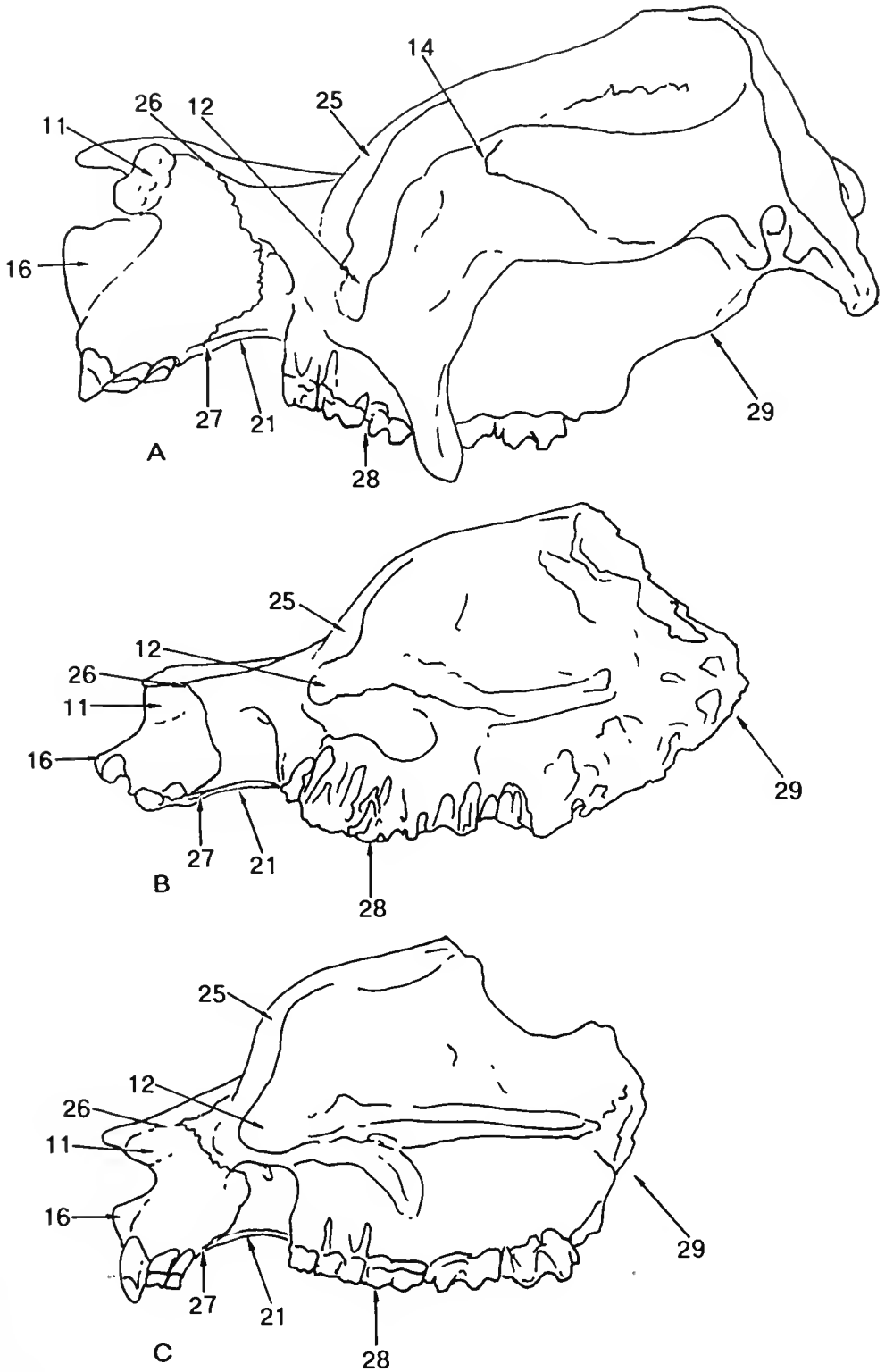


Fig. 6. Lateral aspects of crania of **A**, *Zygomaturus trilobus* (after Owen 1877); **B**, *Hulitherium tomasettii* (after Flannery and Plane 1986); **C**, N.G. *Gen. nov.* NTM P8660-1 showing *Zygomaturus* synapomorphies (large numerals, Tables 1-2); compare with previous figure (Fig. 5), the shape of the premaxillary-maxillary suture, position of orbit, profile of frontal, profile of narial aperture, proportions of cheek tooth row relative to rostrum.

MATERIALS

Northern Territory Museum (NTM) collection of Alcoota and Bullock Creek Local Fauna Diprotodontidae (*Kolopsis*, *Plaisiodon*, *Alkwertatherium*, *Pyramios* Woodburne, *Neohelos*); cranium and dentitions of *Z. trilobus*, Mcleay, Victoria Cave, South Australia; *Z. trilobus*, Mowbray Swamp, Tasmania (casts); cranium and two dentaries of *Zygomaturus* sp. nov., University of California, Santa Barbara, Department of Anthropology (original and NTM casts, P8660-1, P8660-2, P8660-3) Late Pleistocene, Baliem Valley, New Guinea.

RESULTS

Characteristics of *Zygomaturus*. *Kolopsis* is the plesiomorphic sister taxon of *Zygomaturus* on the basis of its synapomorphic possession of a divided para-metacone on the P³ which, however, is plesiomorphic with regard to *Zygomaturus* in that the paracone and metacone are closer together, and the postmetacrista remains comparatively long. *Zygomaturus* apomorphies of the P³ include closer approximation of the parastyle to the paracone and greater separation of the parastyle from the paracone from the metacone. The difference can be readily determined by noting the transverse alignment of the metacone with the hypocone in all known species of *Zygomaturus*, whereas in *Kolopsis* species the metacone is transversely aligned with the sulcus between the protocone and the hypocone (Figs 3-4).

Some other proportional differences are also apparent. For example, the para-metaconal crest in *Kolopsis* spp. is situated near the longitudinal midline of the crown whereas in *Zygomaturus* spp. it lies closer to the buccal margin (Fig. 3). In *Kolopsis* spp. the metastyle and parastyle of M² are large, flange-like crests. These structures are comparatively small in *Zygomaturus* spp. In *Zygomaturus* spp. the P³ length is considerably less than the M² length. In *Kolopsis* spp. the M² is nearly equal in length or only slightly longer, than the P³.

Zygomaturus possesses many other striking apomorphic contrasts with *Kolopsis* (Figs 5-10, Tables 1-2). Among the more obvious characters are the markedly reduced incisive foramina, anteriorly situated orbital margins, deep, bowed zygomatic arches and long transversely flattened zygomatic processes, presence of a flange-

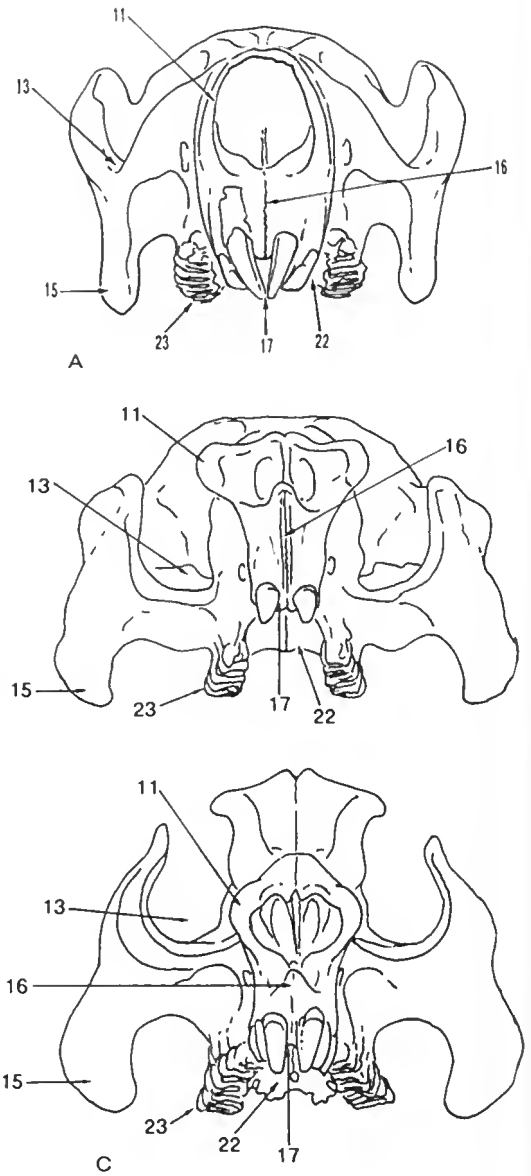


Fig. 7. Frontal aspects of crania of A. *Kolopsis torus*; B. *Zygomaturus trilobus* (after Owen 1877, note absence of sagittal crest in Owen's specimen in contrast to the well developed sagittal crest in the Tasmanian specimen); C. N.G. Gen. nov. NTM P8660-1 (tracing of a computer generated mirror-image restoration). Small numerals represent the plesiomorphic state of the morphocline, large numerals indicate *Zygomaturus* synapomorphies (Tables 1-2). Note the following strong contrasts in B and C with *Kolopsis torus* (A): transversely wide, low nares aperture with thickened dorsal margins compared to transversely narrow nares aperture with thin dorsal margins (11); frontally directed orbits compared to laterally directed orbits (13); laterally directed flange-like zygomatic processes compared to straight, conical processes (15); anterior convergence of cheek teeth (23).

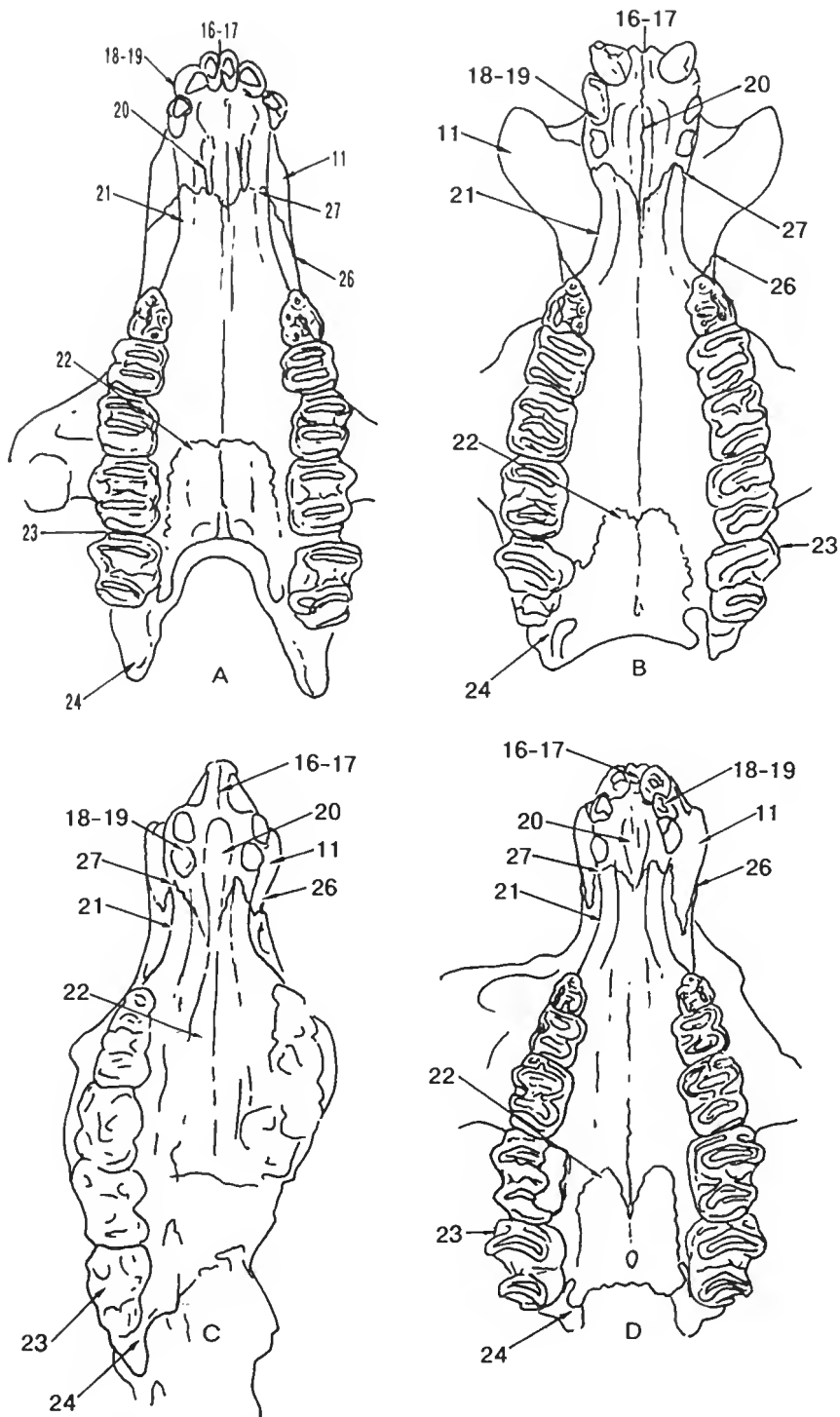


Fig. 8. Palatal aspects of crania of A, *Kolopsis torus*; B, *Zygomaturus trilobus*; C, *Hulitherium tomasettii* (after Flannery and plane 1986); D, N.G. Gen. nov. NTM P8660-1. Small numerals indicate plesiomorphous states, large numerals indicate apomorphous states (Tables 1,2); note synapomorphic reduction of incisive foramina (20), robust premaxillary eminence between widely separated central incisors (16-17), markedly constricted diastemal palate (21), position of premaxillary suture immediately behind the I¹ alveolus (27) and convergent cheek tooth rows (23).

like premaxillary crest between and above the central incisors, I¹ crowns widely separated and often divergent at the tips, chevron-shaped premaxillo-maxillary suture commencing immediately posterior to I³, steep frontal profile and strongly deflected basicranial axis. These features are apparently interrelated in a functional complex that serves to place the bite force of the molars and the incisors closer to the fulcrum of the jaw.

Two primary modifications from the plesiomorphic state (*Kolopsis*) have occurred in *Zygomaturus*: 1) the ascending ramus of the dentary is reflected anteriorly, reducing the angle between the tips of the incisors and the digastric process and from the digastric process to the dentary condyle; 2) the width between the dentary condyles and the glenoid fossae is increased in relation to the distance from the condyles and glenoid fossae to the upper and lower incisor tips (Figs 11-12).

These modifications result in a relative lengthening of the lever arm for the m. masseter while reducing the length of the load arm of the dentary. As the ascending ramus has become more vertical, the maxillary alveolus has deepened in order to retain its occlusal relationship. On the inside of the jaw, the digastric fossa, due to its elevation, has become separated from the pterygoid fossa. In the more obtusely angled jaws of *Kolopsis* and *Neohelos*, the fossae are confluent (Fig. 9).

The position of the glenoid fossa is correspondingly elevated in relation to the occlusal line, resulting in a marked degree of upward flexion of the neurocranium. Because the linear dimension of the dorsal surface of the neurocranium is considerably shortened, the naso-frontal angle becomes less obtuse. The dorsiflexion of the neurocranium is also responsible for the anterodorsal rotation of the jugal, which results in a distinctive lateral emargination of the orbit.

The splanchnocranium retains its upper incisive occlusal relationship with the increased recumbency of the lowers by a reduction of the length of the ventral premaxillary portion of the diastema. The complex shape of the premaxillo-maxillary suture in *Zygomaturus* is directly related to the overthrust of the fronto-naso-maxillary relationships dorsally, in response to neurocranial elevation and the ventral reduction of the length of the premaxilla.

The widening of the base of the triangle formed by the condyles and incisor tips reduces

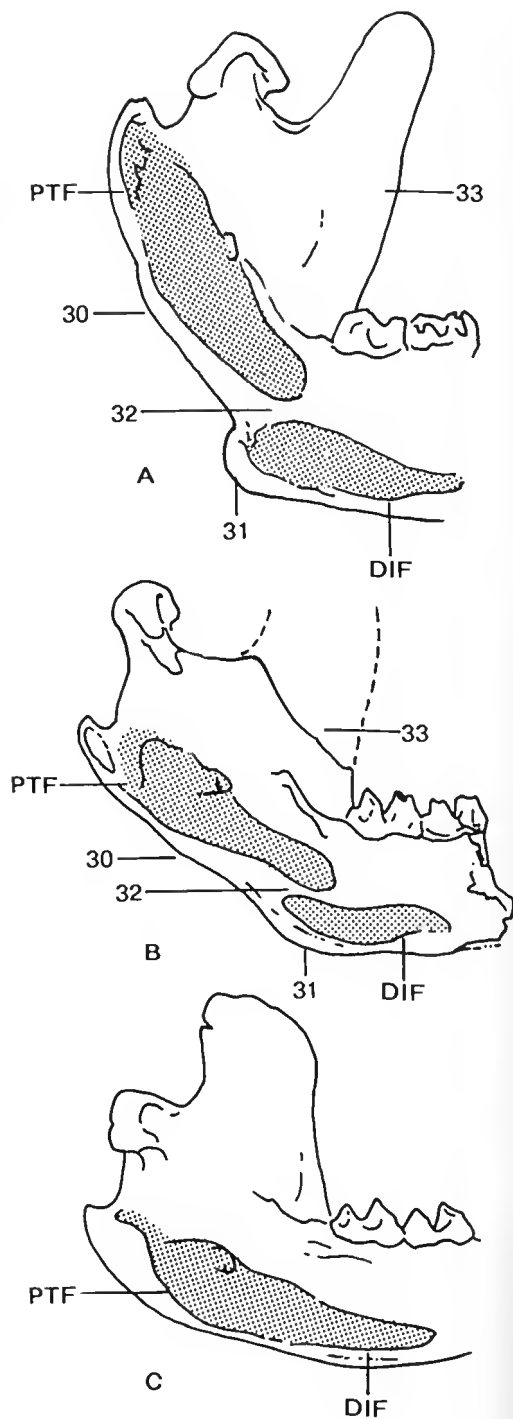


Fig. 9. Internal surfaces of dentary ascending rami A, *Z. trilobus*, Mowbray Swamp LF, Tasmania; B, *N.G. Gen. nov.* Baliem LF; C, *Kolopsis torus*, Alcoota LF. Note confluent digastric and pterygoid fossa in *K. torus*. Apomorphic states in A and B include erect or anteriorly inclined coronoid process (33); elevated angular process (30); separation of pterygoid and digastric fossae (32); posteriorly situated digastric eminence (31). Not to scale.

the amount of lateral excursion of the lower incisors in relation to the uppers but increases the vertical bite force exerted at the tips (Fig. 12). In *Kolopsis* the upper incisor arcade is broad, with small central incisors, whereas in *Zygomaturus* it is correspondingly narrow, with enlarged, tusk-like central incisors. Because relatively larger forces are exerted at the tips of the central incisors in *Zygomaturus* than in *Kolopsis*, the height of the narial aperture is reduced but widened, with concomitant bony thickening of the lateral and dorsal margins to resist bending moments on the rostrum.

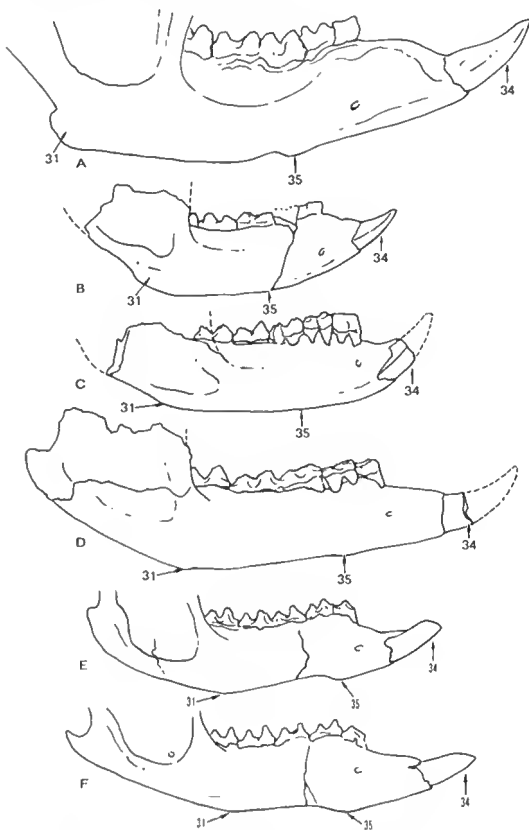


Fig. 10. Outlines of lateral aspect of horizontal rami of zygomaturines, drawn approximately to scale; A, *Zygomaturus trilobus*, Mowbray Swamp, Tasmania; B, N.G. *Gen. nov.* (P8660-2, P8660-3) Baliem LF, New Guinea; C, *Kolopsis rotundus*, Awe LF, New Guinea; D, *Z. keanei*, Keane Quarry, Palnkarinna, S.A.; E, *Kolopsis torus*, Alcoota LF, N.T.; F, *Neohelos* sp., Bullock Creek LF, N.T. Small numerals indicate plesiomorphous character states, large numerals indicate apomorphous states (Table 1). Note pointed, recumbent lower incisors in A-C. The lower incisor of *Z. keanei* (D) is broken off. Other specimens are worn. However, they appear to have been as strongly curved as *Z. trilobus*. In P8660-2, the lower incisors are divergent as in *Z. trilobus*. Synapomorphic *Zygomaturus* features include pointed, divergent recumbent lower incisors (34); long symphysis (35); posteriorly situated digastric eminence (31).

In *Z. trilobus*, a large, thick bony flange of the premaxilla may also assist in the reduction of torsion on the snout, particularly in relation to asymmetrical biting on its divergent central incisor tips. However, the premaxillary flange also may have supported the labial retractor muscles of a prehensile upper lip. Many large, short-faced herbivores (e.g. elephants, rhinos) have evolved selective feeding mechanisms to compensate for the absence of a long, narrow snout.

The anterior end of the cheek tooth arcades are more convergent in *Zygomaturus* than in *Kolopsis* (Figs 7-8, 12). According to Greaves (1978), anterior convergence of the cheek dentition acts to increase the force at the anterior teeth by shortening the resistance lever arms. Moreover, in conjunction with the increased bite force along the posterior portion of the cheek tooth row, the front-to-back gradient is greatly increased, with conspicuous enlargement of M^{4-5} , while the anterior end is correspondingly reduced in both length and width, especially P^3 and M^2 . The cheek tooth arcade is curved, retaining the same linear proportions as in *Kolopsis* but simultaneously increasing the occlusal surface area of the posterior half of the molar row. In lateral aspect, a slight curve of Spee is developed in response to the higher angle of occlusal moment.

I consider the inferred functional features of the skull outlined above to be co-dependant with the dental apomorphies that have long served to distinguish known *Zygomaturus* spp. from *Kolopsis* or *Plaisiodou* (Stirton *et al.* 1967), (Fig. 4, Tables 1-2). The upper third premolar of the genus *Zygomaturus* shows a clear trend towards molarization and antero-posterior compression of the anterior portion of the cheek tooth arcade, which is in agreement with Greave's (1978) functional interpretation of short-faced browsers. At the generic level, the unique features of the cheek teeth of *Zygomaturus* are integral components of its trophic specializations.

Because the characters used in this analysis are all considered to be part of a distinctive adaptive complex not manifestly present in the outgroup (*Kolopsis torus*), it follows that they collectively represent a synapomorphy for *Zygomaturus*. However, the states of various characters within the apomorphic complex may be indicative of the phylogenetic relationships of respective clade members. The horn-like nasal protuberances (naso-premaxillary eminences), greatly enlarged premaxillary flange (premaxil-

Table 1. Character state polarities of *Zygomaturus* determined by comparison of *Zygomaturus* species with *Kolopsis torus* outgroup.

	CHARACTER	APOMORPHIC	PLESIOMORPHIC	
P³	1	PAC & MEC	widely separated	close together
	2	para-metacristae	buccal	near midline
	3	postmetacrista	short, steep	long, inclined
	4	PAS to PAC gap	narrow	wide
	5	PAS width	broad	narrow
	6	occlusal shape	short, broad	long broad
	7	buccal cingulum	weak-absent	strong
M²	8	occlusal shape	square, broad	trapezoidal
	9	styles	reduced	large
	10	mid-valley	narrow, occluded	wide, open labially
CRANIUM	11	narial aperture	low, broad, thick	high, narrow, thin
	12	orbit position	above P ¹	above M ³
	13	orb. orientation	frontated	lateralized
	14	zygomatic arch	short, deep, bowed	long, straight
	15	zygom. process	long, transverse	short rounded
	16	pmx crest	present	absent
	17	upper I ¹	I ¹ large separated	I ¹ small, convergent
	18	upper I ²⁻³	small	large
	19	incisor arcade	narrow, u-shaped	broad, c-shaped
	20	incisive foramen	small, vestigial	very large
	21	upper diastema	short, constricted	long, wide
	22	palate	deep, arched	shallow, flat
	23	cheek tooth row	convex, convergent	straight, parallel
	24	postalv. proc.	Short	long
	25	frontal crests	large, vertical	moderate, inlined
	26	sup. PMX-MX sut.	Anterior	posterior
	27	inf. PMX-MX sut.	Close to I ³	far from I ³
	28	occlusal plane	convex	straight
	29	cranial base	marked flexion	slight flexion
DENTARY	30	ascending ramus	elevated, upright	low, inclined
	31	digastric proc.	Strong, posterior	weak, anterior
	32	ramal fossae	separated	confluent
	33	coronoid process	projects anteriorly	inclined posteriorly
	34	lower incisor	recumbent, pointed	procumbent, blunt
	35	symphysis	long, deep	short, shallow

lary eminence), extremely large body size and the exaggerated frontal and orbital protuberances of *Zygomaturus trilobus* are autapomorphic features of that species. Conversely, the plesiomorphic retention of a well-developed buccal cingulum on the P³ of *Z. trilobus* might indicate that it is a relatively early derivation of the clade. However, the expression of this relatively minor and variable character might also be

interpreted as a size-related manifestation. In most other anatomical respects, *Z. trilobus* is fairly typical of the group.

I give the basic attributes of the skull and dentition of *Z. trilobus* greater taxonomic weight than its rather spectacular allometric distortions and autapomorphic protuberances. Consequently, my view of the phylogenetically significant synapomorphic features of the genus differs

Table 2. Distribution of character states in representative advanced zygomaturines; A=apomorphic state; P=plesiomorphic state; numerically designated characters defined in Table 1.

CHARACTER		<i>Kolopsis torus</i>	<i>Kolopsis</i> sp.	<i>Kolopsis rotundus</i>	<i>Zygomaturus gilli</i>	<i>Zygomaturus</i> cf. <i>trilobus</i>	<i>Zygomaturus trilobus</i>	<i>Zygomaturus keanei</i>	<i>Zygomaturus</i> sp. Lawson - Daily	<i>Hulitherium tomasettii</i>	N. G. Gen. nov.
P ³	1	A	A	-	A	A	A	A	A	P	P
	2	A	A	-	A	A	P	A	A	P	P
	3	A	A	-	A	A	A	A	A	P	P
	4	A	A	-	A	A	A	A	A	A	P
	5	A	A	-	A	A	A	P	A	A	P
	6	A	A	-	A	A	A	P	A	A	P
	7	A	A	-	A	P	P	A	A	A	P
M ²	8	A	A	A	A	A	-	-	-	P	P
	9	A	A	A	A	A	-	-	-	P	P
	10	A	A	P?	A	A	-	-	-	P	P
CRANIUM	11	A	A	-	-	A	-	-	-	-	P
	12	A	A	-	-	A	-	-	-	-	P
	13	A	-	-	-	A	-	-	-	-	P
	14	A	A	-	-	A	-	-	-	-	P
	15	A	-	-	-	A	-	-	?	P	P
	16	A	A	-	-	A	-	-	-	-	P
	17	A	A?	-	A?	A	-	-	A?	-	P
	18	A	A	-	A?	A	-	-	-	P?	P
	19	A	A	-	-	A	-	-	-	-	P
	20	A	A	-	-	A	-	-	-	-	P
	21	A	A	-	-	A	-	-	A?	-	P
	22	A	A	-	-	A	-	-	-	-	P
	23	A	A	-	-	A	-	-	-	-	P
24	A	A	-	-	A	-	-	-	-	P	
25	A	A	-	-	A	-	-	-	-	P	
26	A	A	-	-	A	-	-	-	P	P	
27	A	A	-	-	A	-	-	-	P	P	
28	A	A?	-	-	A	-	-	A?	-	P	
29	A	A	-	-	A	-	-	-	-	P	
DENTARY	30	A	-	-	-	A	-	-	A?	P	P
	31	A	-	-	-	A	-	-	A	P	P
	32	A	-	-	A?	A	-	-	A?	P	P
	33	A	-	-	-	A	-	-	A?	-	P
	34	A	-	-	A?	A	-	-	A	-	P
	35	A	-	-	A	A	-	-	A	-	P

somewhat from that of Flannery and Plane (1986). Polarities for the expression of characters in *Zygomaturus* were obtained by contrasting *Zygomaturus trilobus* with *Kolopsis torus* (Tables 1,2).

Small New Guinea species (*Hulitherium* and N.G.Gen. nov.). Outgroup comparison of the distribution and expression of characters among the species under consideration (Tables

1-2) indicates that *Hulitherium* and N.G. Gen. nov. are members of the *Zygomaturus* clade (Figs 4, 14). Both genera share virtually all uniquely *Zygomaturus* features such as arcuate premaxillary suture commencing immediately behind I³, markedly reduced incisive foramina, precipitous frontal profile, infraorbital foramen situated close to anterior orbital margin, anterior orbital margin situated well forward over P³,

premaxillary crest developed between and above central incisors, thickened premaxillary margins of the external narial aperture and a strong meristic gradient between anterior and posterior cheek teeth. It follows that if *Hulitherium* and N.G. *Gen. nov.* are considered to be separate genera, then on cladistic grounds the differences among the other *Zygomaturus* species might also qualify them for separate genus rank distinctions.

Flannery and Plane (1986:66-67) state that *Hulitherium* "...possesses high vaulted frontals that are otherwise seen only in the species of *Plaisiodon* and *Zygomaturus*, and a reduced paracrista on M_2 and an anterodorsally directed maxillary-premaxillary suture, features otherwise seen only in species of *Zygomaturus*." A chip of enamel from the buccal side of P^3 shows that the paracone and metacone of *Hulitherium* are widely separated and that the postmetacrista

is very short and steep. Moreover, Flannery and Plane (1986) noted that the P^3 of *Hulitherium* differs from *Z. gilli* "...in having the paracone and metacone closer at the buccal margin." The character distribution indicates that this is a derived feature of *Zygomaturus* species. In *Kolopsis* and primitive *Zygomaturus* species, the paracone and metacone slope lingually towards the midline of the crown. Consequently, *Hulitherium* expresses a more derived state of the *Zygomaturus* P^3 morphocline than does *Zygomaturus gilli* (Tables 1-2). Flannery and Plane (1986:74) place *Hulitherium* in its own genus as a possible sister taxon of *Zygomaturus* because: "In many features, *Hulitherium tomasettii* is more plesiomorphic than *Z. trilobus*...and because the postcranial morphology is markedly different from that of *Z. trilobus*, indicating an apparently long period of specialization..."

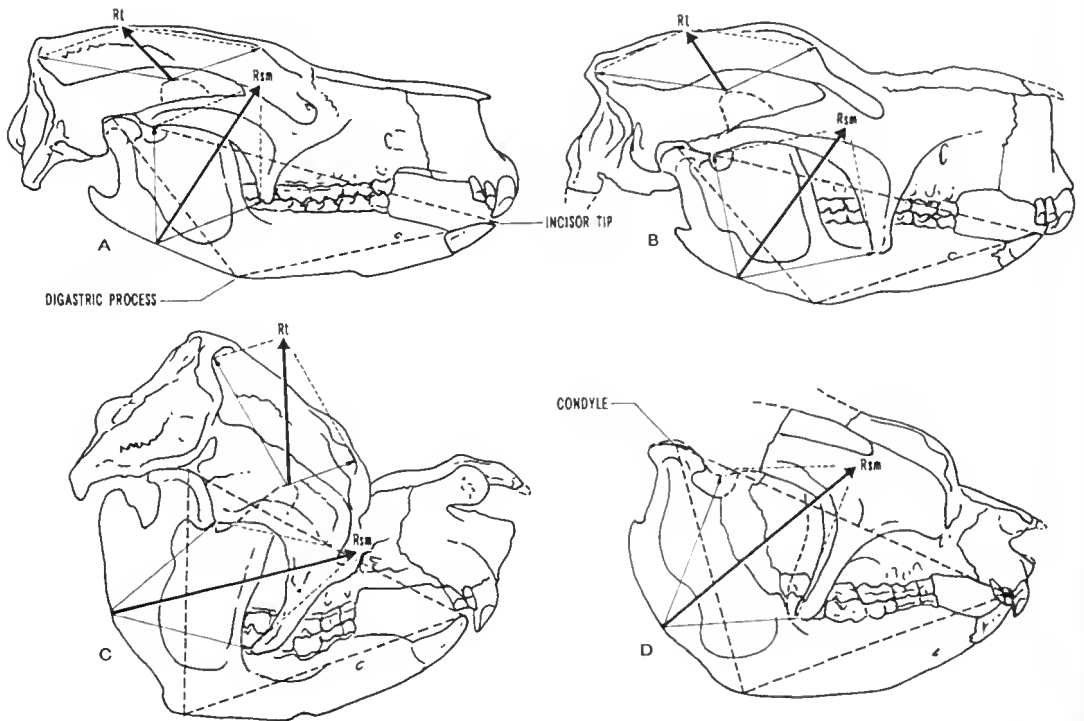


Fig. 11. Comparison of lateral aspect of skulls of plesiomorphic and derived zygomaturines; A, *Neohelos* sp.; B, *Kolopsis tarus*; C, *Zygomaturus trilobus*; D, N.G. *Gen. nov.* NTM P8660-1, P8668-2, P8668-3. Functional interpretation contrasts features of a distinctive trophic complex which members of the genus *Zygomaturus* (C-D) appear to share; A-D depict estimated resultant vectors for the m. temporalis (Rt) and m. superficial masseter (Rsm). Dashed triangles connecting condyle, incisor tip and centre of digastric process facilitate comparison. Though differing markedly in size, N.G. *Gen. nov.* (D) shows the same biomechanical modifications as *Z. trilobus* (C) in contrast to plesiomorphic zygomaturines (A-B). Measurements of individual components indicate that these modifications are predominantly isometries (rotations and translations); anisometries include shear in the rostrum, stretching in ventral border of the horizontal ramus and compression in the mid-face and zygomatic arches. Proportional sliding associated with scaling (enlargement-reduction) and allometry does not account for the modifications seen in C and D relative to A and B. However, allometry does account for differences between C and D, therefore small New Guinea zygomaturines show no specific anatomical relationships with small plesiomorphic Miocene zygomaturines.

Although they do not make the many plesiomorphic features of *Hulitherium* explicit, their statement conveys the idea that *Hulitherium* is a plesiomorphic sister taxon of *Zygomaturus* and that the affinities of *Hulitherium* are more with the Miocene genera *Kolopsis* and *Plaisiodon* than with other species of the genus *Zygomaturus* (i.e. *Z. gilli* and *Z. keanei*). However, in the absence of comparable cranial material from the primitive *Zygomaturus* species *Z. gilli* and *Z. keanei* and in the absence of synapomorphic features of *Hulitherium* with *Kolopsis*, there appears to be no substance to their argument.

Based on NTM P8660-1, the recently proposed New Guinea genus (Flannery, pers. comm.), (*N.G. Gen. nov.*), (Figs 1-3) appears to be closely related to *Hulitherium* with respect to P³ morphology (short steep postmetaerista), paracone and metacone lying close to buccal margin; strong front to back gradient in the cheek dentition, curved arcades with crowns large relative to the splanchnocranium, narrow, thin, high frontal crests and "dished out" frontal depression, deeply arched palate, low but distinct septal process of the premaxilla and small size compared to *Zygomaturus trilobus*. *N.G. Gen. nov.* differs from *Hulitherium* in being significantly smaller, in having a steeper, higher frontal profile, in possessing a more distinct nasomaxillary eminence and premaxillary interdiastemal crest. The orbital margins are more anteriorly situated,

the rostrum is shorter and the molar crowns are more complex.

The shorter, relatively deeper rostrum of *N.G. Gen. nov.*, combined with incipient premaxillary-nasal eminences and a more prominent premaxillary crest, gives a closer resemblance to *Zygomaturus trilobus* than to *Hulitherium*. The similarities between *N.G. Gen. nov.* and *Z. trilobus* are more compelling in a restored comparison in which the large masseteric process and lateral orbital margin are shown (Figs 1-2). The zygomatic processes are unknown for *Hulitherium*. Also in common with *Z. trilobus*, the I¹ crowns of *N.G. Gen. nov.* (P8660-1) are slightly divergent in contrast to the markedly convergent crowns of *Kolopsis*, *Plaisiodon* and *Neohelos*. The state of this feature is not known for *Hulitherium*.

Although the dentition of *N.G. Gen. nov.* appears to be derived relative to *Hulitherium*, both genera are clearly synapomorphic with *Zygomaturus* and show strong polarity contrasts with *Kolopsis*. Due to the incompleteness of material available for an outgroup comparison at the species level, the question as to whether the more detailed similarities of *N.G. Gen. nov.* to *Zygomaturus trilobus* are genus rank parallels or species-rank synapomorphies cannot be resolved at present. At minimum, the phylogenetic evidence summarized in the figures and tables supports the inclusion of *N.G. Gen. nov.* and

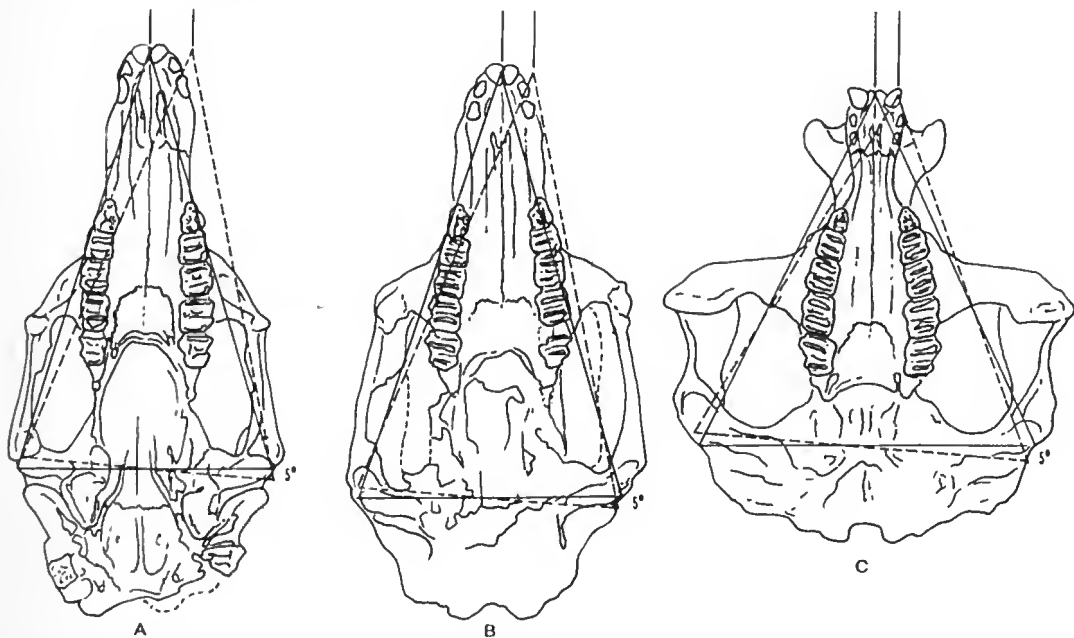


Fig. 12. Ventral aspects of A, *Neohelos* sp.; B, *Kolopsis torus* and C, *Zygomaturus trilobus* showing the extent of lateral excursion of the tip of the lower incisors in relation to a 5° displacement of the condyles.

Hulitherium within the *Zygomaturus* clade. If the more recent generic distinctions are to be retained, it may be useful to propose a new rank, Tribe Zygomaturini, to signify the clade affiliation and designate *Zygomaturus gilli* as a plesion or assign a new generic name to the species (Fig. 14).

***Zygomaturus nimborensis* Hardjasasmita.** *Zygomaturus nimborensis* is a larger Pleistocene form about which very little is known. I have translated Hardjasasmita's (1985:1000) diagnosis from Bahasa Indonesia, which is here quoted in full: "Species diagnosis: A diprotodontid, Genus *Zygomaturus* that is much smaller than *Zygomaturus keanei*, but much larger than

Zygomaturus gilli; mandible robust; ramus approximately horizontal; symphysis arises commencing at position of second molar; the hollow [internal contour] of the symphysis is diagonally slanted and bent in the letter U-shape. The height of the mandible is relatively great compared to molar height. Mental foramen diameter 0.5mm, situated under a line level with the molar crown. The valley between the anterior and posterior moiety (see figure 1 and figure 2) is curved like the letter U that is widest above. Type locality: near Nimboran, District Head, Genyem, near Sentani Jayapura, Irian Jaya. The exact location was not known [recorded]. Age: Estimated to be Pleistocene".

The description, which merely elaborates on the fragmentary condition of the fossil, provides no additional information relevant to systematic assessment. My photocopy of the article contains no illustrations. The measurements given for the lower dentition of *Z. nimborensis* are of interest because of their approximate similarity in size to the upper molars of the Lake Palankarina Lawson-Daily Quarry *Zygomaturus* (UCMP 70126), (Hardjasasmita 1985, Stirton 1967).

	M1	M2	M3	M4
<i>Z. nimborensis</i> (lowers)	—	29.8	32.8	36.2
<i>Z. sp.</i> UCMP 70126 (uppers)	—	30.0	34.3	33.7

The amount of variation between the upper and lower molars of the two species shown above is probably within the range of variation of a single species of the Zygomaturinae. However, Hardjasasmita's measurements also roughly correspond with the dimensions of *Nototherium watutense* Anderson, and should be considered particularly suspect with regard to the lack of reduction of M4, a feature also characteristic of *N. watutense*. I lack sufficient information to discuss this species any further.

***Kolopsis rotundus*.** *Kolopsis rotundus* Plane, 1967 is a small Late Pliocene zygomaturine from the New Guinea Awe Fauna, Otibanda Formation (Figs 4, 10, 13). Its cheek dentition is slightly smaller than that of *Hulitherium* (Plane 1967, Flannery and Plane 1986). The specific diagnosis of *K. rotundus* (Plane 1967:111) includes a substantial inventory of *Zygomaturus* apomorphies: "Upper incisor not transversely compressed...; P³ of similar size to that in *K. torus*; length 19.6... paracone and metacone 6.2 apart... [compared to 3.4 apart in a 21.0 long *K. torus* P³] separated by wide lingual and labial

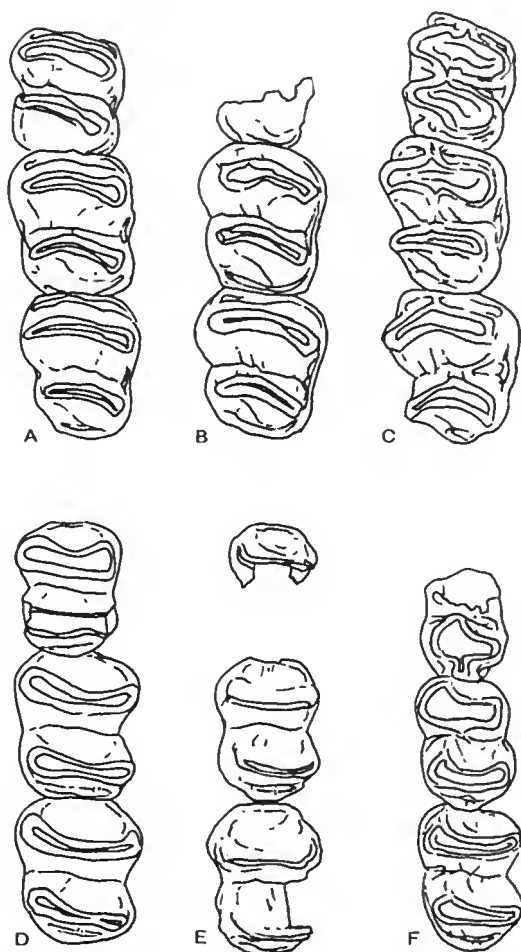


Fig. 13. Outlines of upper (A-C) and lower (D-E) cheek dentitions of A, Lawson-Daily Quarry *Zygomaturus*, Palankarina LF (X2/3); B, *Kolopsis rotundus*, Awe LF (X1); C, N.G. Gen. nov., NTM P8660-1, Baliem LF (X1); D, *K. rotundus*; E, *Hulitherium tomasettii*, Puren LF (X9/10); F, N.G. Gen. nov. NTM P8660, (X9/10); scaled to length of M¹ for comparison.

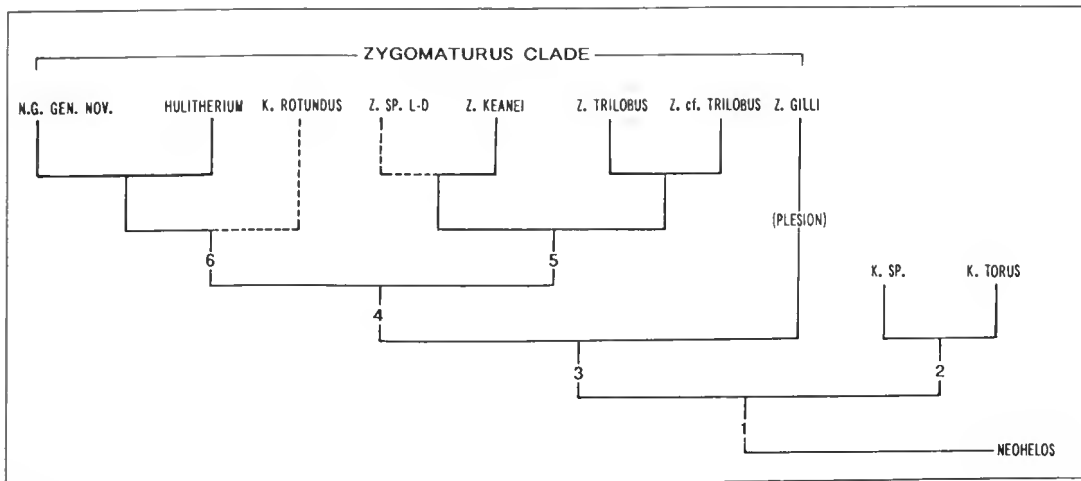


Fig. 14. Cladistic hypothesis of speciation in some representative Zygomaturini based on P^3 and M^2 ; N.G. GEN. NOV.=NTM P8660; Z. SP. L-D=Lawson Daily *Zygomaturus* sp.; Z. cf. TRILOBUS=Chinchilla *Zygomaturus* sp. (Archer and Bartholomai 1978); Apomorphics designated by numerals: 1, P^3 with 5 cusps; 2, incipient division of paracone and metacone on P^3 , enlarged parastyles and metastyles on M^2 ; 3, P^3 paracone and metacone widely separated and enlarged, reduced parastyle and metastyle on M^2 ; 4, P^3 broad, short, reduced relative to M^2 ; 5, Wide labial sulcus with mesostyle and strong buccal cingulum on P^3 ; 6, P^3 paracone and metacone situated close to buccal margin, very reduced postmetacrista, narrow buccal sulcus and weak or absent mesostyle and buccal cingulum. Broken lines indicate possible closer connection between *K. rotundus* and Lawson-Daily *Zygomaturus* sp.

grooves; crest from metacone to posterior end of tooth short and steeply inclined...paracone and metacone more rotund than in *K. torus*; parastyle separated from paracone by much narrower transverse cleft than in *K. torus*...". The upper molars are larger relative to P^3 than in *K. torus*; the dentary is more robust; the digastric eminence and fossa are stronger. The lower incisor of *K. rotundus* is strongly curved, recumbent and pointed, unlike that of *K. torus* (straight, procumbent and blunt).

Plane (1976) does not elaborate on his reasons for excluding *Kolopsis rotundus* from the genus *Zygomaturus*. The specific contraindications are spelled out subsequently in Stirton *et al* (1967:156): the P^3 of "...the New Guinea species is more primitive than *Z. gilli* from Sandringham Sands... [in that the] posterolingual base of the protocone in *K. rotundus* not expanded to contact the anterolateral base of the metacone as in *Z. gilli*, small depression between protocone and paracone not developed in *K. rotundus*, shallower labial groove between paracone and metacone than in *Z. gilli*".

Such characters, particularly the small basin between the protocone and paracone, are not always present in *Zygomaturus trilobus*. I give more weight to the wide separation and robustness of the paracone and metacone, the short, steep para-metacrista, and broad, closely ap-

proximated parastyle of *K. rotundus* than to the apparently variable contraindicating features.

My interpretation of the character states for the genus *Zygomaturus* suggests that *K. rotundus* is a relatively derived species in having the P^3 paracone and metacone very widely separated and situated close to the buccal margin of the crown, also in possessing recumbent, pointed lower incisors and in several features of the dentary including a posteriorly situated digastric eminence and a conspicuously elevated ascending ramus (Tables 1-2, Figs. 4, 10, 13).

Lawson-Daily Quarry *Zygomaturus*. Stirton (1967) reported on a *Zygomaturus* species recovered from the Lawson-Daily Quarry at Lake Palankarina, South Australia, which he describes as being intermediate in size between *Z. keanei* Stirton and *Z. gilli* Stirton. Remarking on the upper molars of the specimen, he states: "the loph arcs much as they are in *Z. keanei*, but even more like those in *Kolopsis rotundus* Planc, 1967 from New Guinea..." (Stirton 1967:145). They are indeed very similar (Fig. 13), *K. rotundus* differing only slightly in size and in having slightly more development of the lingual cingulum, anterior cingulum, crista obliqua and a relatively wider metaloph on M^5 . The close similarities between *Kolopsis rotundus* Plane, 1967, and the Lawson-Daily *Zygomaturus* sp.

would indicate that both species represent the same genus and that they possess similarly derived character states.

Having remarked on the Lawson-Daily *Zygomaturus*'s greater similarity to *Kolopsis rotundus* than to *Zygomaturus keanei*, it is unclear why Stirton (1967) did not propose placing them in the same genus. Presumably the decision to keep them separate was influenced by the apparent early Pliocene age of *Kolopsis rotundus* in the Awe Fauna, that was believed at the time to date between 7.6 and 5.7 million years BP (Everenden *et al.* 1964). That age determination has subsequently been adjusted upwards to between 2.5 and 3.5 million years BP (late Pliocene) (Page and McDougal 1972, Hoch and Holm 1986).

The revised K/Ar dates place *K. rotundus* in a biochronological context more compatible with the Lawson-Daily *Zygomaturus*. Simultaneously, the much younger revised age serves only to magnify the biochronological anomaly created by the apparent persistence in the late Pliocene of a *Kolopsis* species. Thus, the data support an alternative hypothesis suggesting that the earliest New Guinea Zygomaturini exhibit a stage of evolution comparable to that of a late Pliocene species of *Zygomaturus* from the southern portion of continental Australia.

DISCUSSION

If my hypothesis regarding the cladistic relationship of these zygomaturines is correct, the question of the origin and earliest time of arrival of *Zygomaturus* in New Guinea is virtually answered (Fig. 15). The Palankarinna LF is considered to be Kalimnan Stage equivalent. Thus, the Lawson-Daily *Zygomaturus* sp. is a late Pliocene form. The earliest known New Guinea zygomaturine, the Awe LF *Kolopsis rotundus*, is also a late Pliocene form. Evidence of a close relationship between *Hulitherium*, N.G. *Gen. nov.* and *K. rotundus* would result in a parsimonious explanation of the subsequent zygomaturine radiation in New Guinea.

Although the upper dentition of *Hulitherium* is poorly represented, the lower molars compare reasonably well with *K. rotundus*, differing primarily in size and in being slightly narrower relative to their length (Fig. 13). Flannery and Plane's (1986) description of the lower premolar fragment and molars of *Hulitherium* indicate a number of proportional and detailed structural

similarities to *K. rotundus*, including crown and lophid shape, weak paraeristid development, weak anterior cingulum, strong, rounded, centrally raised postcingulid, especially on M_{3,4} and faint eristid obliqua development. The fragment of *Hulitherium* P¹ indicates that it was similar to that of *K. rotundus* and N.G. *Gen. nov.* in having a widely separated paracone and metacone and a steep-sided, nearly vertical para-metaconal crest. There appear to be no features of the lower dentition of *Hulitherium* that could not have been derived from *K. rotundus*.

The dentition of N.G. *Gen. nov.* is elaborated in comparison to *K. rotundus* and *Hulitherium*. The molars are higher crowned, with thicker enamel, more prominent development of crests and cingulae and display a more marked front to back size gradient. The structure of the cheek dentition is basically similar compared to *K. rotundus* in the uppers and compared to *Hulitherium* in the lowers (Fig. 13). The primary difference is in the development of distinct mid and hind links, which could have been derived from homologous, though much weaker structures present in *K. rotundus* and possibly *Hulitherium*, based on the analogous condition of its lowers. It is reasonable to suggest that a species with a lower molar morphology similar to *Hulitherium* or *K. rotundus* could have given rise to that of N.G. *Gen. nov.* (Figs. 13-15).

Arrival of *Zygomaturus* in New Guinea. The stage of evolution similarities between *K. rotundus* and the Lawson-Daily *Zygomaturus* would indicate that the genus *Zygomaturus* entered New Guinea no earlier than mid Pliocene. There is no evidence to support an earlier isolation of members of this or any other generic clade of the Diprotodontidae (Fig. 15). The Awe diprotodontine *Nototherium watutense* Plane, 1967, is also a derived species with closer affinity to the Pleistocene *Nototherium inerme* than to the late Miocene *Pyramios alcootense* (Stirton *et al.* 1967). *Kolopsoides cultridens* appears to represent an independent zygomaturine lineage, with no close affinities to *Kolopsis* or *Zygomaturus*.

I previously suggested (Murray 1990) that *Kolopsoides* may represent a parallel *Zygomaturus*-like development from a *Plaisiodon*-like ancestor. If this hypothesis is correct, *Kolopsoides* represents a stage of evolution structural equivalent to *Zygomaturus*. Because the mid to late Pliocene is poorly represented in northern Australia, no *Kolopsoides* annectants have been found. However, I specu-

late that these may eventually turn up on the mainland, possibly among the Riversleigh "System C" diprotodontids (Archer *et al.* 1989).

The character states of both *Hulitherium* and N.G. *Gen. nov.* suggest that they arose from a relatively derived species of the genus *Zygomaturus*. By analogy with certain other fossil taxa that make their appearance in the late Pliocene, I speculate that 3.5 million years could have been sufficient time for the development of their respective specializations, commencing with a form similar to *K. rotundus*.

Insular dwarfing or small plesiomorphs?

The evidence does not support the hypothesis that *Hulitherium* and N.G. *Gen. nov.* represent relict small-sized plesiomorphic zygomaturines closely related to those from the Australian Miocene. The relatively small size of these two Pleistocene species might therefore be due to the

phenomenon of insular dwarfing. Examples of very rapid and quite drastic body size reduction in mammoths are recorded in the late Pleistocene of North America and the Mediterranean in terms of thousands of years.

The most telling attribute of the small New Guinea Pleistocene zygomaturines is the conspicuous proportional differential between the cheek dentition and the facial skeleton. The basic configuration seen in *Zygomaturus trilobus* appears to be exaggerated in that the cheek dentition and the adductor muscle armatures are enlarged relative to the facial skeleton. This positive allometry of the trophic complex may indicate that the New Guinea zygomaturines are scaled down from a considerably larger species of *Zygomaturus*. The cheek dentitions of Miocene zygomaturine species are relatively small in proportion to their facial skeletons.

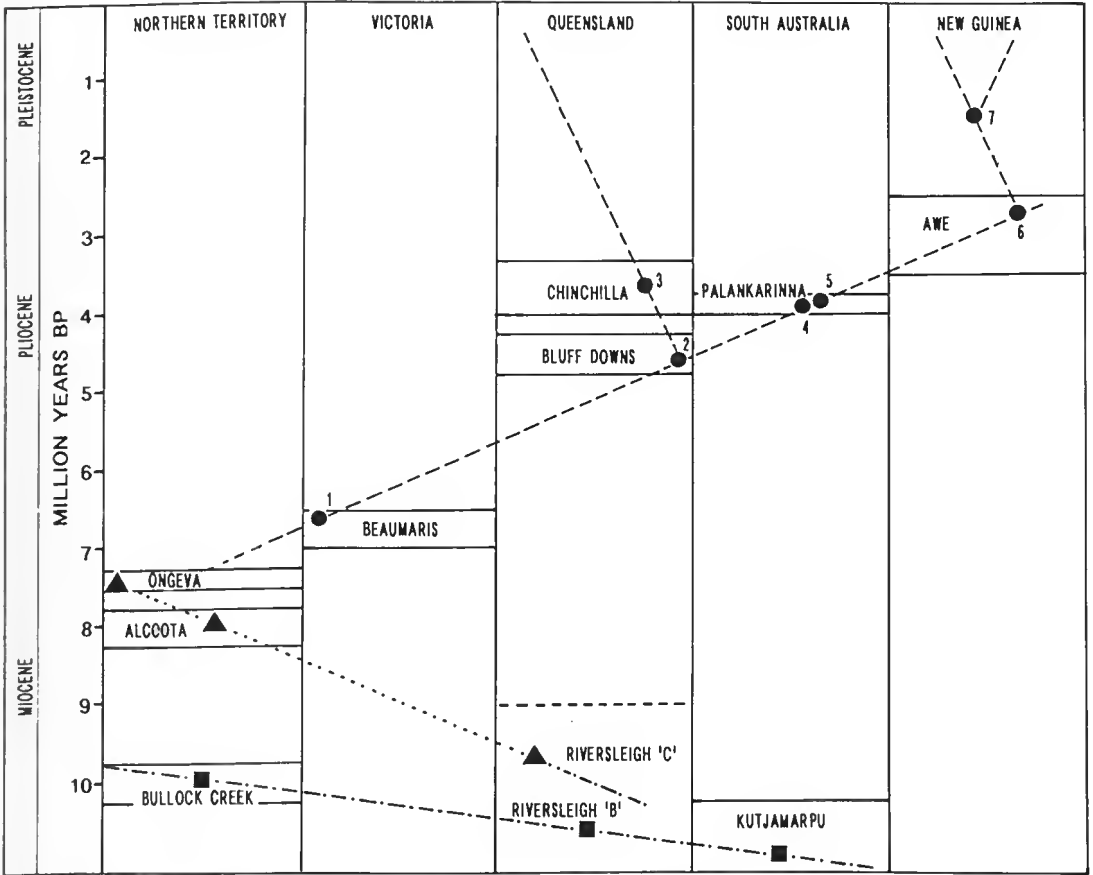


Fig. 15. Stratigraphic diagram depicting a hypothesis of phyletic branching of zygomaturine annectants in relation to chronology; Dots=*Zygomaturus* clade; squares=*Neohelos* clade, triangles=*Kolopsis* clade; broken lines depict phyletic lineages connecting Local Fauna species as they occur in stratigraphic superposition; numerals designate *Zygomaturus* species: 1, *Z. gilli*; 2, *Z. sp.*; 3, *Z. cf. trilobus*; 4, *Z. keanei*; 5, Lawson-Daily Quarry *Zygomaturus*; 6, *Kolopsis rotundus*; 7, small Pleistocene New Guinea *Zygomaturus* spp.; *Z. nimborensis* is not included as there are no specific morphological details upon which to base its position. Chronology is based on Woodburne *et al.* (1985).

It is unlikely that a simple size reduction in *Kolopsis torus* would result in a form similar to that of either *Hulitherium* or N.G. *Gen. nov.* and it is plainly evident that the only other explanation that would allow for the retention of a relict Miocene *Zygomaturus*-like form in New Guinea is to unparsimoniously postulate a highly detailed structural convergence with *Zygomaturus trilobus*.

The other Awe diprotodontids (*Nototherium watutense* and *Kolopsoides cultrideus*), though apparently highly derived, are also much smaller than their closest late Miocene and Pliocene relatives in Australia. It seems unlikely that all of these species are expressing independent parallel specializations in response to different selective pressures. A more parsimonious explanation for the phenomenon is insular dwarfing.

Implications for New Guinea palaeozoogeography. It now seems evident that an apparently minor systematic oversight has resulted in well over two decades of misguided theorizing about New Guinea zoogeography and an apparently anomalous zygomaturine biochronology (Stirton *et al.* 1967, Flannery 1988). Two misconceptions conspired to produce the notion that the New Guinea diprotodontid fauna represented a relict of Miocene Australia. By far the most influential factor was the initially incorrect radiometric age of the Otibanda Formation published by Everenden *et al.* (1964).

An age of 7.6-5.7 million years makes it seem just possible that the smaller mid to late Miocene diprotodontids might have hung on in isolation. The second factor is the pervasive influence of the small size of the skulls of the New Guinea zygomaturines which, in combination with the apparent age of the fauna, seems to have exerted a subtle bias on the interpretation of the character states of *Kolopsis rotundus*.

Stirton *et al.* (1967:151-156) observed that: "*Kolopsis rotundus* Plane 1967, represents a genus previously common in the Miocene in the middle latitudes of Australia, which lingered on into the Pliocene in the equatorial latitudes of New Guinea...", [and in relation to relict North American Tertiary faunas]... The somewhat anomalous geochronological position of *Kolopsis rotundus*, which maintains certain primitive features [those discussed previously and dismissed as trivial] in relation to members of the subfamily occurring in somewhat older Australian faunas, indicate that a similar phenomenon has

occurred in the Australian region". In light of the revised age of 2.5-3.5 million years BP for the Awe Fauna (Page and McDougal 1972, Hoch and Holm 1986), their weighting of certain characters of the P³ of *K. rotundus* might have been different.

The heightened biochronological dissonance resulting from the revision of the age of the Otibanda Formation would seem to compel one to seek another explanation, or at least to proceed with caution. Flannery's (1988) observations seem to indicate that the relict nature of New Guinea's fauna has been fully substantiated: "By the early Miocene, geological changes had split the Australidelphian/monotreme faunas of the region into two units, a New Guinean one and an Australian one. These faunas had separate histories until the Pleistocene" (Flannery 1988:23). And "... mammalian assemblages ... from Riversleigh, Alcoota and Bullock Creek (central and northern Australia) show some striking similarities with the New Guinean mammal fauna. These assemblages include *Dorcopsis*-like macropodines ... zygomaturine diprotodontids" (Flannery 1988:18).

On the contrary; the fauna of New Guinea seems to be more representative of relatively recent adaptations to its extreme habitat diversity rather than being a refugium for archaic species. Unlike Madagascar or New Zealand, New Guinea has no radiations of disjuncts equivalent to the Malagasy lemuroids or New Zealand ratites. The unique character of the predominant large mammal elements of the New Guinea mammalian fauna (zygomaturine diprotodontids and macropodine kangaroos) appears to have originated very late in the Tertiary, probably since the mid Pliocene. However, this view does not exclude an assumption that animals had begun to colonize the presumptive New Guinea land masses since the time they had become inhabitable. The point is that the colonization of the island(s) appears to be predominantly successional over the late Tertiary as opposed to predominantly disjunct since the mid Tertiary.

CONCLUSIONS

The major conclusions drawn in this study are: 1) *Hulitherium tomasettii* and N.G. *Gen. nov.* represent species recruited from within the *Zygomaturus* clade and as such are more derived than *Zygomaturus gilli*; 2) *Kolopsis rotundus* from the late Pliocene Awe Formation of New

Guinea is more closely related to *Zygomaturus* than to *Kolopsis*; 3) *Kolopsis rotundus* appears to be most similar to the Palankarina Lawson-Daily *Zygomaturus* sp.; 4) the stage of evolution equivalents of the Lawson-Daily Quarry *Zygomaturus* sp. or *Kolopsis rotundus* could have given rise to all later (Pleistocene) New Guinea species of the *Zygomaturus* clade (or genera of Tribe Zygomaturini) commencing in the Late Pliocene; 5) the two small Pleistocene New Guinea zygomaturines and possibly *K. rotundus* probably represent insular dwarfs; 6) the larger terrestrial fauna of New Guinea does not represent a relict Australian Miocene fauna, but does represent a mid to late Pliocene "barrel-filling" phenomenon in which a relatively few derived Australian genera have speciated prolifically and rapidly in response to availability of unoccupied niches, geographic isolation and vertically stratified habitat.

ACKNOWLEDGEMENTS

For so short a polemic the debt to my colleagues might appear disproportionately heavy, though no less true: I thank Rod Wells, Flinders University, and Dick Tedford, American Museum of Natural History, for their constructive criticism of my original draft. Dirk Megirian and Tim Flannery are to be thanked for enduring long telephone discussions on the topic. Discussions of zygomaturines with Brian MacNess, University of NSW, have also been influential. I thank Phil Walker University of California, Santa Barbara and Doug Hayward Biola University for entrusting me with the Baliem zygomaturine. Rod Wells provided me with the Victoria Cave *Zygomaturus trilobus* material. I thank Chris Tassel of the Queen Victoria Museum for providing me with a fine cast of the Mowbray Swamp *Z. trilobus*, and Don Gregg and Noel Kemp for allowing me to examine the Tasmanian Museum *Z. trilobus* specimen. Finally I thank the students of Flinders University for their help in excavation and preparation of the Alcoota and Camfield material, especially Sue Jennings and Leanne Dansie, and my volunteer preparator Pauline Cockrill.

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THE WEIRD WONDERFUL WOMBAT WARENDJA WAKEFIELDI HOPE & WILKINSON.

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EXTENDED ABSTRACT

Warendja wakefieldi Hope and Wilkinson, 1982 was first described from two dentaries and six isolated teeth from a cave near Nelson, Victoria. Subsequently, a maxilla was described (Flannery and Pledge 1987) from a small cave near Comaam, South Australia. More material from the latter site has been recognised by J. McNamara, who was able to fit it to the original specimen and reconstruct most of the skull. This is described briefly below.

The skull of *Warendja* is slightly smaller than that of an adult common wombat and very lightly built. With the length of more than 155 mm (nasals and occipitals are missing), the rostrum is relatively long (about 50 mm), narrow (25 mm) and high. The zygomatic arch is low and slender, the cranium distinctly constricted anteriorly and domed behind, and there is a weak sagittal crest. The highest point of the skull is at the frontals which have a slight post-orbital prominence. The premaxillae are not complete, lacking the palatal area and posterodorsal contacts, but suggest that the narial opening was cylindrical rather than flattened and laterally expanded as in *Vombatus* Geoffroy. The maxillae are better preserved, both in the reconstructed skull (SAM P24105) and the skull fragment (SAM P31836). Contact with the frontal is unclear, but it seems there was not a narrow posterodorsal extension of the maxillary as seen in *Vombatus* and *Phascolarctos* Gray. It is not likely that the nasal made contact with the lachrymal. The palatal part of the maxilla is distinctive as indicated by Flannery and Pledge (1987), being very broad and relatively flat - unlike that of living wombats. The palatine bones bound a large palatal fenestra, extending forward to the middle of M¹. The alisphenoid is not clearly defined on all sides, but its suture, with the squamosal, skirts the anterior base of the tympanic process. The lachrymal appears not to have the tubercle that is prominent in *Vombatus* and

Phascolarctos. The parietals are almost rectangular and smoothly convex except for the lip along the medial edge where the sagittal crest is formed, and the occipital edge. The brain case is 50 mm wide at the anterior squamosal root of the zygoma.

The squamosal is incompletely known since the auditory regions are damaged in all specimens. It is rectangular in its cranial part which is evenly convex and not perforated by foramina as in modern wombats. The zygomatic wing is not as laterally extensive or as robust as in *Vombatus* and *Lasiorhinus* Gray but is wombat-like in being dorsally flat with a well defined posterolateral rim. Its simple overlapping contact with the jugal is unlike the intertonguing contact seen in modern wombats and most other living marsupials but is similar to that seen in *Ngapakaldia* Stirton and *Muramura* Pledge. The ventral surface of the squamosal has much gentler relief than in *Vombatus*, with a broad flat glenoid facing anteroventrally. The epitympanic sinus is moderately deep, the postglenoid foramen large and ovate, and the tympanic cavity is large (7mm transverse diameter) and lined by squamosal bone. The auditory region, as preserved, is a reduced version of that seen in *Vombatus* with lower and rounder prominences.

A wombat-like femur (SAM P31854) is tentatively referred to *Warendja* because of its differences from *Vombatus* femora also preserved in the deposit. It has a smaller head, a more pointed greater trochanter closer to the axis of the shaft, a sharper shorter and lower lesser trochanter, and larger lower third trochanter. At the distal end, the anterior face is rounded rather than having a shallow saddle, the lateral condyle narrower and the intercondylar channel is parallel-sided rather than tapering upwards. These and other differences indicate that *Warendja* had a slightly different gait to *Vombatus*.

The skull of *Warendja* shows a number of features that are considered to be plesiomorphic

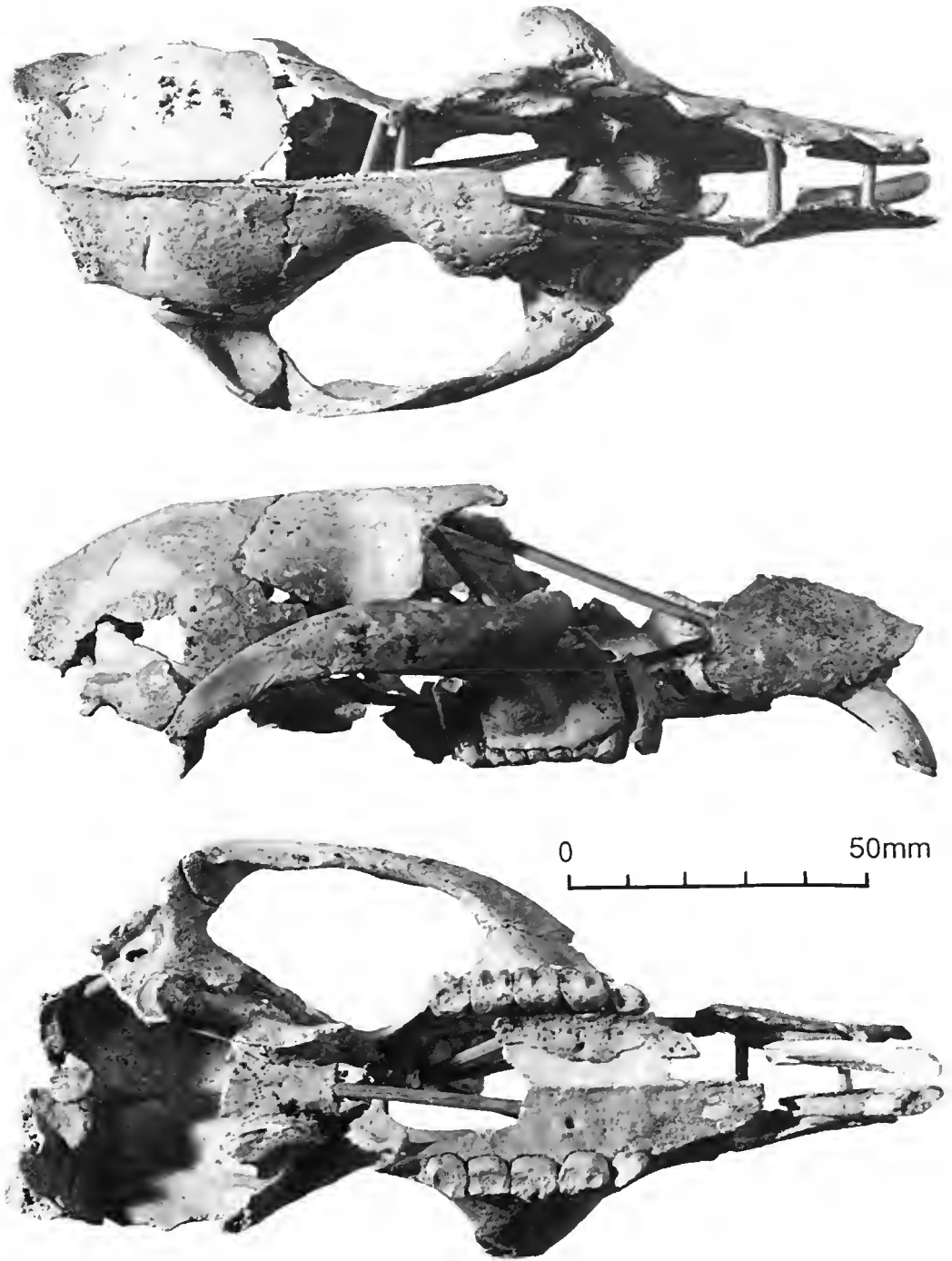


Fig. 1. Skull of *Warendja wakefieldi* in dorsal, right lateral and palatal views.

with respect to other wombats, while at the same time possessing several wombat synapomorphies. The synapomorphies include rootless incisors, premolars and molars, and the sole involvement of the squamosal in the tympanic process. The plesiomorphic features include: broad palate, parallel molar tooth-rows, lightly built zygomatic arches, convex rather than flattened dorsal cranial surface, and a simple glenoid region. These features further support the contention of Flannery and Pledge (1987) that *Warendja wakefieldi* was a very primitive wombat with a more gracile build than the lumbering modern wombats.

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THE CURRAMULKA LOCAL FAUNA: A NEW LATE TERTIARY FOSSIL ASSEMBLAGE FROM YORKE PENINSULA, SOUTH AUSTRALIA.

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ABSTRACT

Discovery of fossil bones in the unflushed core of a joint-controlled cave at Curramulka, Yorke Peninsula, has revealed a rich and diverse vertebrate fauna, consisting of at least 27 species, most of which are marsupials. A preliminary list is given, in which few taxa are identified to a specific level. Several new species are recognized, but most, except a giant koala, a giant ringtail and a new species of *Simosthenurus*, are not named or described in detail, pending the discovery of more diagnostic material. The apparent absence of several taxa, *viz.* bandicoots and rodents, is discussed in view of the postulated Pliocene, or even late Miocene, age suggested by the generic composition of the fauna.

KEYWORDS: Tertiary, cave, Curramulka, vertebrates, marsupials, Miocene-Pliocene, arboreal, new species, new genera.

INTRODUCTION

Curramulka is a small farming town in the middle of a topographic basin of flat-lying Lower Cambrian Parara and Kulpara Limestones (Crawford 1965, Daily 1957) in central Yorke Peninsula (Fig. 1), South Australia. These limestones contain two caves, known from earliest times of settlement (e.g. Griffiths 1988). Near the centre of the town is Town, or Town Well, Cave (5Y2) with a 30 m shaft down to water, which for many years provided the town's water supply. About 3 km south, on a hill-top near the basin rim, is the small doline of another cave, known variously as Correll's or Corra Lynn (5Y1) (Fig. 2). About midway between these caves is the local council quarry, still occasionally worked for road-metal. Both caves are joint-controlled, and sediment-filled joint fissures are visible in the quarry.

Bones of a (?late) Pleistocene vertebrate fauna can occasionally be found in breccia in some of the quarry fissures, and late Pleistocene fossils have been collected by the South Australian Museum from Town Well Cave. The latter has also yielded a surficial deposit of Holocene subfossils, and a single tooth of a diminutive

marsupial lion, *Thylacoleo hilli* Pledge, 1977, of postulated Pliocene or earlier age, which was cemented to the wall in a distant passage.

Corra Lynn Cave is on private land, with severely restricted access negotiable only through the Cave Exploration Group of South Australia. Known for more than a century, it had long been visited by locals seeking a different thrill. Yet until recently, cavers rarely ventured beyond the larger passages close to the entrance, and while collections, mainly of skulls of the locally-extinct potoroid *Bettongia lesueur* (Quoy and Gaimard) were made in 1955 and 1964, no truly fossil material had been encountered. About sixteen years ago, members of the Cave Exploration Group of South Australia (CEGSA), particularly Messrs I. Lewis, G. Pilkington and M. Meth, began detailed surveys of this cave, in the process finding and excavating hundreds of metres of choked passages. Compilation and plotting of the many weekend surveys produced an intriguing picture. The cave was seen to be a three-dimensional joint-controlled maze, on at least three levels, with (by 1985) more than twelve kilometres of passage fitting within a surface area of only 450 x 205 m (11.25 ha) and a depth of 40 m). Within this system, there was

a blank zone that had not been penetrated. Deliberate searching eventually found a route into this region, and resulted in the recovery of the first vertebrate fossils from the cave.

The first fossils to be brought out, in January 1985, represented several small macropodids and a fragment of *Protemnodon* sp. Upon request for more and better material, Pilkington shortly afterward (9 March 1985) recovered a spectacular specimen of a giant koala (Pledge 1985a, Anon. 1985a, 1985b). Subsequently (30 March 1985), the author was taken to the area, a one-way journey taking about 1 hours, much of it spent crawling through very low 'flatteners' (Fig.2). This difficulty of access means that only small quantities of bone and silt can be brought out at any time. On that and several later trips (e.g. Pilkington 1985), more specimens were collected with the faunal list growing to at least 27 taxa (Table 1).

Two new genera and three new species are described, and a new descriptive term-of-convenience, the 'endoeristid', is introduced. The endoeristid is defined as a continuous longitudinal, full-length blade formed on the lingual edge of lower molars by the concurrence of pre- and postmetaeristids and pre- and postentoeristids with no break or gap at the mesostylid. It is distinguished from the entoeristids which derive solely from the entoconid and are restricted to the posterolingual quarter of the lower tooth, by the spelling of the term, and is the analogue of the 'ectoloph' of upper molars.

The material is all registered in the Palaeontological Collections of the South Australian Museum, prefix SAM P.

SYSTEMATICS

Class Amphibia

Order Anura

Neobatrachus pictus Peters

Tyler (1988) referred specimen SAM P27928, a right ilium, to this living species. The only other frog material found is an unidentifiable propodial.

Class Reptilia

Order Chelonia

Family Chelidae sp. indet.

This family is represented by two fragments of plastron which are insufficient for further identification.



Fig. 1. Locality map.

Family Meiolaniidae

? *Meiolania* Owen

Two fragments of large, unsculptured carapace may represent this extinct armoured land tortoise. The genus is widespread in north-eastern Australia, from Gulgong (the Miocene or Pliocene Canadian Deep Leads) to Riversleigh (early Miocene) and the Lake Eyre region (Oligocene to Miocene) to Lord Howe Island (Late Pleistocene/Holocene) and Walpole Island. If valid, this record extends the range considerably southwards.

Order Squamata

Family Madtsoiidae

Wonambi Smith

Wonambi sp. cf. *W. naracoortensis* Smith (Fig. 3)

Some twenty vertebrae of this large, primitive, Gondwanan boid snake have been collected, together with several rib fragments and a few teeth. A fragment of pterygoid with three teeth (P31801) and an edentulous fragment of maxilla (P31785) have also been recognized. Since the remains have been found in several widely separated localities around the deposit, the species seems to have been fairly common. *Wonambi naracoortensis* is known from the Late Pleistocene at Naracoorte (Smith 1976, Barrie 1990) and has also been found in the Pliocene Pleistocene Kanunka Local Fauna of the Katipiri

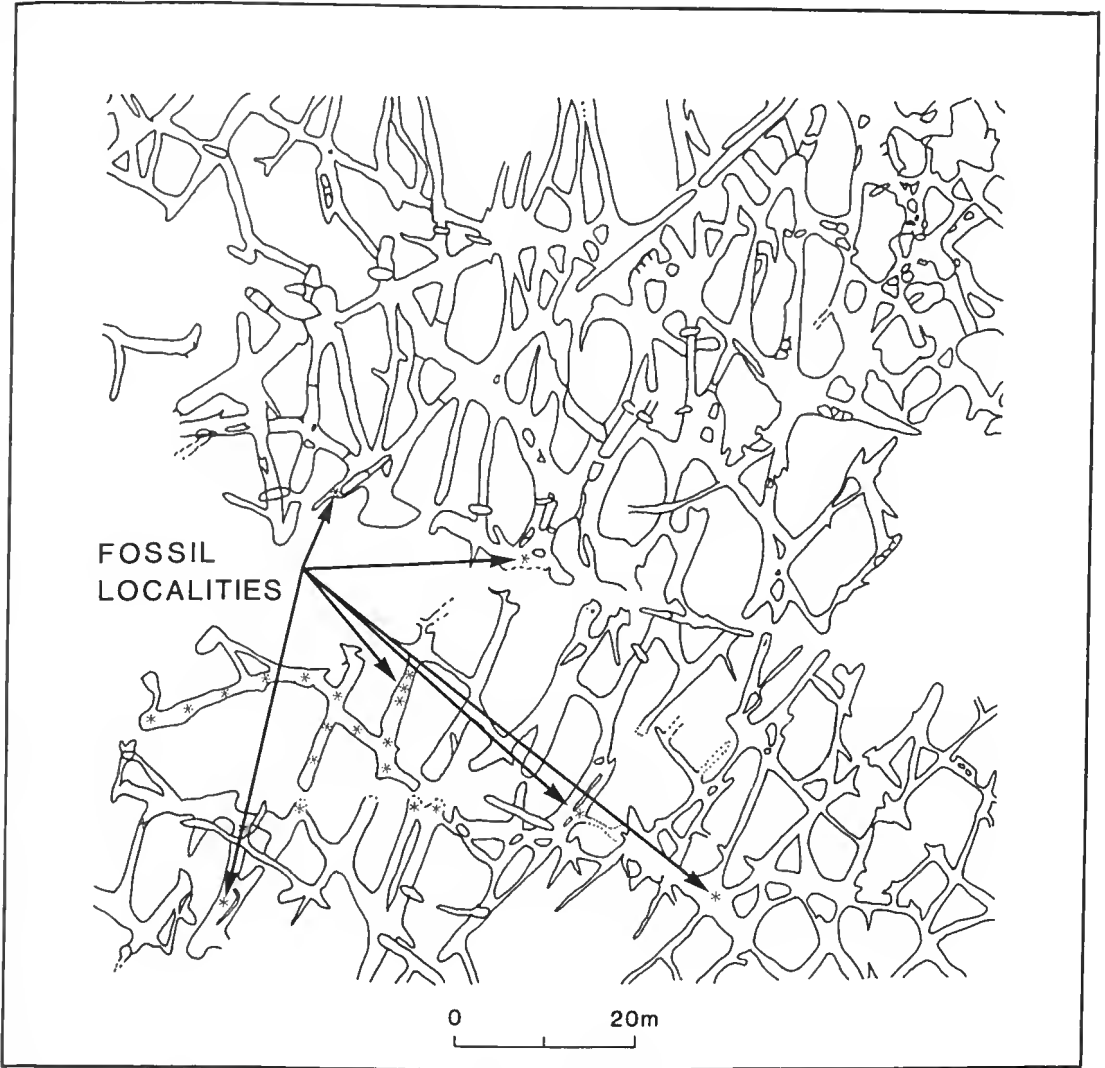


Fig. 2. Detail of a small part (100 m x 100 m) of the fossil bearing level of Corra Lynn Cave 5Y1.

Table 1. Faunal list for the Curramulka Local Fauna, Corra Lynn Cave.

AMPHIBIA	<i>Neobatrachus pictus</i>	MARSUPIALIA (cont.)	
CHELONIA	Chelidae sp. indet. <i>?Meiolania</i>	Diprotodontidae	Zygomaturine sp. indet.
SQUAMATA	<i>Wonambi</i> sp. Elapidae sp. indet. <i>Varanus</i> sp.	Palorchestidae	<i>Palorchestes</i> sp. cf. <i>P. painei</i>
Scincidae	<i>Tiliqua</i> sp. cf. <i>T. scincoides</i>	Vombatidae	<i>Vombatus</i> sp. indet. <i>Phascolonus</i> sp. <i>Phascalomys</i> sp. cf. <i>P. medius</i> Vombatidae sp. indet.
AVES	cf. <i>Ibandornis</i> sp.	Thylacoleonidae	<i>Thylacoleo</i> sp. cf. <i>T. hilli</i>
MARSUPIALIA		Pseudocheiridae	<i>Corracheirus curramulkensis</i> gen. et sp. nov.
Dasyuridae	cf. <i>Dasyuroides/Dasyercus</i> sp. cf. <i>Glaucodon</i> sp.	Petauridae	<i>Petaurus</i> sp. cf. <i>P. norfolcensis</i>
Thylacinidae	<i>Thylacinus</i> sp.	Potoroidae	<i>Potorous</i> sp.
Phascolarctidae	<i>Phascolarctos</i> sp. cf. <i>P. cinereus</i> <i>Cundokoala yorkensis</i> gen. et sp. nov.	Macropodidae	cf. <i>Baringa</i> sp. cf. <i>Baringa nelsonensis</i> <i>Troposodon</i> sp. cf. <i>T. bowensis</i> <i>Protemnodon</i> sp. <i>Sinosthenurus cegsai</i> sp. nov.

Sands at Lake Kanunka. Other madtsoiid species are known from the Oligo-Miocene deposits at Riversleigh, north-western Queensland (Scanlon 1988).

Elapidae indet.

Three vertebrae referable to this family have been found.

Family Varanidae

Varanus Merrem

Varanus sp. indet.

Goannas are represented by an anterior caudal vertebra (SAM P29909) and a frontal bone (P30003), both of a size to indicate a head-vent length of about 600 mm (M. Hutchinson, pers. comm., 12 September 90). There is also a damaged posterior caudal vertebra.

Family Scincidae

A dentary (P29871), a fragment of vertebra and a pair of damaged frontals represent this family. The size suggests *Tiliqua* sp. cf. *T. scincoides* Shaw (M. Hutchinson, pers. comm., 14 September, 1990).

Class Aves

Family Dromornithidae

Ilbandornis Rich

cf. *Ilbandornis* sp.

(Fig. 4)

Six bones have been referred to this taxon, by elimination: a large fibula (SAM P26530) lack-

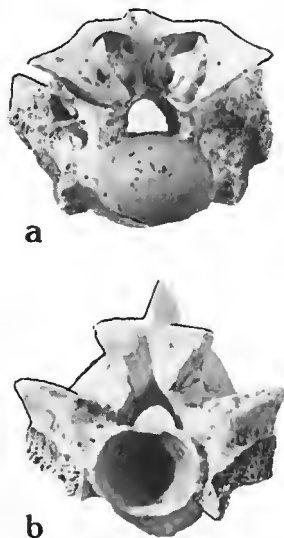


Fig. 3. Vertebrae of *Wonambi* sp. cf. *W. naracoortensis*; a, P29908; b, P26535. Natural size.

ing the distal end, an atlas vertebral centrum (SAM P26545), a damaged tibiotarsus (P31781), the proximal end of another (P31790), the head of a femur (P31791) and a toe bone (P31799). These are much larger than *Dromaius* Vieillot but smaller than *Geuynornis* Stirling and correspond in size and form to *Ilbandornis* sp.. Atlas cervical vertebrae of dromornithids are rare in the fossil record, and this identification is particularly tentative. However, its presence does suggest some antiquity for the deposit. *Ilbandornis* is known from the Late Miocene Alcoota Fauna of central Australia (Rich 1979).

Class Mammalia Australidelphia Family Dasyuridae (Fig. 5)

Two specimens are tentatively referred to this group of Dasyurini. Of one, SAM P26527, little can be said since the broken dentary contains only M_5 . The other specimen, SAM P29808, is a more complete dentary, lacking only incisive teeth and alveoli, all premolars and $M_{3,4}$. The presence of M_2 , however, and the premolar alveoli allows an attempt at generic allocation. Its M_5 is similar to but slightly smaller than that of P26527.

The M_2 is similar in general size to that of *Dasyuroides byrnei* Spencer, *D. achilpatua* Archer and *Dasyercus cristicauda* (Kreff), but differs considerably in form, having a relatively large metaconid with an expanded lingual margin (making this the widest part of the tooth). The paraconid is larger and more distinct, the entocoonid larger, the talonid relatively narrower and the posthypocristid shorter. M_5 is similar to that of *Dasyuroides* Spencer and *Dasyercus* Peters except in having a more open pre-post protocristid angle and a narrower trigonid. Premolar alveoli indicate a single rooted P_3 (as in *Dasyurus dunmalli* Bartholomai, 1971, and *Dasyuroides achilpatua* (Archer, 1982)), and P_1 and P_2 slightly divergent anteriorly.

Because of these features and the paucity of other characteristics, the affinities of the specimen cannot yet be determined.

Glancodon Stirton cf. *Glancodon* sp.

The protoconal corner of an upper molar (M^3 or M^4 , SAM P26526) of a species intermediate in size between *Dasyurus maculatus* (Kerr) and

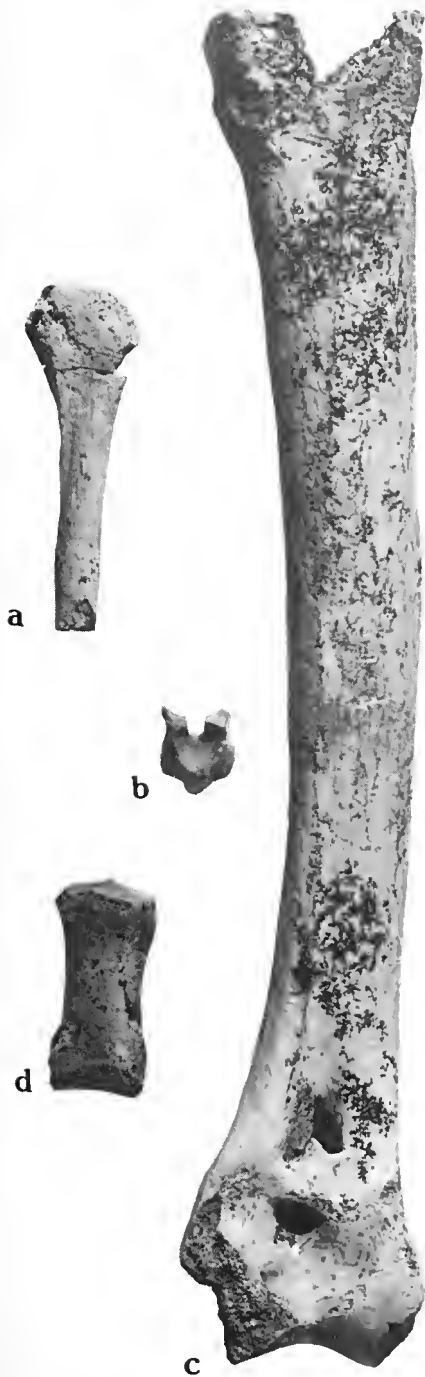


Fig. 4. Cf. *Ilbandornis* sp; a, fibula P26530; b, anterior view of atlas P26545; c, anterior view of tibiotarsus P31781; d, phalange P31799. Half natural size.

Sarcophilus laniarius (Owen) has been recognized and is tentatively referred to *Glaucodon* as the only taxon of appropriate size. Unfortu-

nately, *Glaucodon ballaratensis* (Stirton, 1957) is known only from an incomplete dentary, found in a well at Smeaton, near Ballarat, Victoria, and believed to be of Pliocene-Pleistocene age, and from a referred dentary and M³ from Fisherman's Cliff, near Wentworth N.S.W. (Marshall 1973). The new specimen is unfortunately too fragmentary to be closely compared with the M³ from Fisherman's Cliff.

Family Thylacinidae
Thylacinus Temminck
Thylacinus sp.
(Fig. 6)

Believed to be a new species, SAM P29807 is a well-preserved but incomplete left dentary, retaining C₁, P₁₋₃ and M_{3,4}. Its premolars are up to 10% larger than (P_{1,2}) or equal (P₃) to those of a modern Tasmanian sample (Dawson 1982) while its molars are about 10% smaller. In addition the premolars have a more prominent "taloid" cuspid than modern representatives, and a small anterior basal cuspid not seen in modern teeth. (Table 2).

Family Phascolarctidae
Phascolarctos Blainville
Phascolarctos sp. cf. *P. cinereus* (Goldfuss)
(Fig. 7)

Koalas are represented by four dentary fragments, two of which retain teeth (SAM P26513, 26514), a left M² (P26512) and a right maxillary with M^{3,4} (P29933). These specimens are roughly the same size (Table 3) as equivalent teeth of a Queensland male koala SAM M774, and the teeth are very similar. Differences include slightly narrower and higher lower molars, thicker but more acute cusp(id)s, paracone and metacone more medial, slightly larger styler cusps, greater development of the columnar stylids and metastylid on lower molars, flat molar occlusal plane, and (more or less) constant depth of the mandibular ramus (best seen in edentulous SAM P29932), not increasing posteriorly. There is also a humerus (P31783) which differs slightly in proportions from modern koalas.

Modern koalas show a latitudinal size variation, becoming larger in southern populations ("Bergmann's Law"), and there is considerable morphological variability, e.g. in the size and shape of premolars, but there are features in these fossils which lie outside this variability, which support a new species status. Study of this taxon is continuing.

Phascolarctidae n. gen.

The most striking taxon of this fauna is the giant koala (Pledge 1985a, Anon. 1985 a,b), whose lower molars are 50% or more longer than those of *P. cinereus* (Goldfuss). Apart from its large size and the concomitant greater massiveness of the dentary, the molars show typical phascolarctid features (e.g. selenodonty) but differ in detail. Specifically, the 'entolophid' is constructed more simply than in *P. cinereus*, and much more simply than in its contemporary 'normal' koala taxon.

Cundokoala gen. nov.

Type species. *Cundokoala yorkensis* n. sp.

Diagnosis. As for *C. yorkensis* until other species are described.

Etymology. *Cundo-*, thunder, in an aboriginal language recorded from the Yorke Peninsula (Snell, in Griffiths 1988); *-koala*: the common name, in English usage, of members of the Phascolarctidae. The allusion is to the large size of the type species. Gender is considered to be masculine.

Cundokoala yorkensis n. sp.

(Fig. 8)

Type material. HOLOTYPE: SAM P24904, a left dentary with $M_{2,5}$ and alveolus for P_3 ; lacking anterior tip of jaw with incisor alveolus, and tip of ascending ramus and condyle. Collected by G. Pilkington, 9 March, 1985.

Referred Specimen. SAM P24905, a partial left $M_3(?)$ in alveolo.

Type locality. Corra Lynn Cave (5Y1), 3 km south of Curramulka, Yorke Peninsula, South Australia.

Age. Mio-Pliocene?. See discussion below.

Diagnosis. *Cundokoala yorkensis* differs from all other koalas in its very large size (Table 3), its relatively short and massive dentary, its P_3 short relative to its molars, and its M_2 being shorter than each of the other lower molars. *Cundokoala yorkensis* differs from *Phascolarctos cinereus* in that its lower molars are at least 50% larger (Table 3), and have a simpler endocristid and mesostylid, reduced columnar stylids, non-crenulated enamel in the longitudinal valley, and no plications on the cuspule in the buccal end of the transverse valley. Its M_2 bears a fine crest linking the anterior end of the protostylid crest to the protoconid (and not to the paraconid). It differs from *P. maris* Pledge, 1987a, in that its lower molars are 30% larger and have much simpler endocristid and mesostylid, much simpler columnar stylids, almost no entoconulid, absence of plications on the buccal cuspule and relatively lower crown. It differs from *Madakoala* Woodburne, Tedford, Archer and Pledge in that its lower molars are much larger, have more prominent columnar stylids, lack protoconid-metaconid and hypoconid-entoconid crests, and have a much greater protostylid on M_2 . It differs from *Perikoala* Stirton (Woodburne *et al.*, 1987) in its lower molars being much larger, having a stronger continuous endocristid, greater development of selenodonty, slightly stronger columnar stylids, no protoconid-metaconid or hypoconid-entoconid crests, no crenulated enamel, and having a blunter anterior end on M_2 , and greater development of the protostylid. It differs from *Litokoala kaunukaensis* Springer in that its lower molars are very much larger, have greater development of columnar stylids, lesser separation of the protoconid and metaconid, hypoconid and entoconid relative to their widths, sharper posterolingual corner, and no crenulated enamel.



Fig. 5. Dasyurid indet. P29808. Oclusal stereopair and lateral views. Twice natural size.

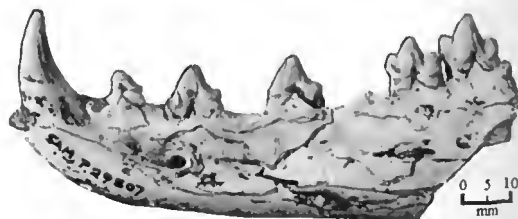


Fig. 6. *Thylacinus* sp. P29807. Lateral view, x 0.7.

Table 2. Measurements in millimetres of *Thylacinus* sp. SAM P29807 compared with ranges of *T. cynocephalus* from Tasmania (modern) and Wellington Caves (Pleistocene), after Dawson (1982) and *T. potens*, from Woodburne (1967b).

	P ₁	P ₂	P ₃	M ₂	M ₃	M ₄	M ₅
P29807	6.6 x 3.4	9.4 x 4.2	10.5 x 4.5	10.0 x 6.2	11.0 x 6.3	12.0 x 6.4	-
Tasmanian	6.0 x 3.4	9.1 x 4.1	10.6 x 5.0	9.6 x 4.4	12.0 x 5.7	14.1 x 6.9	15.7 x 7.6
Wellington Caves	7.8 x -	10.0 x -	12.2 x -	10.7 x 5.1	13.1 x 6.3	15.2 x 7.5	17.4 x 8.5
<i>T. potens</i>					13.0 x 6.8	14.5 x 8.3	15.4 x 8.8

Description. SAM P24904 is a left dentary bearing four molar teeth, and lacking the anterior extremity with the incisive alveolus, and most of the ascending ramus including the condyle, coronoid and angular processes and the posterior masseteric eminence. The digastric process is also damaged. The overall preserved length is 91 mm, with the molar tooth row length being 48.8 mm and the depth of the mandible at M₅ being 34 mm. A short premolar is represented by two alveoli spanning a length of about 6 mm, beyond which point the jaw is broken. There is a small posterior mental foramen below the posterior root of M₃ but no trace of the anterior foramen.

Toothwear ranges from Tedford's (1966) medial wear stage on M₂ to early wear on M₅. The lingual faces of M₂ and M₃ have been slightly damaged by enamel flaking. M₂ is shorter than the other molars and the anterior moiety is noticeably narrower. The anterolingual corner is unfortunately damaged, with the paraconid missing. The high degree of wear has also united the protoconid and metaconid into a single basin. Nevertheless the endocristid can be seen to give only a simple flexure at the metastylid. The columnar stylids evince only slight bulges on the lingual face of metaconid and entoconid. The cristid obliqua curves lingually from the hypococonid, extends two short posterior spurs at the midpoint of the tooth, then meets the postprotocristid. The preprotocristid extends to the paraconid but, less than halfway there, produces a fine anterobuccal crest that meets the anterior end of the preprotostylid. This feature differs from all other koala M₂s. The postprotostylid curves lingually at its posterior end. There is a rather amorphous entoconulid at the posterior end of the longitudinal valley, rather similar to but not as developed as that shown in the M₃ or M₄ of *Plascolarctos maris* (Pledge, 1987a). This feature diminishes in size in posterior teeth and is virtually absent in M₅. Posterior molars are similar. The longitudinal valley is noticeably smooth, with only a slight plication where the cristid obliqua meets the postprotocristid. The metastylid is a simple flexure with the slightest discontinuity where the pre-entocristid meets the buccal face of the end of the postmetacristid. The posthypocristid flows into the postcingulum with only a minor anterior spur for the entoconulid. The preprotocristid converges with but does not reach the parametacristid, there being a separation of about 1.55 mm. Columnar stylids are represented only by lingual swellings on the metaconid and entoconid, unlike the extreme elaborations on *Plascolarctos maris*, or even the lesser ones on *P. cinereus*.

Discussion. Because of its size, *Cundokoala yorkensis* is readily distinguished from all other koalas. The only taxa approaching it in size are

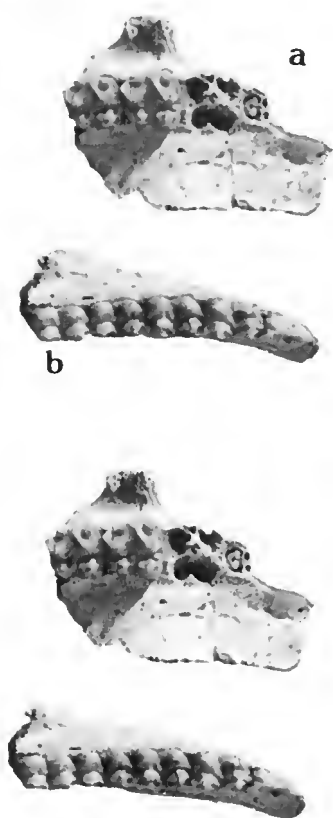


Fig. 7. *Plascolarctos* sp. cf. *P. cinereus*, stereopairs; a, maxilla P29933; b, dentary P26514. Oclusal views, natural size.

Phascolarctos maris, which is morphologically distinct as well as being smaller, and *P. stirtoni*, whose lower molars are unknown. However, because there is a clear equivalent relationship between the lengths of upper and lower molars of all species where both are known, it is immediately apparent that *P. stirtoni* is too small to be this species or even to be considered a senior synonym of the smaller *P. maris*. The morphological simplicity of the lower molars of *Cundokoala yorkensis* also suggest, by analogy with *Phascolarctos cinereus*, that its upper molars are similarly less complicated than those of *Phascolarctos* species

Etymology. This species is named for Yorke Peninsula where it was found.

Family Diprotodontidae Diprotodontid spp. indet.

(Fig. 9)

There are nine teeth that can be referred to this family, but because they are isolated and mostly broken, it is difficult to identify them further. The material comprises an upper incisor (P29937), upper premolar (P26539), two lower incisors (P29942, 31333), two imperfect lower molars that could be associated (P29934-5), two posterior halves of lower molars (P26538, 29904), and an enamel-less fragment with one root of an upper molar (P26540).

The upper incisor seems to be a right I¹. It has a generally zygomaturine form although it is much less compressed laterally. It is highly

Table 3. Length x width measurements in millimetres of teeth of *Cundokoala yorkensis* n.g., n.sp. and *Phascolarctos* sp. cf. *P. cinereus* compared with average *P. cinereus*: e = estimated measurement (alveolar in P24904).

	P ¹	M ₂	M ₃	M ₄	M ₅
<i>Cundokoala yorkensis</i>					
P24904	6.0e	11.8 x 9.0	12.9 x 8.8	12.9 x 8.9	12.7 x 8.6
P24905	-	-	-	-	(13.0 x 8.5)e
<i>Phascolarctos</i> sp. cf. <i>P. cinereus</i>					
P26512	-	8.0 x 8.0	-	-	-
P29933 (upper right)	-	-	8.0 x 8.1	7.5 x 7.6	-
P26514 (left dentary)	7.0 x 4.1	7.8 x 5.1	7.7 x 5.1	7.6 x 5.0	7.6 x 4.5
P26513 (left dentary)	-	-	-	-	8.0 x 4.8
<i>P. cinereus</i> (upper)	7.3 x 5.1	8.0 x 7.7	7.7 x 8.0	7.4 x 7.4	6.6 x 6.5
(lower)	6.4 x 4.1	7.9 x 5.4	8.2 x 5.3	8.2 x 5.1	8.0 x 5.0

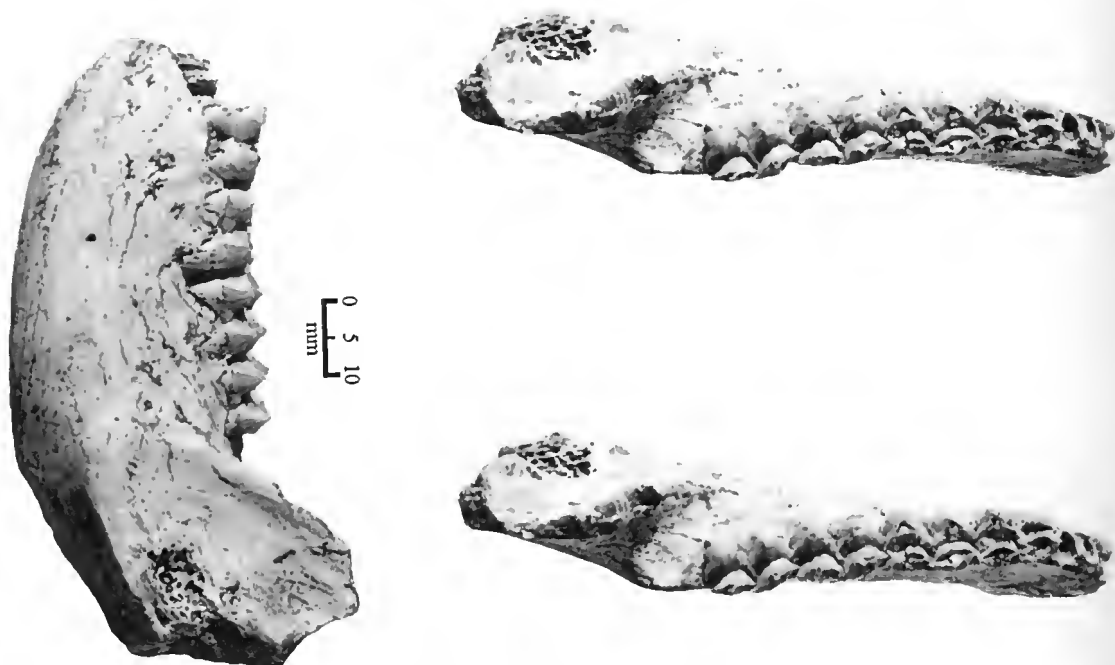


Fig. 8. *Cundokoala yorkensis* gen. et sp. nov.; dentary in oclusal (stereopair) and lateral view. Natural size.

curved with an external radius of about 35 mm. The rather D-shaped or triangular crown cross-section slightly resembles the I¹ of *Pyramios alcootense* Woodburne, and I² of *Kolopsis torus* Woodburne (Woodburne 1967a). In size it agrees with *P. alcootense* best, but it lacks the smooth curve of the lateral surface. There is a faint groove in the labial third of the outer enamel surface, fading out before the base of the enamel, which agrees with I² of *K. torus*, but the Curramulka specimen is much larger (Table 4).

The premolar P26539, although damaged and lacking the posterolingual corner, is distinctly zygomaturine in form. It resembles both *Kolopsis* Woodburne and *Zygomaturus* Macleay in general form, though with differences in detail, but is much smaller than P³ of *Zygomaturus* and has a distinctly transverse parastyle. It is approximately the same size as *Kolopsis*. There is also a close resemblance to certain features of *Alkwertatherium webbi* Murray, 1990, such as size, general shape, large high transversely ovate to bladed parastyle, and distinct mesostyle. It differs from that species, however, in possessing an elongate bladed parametacone, and no buccal cingulum extending from the mesostyle to form a fossette. Unfortunately, the posterolingual corner of the tooth is missing and it is therefore not possible to determine whether there was a hypocone as in *Kolopsis* and *Zygomaturus*, or none as in *Alkwertatherium* Murray. It differs from species of *Zygomaturus* and *Kolopsis* in having a transversely bladed parastyle, rather than a large, regularly conical one. The poorly preserved fragment of upper molar tells nothing except that it is big enough to be from *Zygomaturus* or the large extreme of *Pyramios*.

The lower incisors are very similar except that P31333 is fairly worn and P29942 is only the enamel sheath of an unworn tooth. The latter shows a form very similar to that of *Pyramios alcootense*, although it is considerably smaller than that species. It matches neither size nor proportions of I₁ of *Kolopsis* species or *Plaisiodon centralis* Woodburne.

The lower molars P29934 and P29935 are apparently associated, having been collected at the same site, and having similar preservation and well-fitting interdental appression facets. They are unfortunately badly damaged and lack much of the enamel on the sides of the teeth. Nevertheless, length and approximate width measurements are possible. The size of these teeth immediately rules out *Kolopsis* and *Zygomaturus* (they are too large and too small

respectively), but they fit the ranges of M₂ and M₃, respectively of *Plaisiodon centralis*. However, the morphology of the postulated M₂ does not match that illustrated (Woodburne 1967a, fig. 7 M₁), having a wider protolophid. In this it resembles *Pyramios alcootense*, but the development of the cristid obliqua, which extends almost to the midline in both molars, is closer to that of *P. centralis*. It is conceivable that P29934-5 are in fact M_{3,4} of a small *Plaisiodon* sp. This interpretation avoids the problem of the wide protolophid in P29934.

There is too great a size difference between P29935 and the molar fragments P26538 and P29904 for them to be considered to be the same taxon, particularly if the first is M₁, since P26538 bears a well developed interdental appression facet indicating that it can be no more than M₄ itself. Having only the hypolophid width to judge from, these fragments can be referred to M₄ of *Zygomaturus keanei* Stirton (Table 4).

It is therefore apparent that the specimens at hand represent several diprotodontid species, but there is not yet enough complete material to differentiate and identify them adequately.

Family Palorchestidae

Palorchestes Owen

Palorchestes sp. cf. *P. painei* Woodburne (Fig. 10)

Palorchestes is represented by three upper molars (SAM P26536, 29859, 29938), four lower molars (SAM P29860, 29940, 29999, 30000), a left lower incisor (SAM P29941), and possibly an upper incisor (I³ SAM P29864). There are also two unguis phalanges (P26537, 29893) believed to belong to this species.

Measurements of the molars (Pledge, 1991) suggest that this taxon is intermediate between *P. painei* Woodburne and *P. parvus* De Vis, with the distinctly low crowns aligning the specimens with *P. painei*. However, it is becoming apparent that the composition and phylogeny of *Palorchestes* is more complex than previously thought (e.g. Woods 1958, Woodburne 1967b), so allocation of this material is tentative.

Family Vombatidae

Vombatus Geoffroy

Vombatus sp. indet.

(Fig. 11)

A right upper incisor and right M⁵ (P29931, length 9.5 mm) having a rounder lingual outline

are ascribed to this genus, although they do not closely match *Vombatus ursinus* (Shaw).

Phascolonus Owen
Phascolonns sp. indet.

This taxon is represented by an upper incisor fragment (P26543) which resembles that of *Phascolonus gigas* Owen but is about 45% narrower with a width of 23 mm.

Phascolomys Dumeril
Phascolomys sp. cf. *P. medius* Owen

This species is also represented by an upper incisor (P29862). It is narrower (15 mm) than the *Phascolonus* tooth mentioned above, but thicker medially (8.5 mm). As such, it is close to *Phascolomys medius* Owen as tabled by Dawson (1983). A second specimen (P31797), possibly an incisor of a juvenile, is tentatively referred to this species. It has the same cross-sectional



Fig. 9. Diprotodontids undet; a, right upper incisor P29937; b, zygomaticurine right upper premolar P26539; c, lower left incisor P31333; d, right lower molar P29934; e, right lower molar P29935; f, partial left lower molar P29904; g, partial right lower molar P26538. Natural size.

Table 4. Dimensions in millimetres of miscellaneous diprotodontid teeth from Corra Lynn Cave, compared with Mio-Pliocene species (from Woodburne 1967a, Stirton 1967, and Murray 1990).

Corra Lynn Specimens	tooth		<i>Pyramios alcootense</i>	<i>Kolopsis torus</i>	<i>Plaisiodon centralis</i>	<i>Alkwertatherium webbi</i>	<i>Zygomaturus keanei</i>	
P29937	length	14	1 ¹	15.1 - 20.4	12.3 - 17.5	13.4 - 15.3	-	28.0
	width	11		10.5 - 13.3	6.8 - 10.7	10.5 - 10.9	-	19.4
P26539	length	18.4	p ³	17.4 - 20.9	17.1 - 20.5	23.9 - 28.4	18.7 - 19.2	25.2 - 26.3
	width	17		16.8 - 20.8	13.7 - 16.1	17.6 - 21.8	17.6 - 17.7	19.6 - 21.2
P29942	length	25.8	1 ₁	34.3 - 35.77	13.5 - 16.6	35	-	-
	width	22.2		20.7 - 28.9	22.5 - 26.3	18.0 - 21.2	-	-
P29934	length	26.7	M ₃	20.9 - 21.2	17.2 - 19.0	20.1 - 27.2	19.9 - 21.5	29.2 - 29.6
	width	18		14.8 - 17.3	12.5 - 15.1	14.7 - 17.5	15.0 - 15.1	22.2
P29935	length	30.3	M ₃	24.4 - 29.7	18.7 - 21.6	25.5 - 31.5	23.9 - 26.2	34.0 - 37.7
	width	20		16.1 - 21.4	13.8 - 16.0	18.0 - 21.7	-	25.9 - 28.3
P26538	length	-	M ₄	27.2 - 36.1	21.8 - 25.8	29.9 - 34.6	25.5 - 28.2	40.2 - 42.8
	width	27.5		18.2 - 24.9	15.5 - 18.1	21.0 - 24.3	18.3	28.2 - 29.7
			M ₅	30.1 - 35.8	22.1 - 27.0	25.8 - 37.6	26.2 - 27.5	43.3 - 43.7
				19.8 - 32.6	17.3 - 21.0	23.6 - 27.1	19.5 - 20.5	31.4 - 32.7

shape, but a tapering width of 8.5 to 10 mm and thickness of 5.6 mm.

Vombatidae indet.

Two specimens have not been allocated to a genus. One is a segment of premolar, roundly triangular in section with no vertical grooves. Length and width are subequal, about 8 mm. The other specimen is half of a large molar, though smaller than *Phascolonus gigas*, and with a rounded outline also. The transverse diameter is 8.6 mm, and the (half) length is about 7 mm.

Family Thylacoleonidae

Thylacoleo Owen

Thylacoleo sp. cf. *T. hilli* Pledge

Thylacoleo hilli Pledge was discovered in nearby Town Well Cave, and consists solely of an upper premolar (Pledge 1977). The material from Corra Lynn Cave is, so far, even less diagnostic. SAM P26522 is the tip of a barely worn left I₁, smaller, more gracile and more acute than the equivalent tooth of *T. carnifex* Owen. P29913 is an unworn right I¹, also smaller than the equivalent of *T. carnifex*, and preserving the characteristic little medial cusp. The teeth are noticeably smaller than those of *T. carnifex* and accordingly are referred to *T. hilli* as being the appropriately-sized species.

A slightly damaged astragalus P26523 is considered to be from *Thylacoleo* and is somewhat smaller than the average adult Pleistocene specimens from Naracoorte. It is possible that one or other (or both) of the ungual phalanges ascribed to *Palorchestes* (above) is in reality from *Thylacoleo*, with the bony sheath entirely broken away.

Family Pseudocheiridae

Another striking species in this fauna is a giant ringtail possum with a dentary (SAM P26542, P31792) as large as that of a modern koala. This differs in detail of molar morphology from all modern species at hand.

Corracheirus gen. nov.

Type Species. *Corracheirus curramulkensis* n. sp.

Diagnosis. As for *C. curramulkensis* until other species are described.

Etymology. *Corra-*, from the name of the cave (Corra Lynn Cave) - the type locality; *-cheirus*, from *Pseudocheirus*, a genus of ringtail possum.

Corracheirus curramulkensis n. sp.

(Fig. 12)

Type Material. HOLOTYPE: SAM P26542, a right dentary lacking P₃ and the anterior part of M₂. Paratype: SAM P31792, a left dentary with P₃₋₄.

Referred Specimens. SAM P29901, a fragment of right dentary with P₃; P26520 a right lower incisor.

Type locality. Corra Lynn Cave (5Y1), 3 km south of Curramulka, Yorke Peninsula, South Australia.

Diagnosis. A giant ringtail possum with molar teeth twice the length of the modern *Pseudocheirus peregrinus* Boddaert and 20% larger than *Pseudokoala erlita* Turnbull and Lundelius (Table 5). Differs from *P. peregrinus* in having rounder, less angular, less acute protoconid and hypoconid crests, protoconid and hy-



Fig. 10. *Palorchestes* sp. cf. *P. painei*. a, b, outer and inner views of lower incisor P29941; c-e, stereo oclusal views of upper molars and, f-i lower molars; c, P29938; d, P26536; e, P29859; f, P29940; g, P29905; h, P30000; i, P29999. Natural size.

poconid level with metaconid and entoconid respectively, postprotocristid continuous with prehypocristid (cristid obliqua), not extending to metastylid; lingual face of endocristid almost flat at metaconid and entoconid; simple metastylid flexure of endocristid, crenulations within the trigonid and talonid basins and a short premolar. Differs from *Pseudokoala erlita* in being larger, having postprotocristid continuous with cristid obliqua and not extending to metastylid, in having a continuous endocristid with simple metastylid flexure, in having simple low protoconid and hypoconid; and shorter broader premolar. Differs from *Pseudochirops archeri* Collett in being twice as large, having rounder protoconid and hypoconid crests; protoconid level with metaconid, hypoconid with entoconid; much simpler endocristid, thinner metaconid and entoconid, with crests less diagonal, continuous postprotocristid and cristid obliqua, absence of entostylid and other basinal crenulations, shorter

P_3 , and absence of P_2/I_2 . Differs from *Hemibelidens lemuroides* (Collett) in being twice as large, having slightly more angular protoconid and hypoconid crests with the cuspid being the buccal most points, endocristid less diagonal, thinner metaconid and entoconid, continuous postprotocristid and cristid obliqua, anterolingual eingulum reduced and only on M_3 , and shorter P_3 . Differs from *Petanroides volans* (Kerr) in being twice as large, protoconid level with metaconid, hypoconid with entoconid, precristids less convex, endocristid with simpler metastylid unconnected to postprotocristid, and postprotocristid continuous with cristid obliqua. Differs from *Pildra magnus* Pledge, 1987b, (from the Oligo-Miocene Ngama Local Fauna of the Etadunna Formation) in being twice as large; in having a continuous well-developed endocristid with a metastylid flexure and incorporating the entoconid; and with rounded protoconid and hypoconid crests. Differs from *Marlu kntjamarpensis*

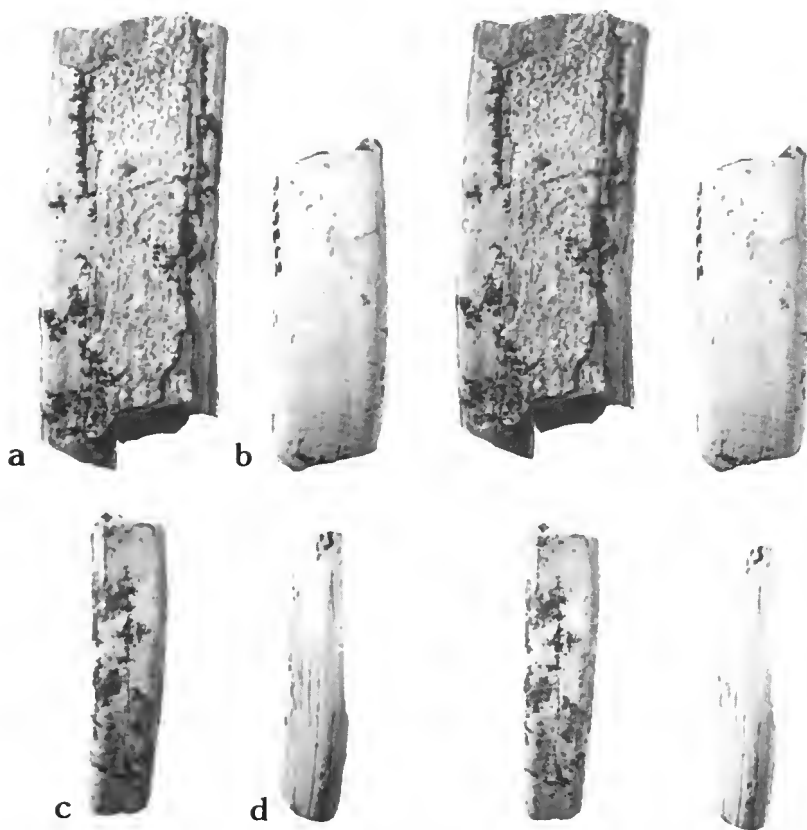


Fig. 11. Vombatids, outer views of upper incisors, stereopairs; a, *Phascolonus* sp. P26543; b, *Phascolomys* sp. cf. *P. medius* P29862; c, P31797; d, *Vombatus* sp. indet. P29931. Natural size.

Woodburne *et al.* (from the mid Mioene Kutjamarpu local fauna of the Wipajiri Formation) in much larger size (2 - 3x), having a continuous endocristid with a connection between slightly overlapping postmetacristid and pre-entocristid, and lacking I_2/P_1 .

Description. SAM P26542 is an almost complete dentary, lacking only the incisor, P_3 , the anterior half of M_3 , and the upper part of the ascending ramus. The incisor root is broken off and shows this tooth to have been greatly compressed laterally. The incisor P26520 is referred to this species by being of the right size, being similar in appearance to *Pseudocheirus* Ogilby and being unlike any of the macropodids. It differs from *Pseudocheirus peregrinus* in having a relatively shorter spatulate bladed crown represented by the unworn referred specimen P26520 (total length 28.2 mm, enamel length about 13 mm).

The dentary is relatively deep-bodied compared with *P. peregrinus*, with the ascending ramus not vertical at the leading edge, but at about 80° to the dental plane. The angular process is much reduced, not extending behind the

condyle while the posterior masseteric eminence does so, unlike *P. peregrinus*. The masseteric fossa is strongly delineated ventrally and posteriorly. The broad condyle itself may be deformed or pathological since its flat articular surface shows a postero-lateral and a medial moiety separated by a deep groove; it is rela-

Table 5. Dimensions of cheek teeth (in millimetres) of *Corracheirus curranulkenensis* n.g., n.sp.

	P_3 (alveolus)	M_2	M_3	M_4	M_5
P26542(holotype)					
length	2.5	>6.5	8.6	8.1	8.2
anterior width	2.0	4.5	5.0	4.8	4.5
posterior width	2.9	5.2	5.0	4.5	4.1
P29901 (referred)					
length		9.3			
anterior width	-	5.3	-	-	
posterior width		5.6			
P31792(paratype)					
length		8.5	8.2		
anterior width	-	5.2	5.3	-	
posterior width		5.5	5.0		

tively low and has little neck. The mandibular foramen is higher than in *P. peregrinus*, lying just below the level of the teeth. A small mental foramen opens below the anterior part of M_2 . The ventral profile of the jaw is similar to *P. peregrinus*, but the incisor may rise more sharply. The symphysis extends back to the level of M_3 , unlike *P. peregrinus*. There is a short diastema of 6 mm between incisor and P_3 , with no indication of the tiny anterior premolars seen in *P. peregrinus*. The dentary is larger than that of *Pseudokoala erlita*, and only generally similar, having a more convex ventral profile, straight alveolar profile and more procumbent less tilted incisor. Measurements are as follows: dentary length (incisor alveolus) parallel to tooth row, 66 mm; depth at M_3 , 18 mm; symphysis length, >17 mm; length of ascending ramus at occlusal level, 29 mm;

transverse width at angular process, 20 mm; alveolar tooth row length P_3 - M_5 , 33.2 mm.

P_3 is missing, but the alveolus, measuring 2.4 mm long and 2.9 mm wide posteriorly, indicates a very short, double rooted tooth.

M_2 is damaged. The anterior quarter, bearing the protoconid, is broken off. The buccal protocristid tends slightly posteriorly. It is not clear whether the cristid obliqua fades out at the transverse valley, meets the postmetacristid, or meets a lingually directed crest from the protocristid/protoconid. The tooth is less worn than NMV P54159 of *Pseudokoala erlita* but is similar in general form except for having a straight endocristid with only a slight thickening at the metastylid, rather than an overlap of the postmetacristid and pre-entocristid. The posthypocristid is slightly convex, unlike those of

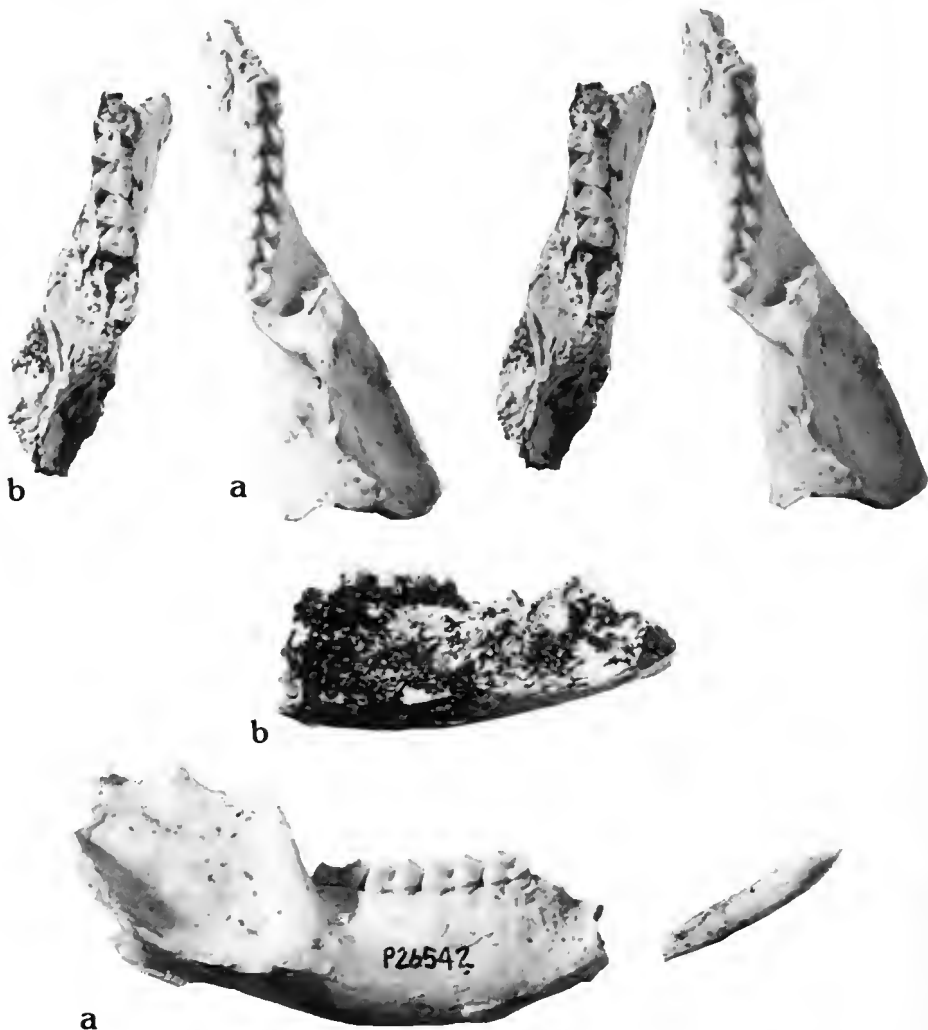


Fig. 12. *Corrachairus curramulkensis* gen. et sp. nov., dentaries; a, holotype P26542; b, referred specimen P31792; oclusal (stereopair) and lateral views. Twice natural size.

P. peregrinus and *P. erlita*. There are crenulations in the talonid basin, mostly extending posterolingually from the cristid obliqua.

The posterior molars have a similar plan. Cuspids are relatively low (although the protoconid and hypoconid appear to be attenuated when unworn: only the apices of these cusps show breached enamel). The paracristid, postprotocristid, cristid obliqua and posthypoerista are all convex buccally, giving rounded angles at the cuspid. The metaconid and entoconid support flat, bladed cristids that are continuous but overlap sigmoidally at the metastylid and are less oblique than those of *P. peregrinus* and *P. erlita*. In profile, the cuspid is obtuse. In the holotype, the postprotocristid meets the cristid obliqua at the mesostylid and does not continue to the postmetacristid (there is a very weak connection in M_3 of P31792). They are separated by a deep crevice. The posthypoerista is likewise separated from the postendocristid. The parastylid is a little in advance of, but lower than, the anterior end of the premetacristid, and is joined to it by a narrow precingulum, about one quarter tooth-width, except in M_3 . There is a small but distinct low level anterobuccal cingulum (and an anterolingual cingulum on M_3) which tends to give the front of the teeth a square outline, and a low buccal cingulum at the mouth of the transverse valley. The lingual face of the endocristid is shallowly scalloped as a consequence of a slight vertical axial thickening at the metaconid and entoconid. The trigonid and talonid basins are only mutedly ornamented compared with M_2 suggesting that crenulations have not been obliterated by wear.

Discussion. *Corracheirus curramulkensis* is considered to be a species roughly contemporary with, or a little earlier than, (see Discussion and Conclusions, below) the somewhat smaller *Pseudokoala erlita* of the Hamilton Local Fauna in western Victoria (Turnbull and Lundelius 1970, Turnbull *et al.* 1987). Although there are only two or three comparable teeth, the Curramulka specimens are seen to be morphologically and mensurally distinct from the Victorian species. The differences are considered to be of generic significance, by comparison with the differences seen in the lower molars of the modern pseudocheirids, *Pseudocheirus*, *Pseudochirops*, *Petauroides* and *Hemibelideus*.

Relationships of *C. curramulkensis* with other species are, however, less easy to deduce because of the lack of knowledge about P_3 and M_2 and upper molars. On the basis of the few characters

preserved in common, there may be a relationship with *Marlukujamarpensis* (Woodburne *et al.* 1987).

A tooth found at Marmor Quarry, southeast of Rockhampton, Queensland, closely resembles the M_3 of *Corracheirus curramulkensis* in size (length 8.0 mm, width 4.1 mm) and differs only in the postmetacristid and postentocristid being medially more convex and the cristid obliqua more concave. These are probably not sufficient grounds to make the Queensland specimen a different species. It should be noted that the Marmor Quarry also has yielded a fragment of molar referable to the large koala *Phascolarctos stirtoni* Bartholomai (? M^4). This species seems also to occur in the Chinchilla Sands (Bartholomai 1968). It is thus supporting evidence for a Pliocene age.

No upper molars have yet been found in the Curramulka Local Fauna, but a fragmentary specimen from the Bow Local Fauna, Merriwa, N.S.W., has characters that are similar to this species and is described as follows. The Bow tooth lacks that part anterior to the protocone and paracone, and while not heavily worn, appears to have been tumbled and abraded so that features are somewhat obscure. It is considered to be a right M^4 . Estimated length is 6.5 to 7 mm (preserved length is 5.8 mm), anterior width approximately 5.5 mm, posterior width 4.7 mm. This may be rather short for *C. curramulkensis*. The buccal face is relatively flat, with only a slight vertical ridge at the mesostyle and slightly concave above the pre- and postmetacristae, the 'ectoloph' is almost straight - a very open W. A strong posterolingual crest also extends from the paracone towards the middle of the tooth, but does not join the crista obliqua which has curved buccally to join the premetacrista just posterior of the mesostyle. A small anterior spur from the crista obliqua trends towards the posterolingual paracrista. The protocone is shorter than all other cusps and appears to give rise to a somewhat diverging set of buccally directed cristae. The postprotoerista is low and meets the crista obliqua rather low on its anterior face. The posthypoerista is almost symmetrical with the crista obliqua, except for the short anterior spur on the latter. The hypocone gives rise to a broad subdued set of three near parallel buccally directed cristae which halt at the bottom of the fossette. There is also a short posterobuccally directed crista arising from the crista obliqua opposite the anterior spur, and a similar faint eminence arising anterobuccally from the posthypoerista. The metacone has a strong lingual axial ridge defined by deep grooves. The posthypoerista does not meet the postmetacrista

- there is a gap of about one millimetre. The Bow Local Fauna is considered to be of Pliocene age.

Etymology. This species is named for the nearby town of Curramulka.

Family Petauridae

Petaurus Shaw

Petaurus sp. cf. *P. norfolcensis* (Kerr)

(Fig. 13)

Gliders are represented by a single right dentary (SAM P29892) preserving P_3M_{2-4} . This matches *P. norfolcensis* (Kerr) in size and general morphology, differing mainly in having a slightly longer P_3 and narrower, more acute M_2 .

Family Potoroidae

Potorous Desmarest

Potorous sp.

(Fig. 14)

Two dentary fragments represent this taxon. SAM P26541 preserves P_3M_{2-4} , while P29925 preserves $M_{2,3}$ and unerupted M_4 . The teeth are similar in size to those of *P. platyops* (Gould) (*P. morgani* Finlayson, SAM P168) but the premolar differs slightly in outline and has five ridges and cusps and much less lingual cingulum. In addition, the dentary is more massive than in the aged *P. platyops* examined and the inflection of the ventral outline is more posterior, below M_5 rather than M_3 .

Family Macropodidae

Kangaroos are the most numerous taxon collected, and represent at least four species, none of which has been identified with certainty (Table 6).

Baringa Flannery and Hann

Species 1: cf. *Baringa* sp.

(Fig. 15)

Eight dentaries (SAM P26547, 26548, 26550, 29863, 29902, 29923, 31337, 31794) including all teeth, and a maxilla P31788, represent this smallest species. The molar teeth are roughly the same size as those of *Thylogale thetis* Lesson and *T. stigmaticea* Gould but are lower and have shorter, wider precingula. The premolar P_3 is longer and more regular in width and height, and the lower incisor is slightly smaller and possibly more spatulate. The dentary is about the same size as that of *T. billardieri* Desmarest, with perhaps a more vertical leading edge to the ascending ramus, and with a slightly shallower

and more even depth below the teeth. The symphysis and diastema are shorter. There is a rather deep buccinator groove from below P_3 to the anterior half of M_4 , more distinct and lower than in *Thylogale* Gray.

The alveolar margin is not arched. A sharp ridge from below the anterior edge of the ascending ramus follows outside of the ventral rim of the masseteric fossa: it is more angular and more pronounced than in *Thylogale* and *Petrogale xanthopus* Gray. In some characters - e.g. buccinator groove, masseteric rim, regular depth of dentary, form of P_3 - the species resembles the early Pleistocene *Baringa nelsonensis* Flannery and Hann 1984, but is considerably smaller.

One worn upper dentition (P31788) has been recognized, on the basis of size and form. It retains P^3M^{2-4} . The premolar is relatively long compared with the molars, unlike *B. nelsonensis*, but is similar to that species except that the posterior cusp seems to be highest and the lingual shelf is well developed.

Species 2: cf. *Baringa nelsonensis*

Flannery and Hann

(Fig. 16)

This is the most numerous of the macropodid taxa with nine dentary fragments and seven referred maxillary fragments: SAM P24887, r. dentary $M_{2,3}$; P26510, r. maxilla, M^{1-3} ; P26511, r. maxilla, P^2M^{1-2} ; P24889, l. maxilla, P^3M^{2-3} ; P26549, r. dentary P_3M_5 , very worn; P26551, l. maxilla M^{1-5} ; P29865, r. dentary, M_1 ; P29869, r. maxilla, M^{2-4} ; P29903, r. maxilla, M^{2-3} ; P29919,

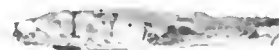


Fig. 13. *Petaurus* sp. cf. *P. norfolcensis*, dentary P29892 in occlusal (stereopair) and lateral views. Twice natural size.

r. dentary, $M_{2,4}$ (M_5 unerupted); P29920, r. dentary P_3M_4 ; P29921, r. dentary, $P_2M_{1,3}$ (P_3 unerupted); P29922, l. dentary, $P_2(P_3) M_{2,4}$; P29927, l. dentary, M_5 P31338, l. maxilla, $M^{1,2}$; P31789, r. dentary, M_4 . As there is some size variation, this sample may not represent a single species.

The molars of this taxon are roughly the size of *Macropus irma* (Jourdan) but differ from *Macropus* Shaw in many respects. No incisor is known, but it would seem not to be procumbent as in *Macropus*. The premolar is long and bladed, as in *Petrogale* Gray, but differs in shape being of regular height and width and with no posterior expansion or hook of the crest. Of the three dentaries showing adult, fully erupted teeth, only two preserve M_5 and one of these is very worn. Nevertheless, these specimens show no great increase in size of the molars; in fact, M_5 is rather smaller than M_4 . In addition, the very old individual, P26559, displays molars with the roots extending backwards beyond their crowns, as in *Dendrolagus* species. Upper premolars (P^1) have a weak lingual cingulum, less than half the length of the tooth, and a distinct posterolingual cusp. P^2 has a stronger lingual cingulum nearly full length and a weaker posterolingual cusp. Several lower incisors (P26509, 29928) may also be referred to the taxon. They are about the size and form of that of *T. billardieri*.

Measurements and morphology of the teeth are similar to *Baringa nelsonensis*, although the I_1 does not show the distinctive wear pattern ascribed to that species (Flannery and Hann 1984).

Troposodon Bartholomai

Species 3: *Troposodon* sp. cf. *T. bowensis* Flannery and Archer (Fig. 17)

A near-complete left dentary lacking I_1 (SAM P26546), a fragment with $M_{3,4}$ (P22918), a fragment with P_2 , part of unerupted P_3 and the remains of I_1 (P24888), a fragment of left dentary with P_3 and M_2 (P31793), and a fragment with unerupted left M_5 (P31795) are all that represent this species.

The species is small and appears closest to *Troposodon bluffensis* (Bartholomai, 1978) and *T. bowensis* Flannery and Archer, 1984. *Troposodon bluffensis* is known from few isolated teeth, only two of which (P_2 , M_5) can be compared with the Corra Lynn material. The M_5 ,



Fig. 14. *Potorous* sp. undet., dentaries in stereoview; a. occlusal, P26541; b. lateral, P29925. Natural size.

although more worn, matches the size of the paratype QM F9055 while the P_3 is somewhat longer than its equivalent, has a crest less curved and lacks the posterolingual cusp.

The dentary is similar in size and profile, and presents the distinctive buccal depression below $M_{2,3}$, seen in *T. bowensis* (and also *T. gnar* Flannery and Archer and *T. kenti* Campbell). The teeth fall generally within the range of measurement given for *T. bowensis* (Flannery and Archer 1984), although these are on the small side, except for the P_3 . While the molars fit the description for *T. bowensis*, the premolars do not. On the unworn P_2 , there is no particularly distinct cuspid at the anterior end of the crest, and there are several grooves on each face, alternating to give the crest a zig-zag form. The posterior end of the crest flexes lingually, but there is no posterolingual cuspid as illustrated in Flannery and Archer (1984; Fig. 2D). P_3 is well worn in the dentary P26546, and all traces of buccal ridges have been obliterated although there seem to have been three lingually. There is no trace of the distinct anterior cuspids seen in *T. bowensis*, and although the crest flexes posterolingually, there is no posterolingual cuspid. On P31793, however, there are four buccal and four lingual ridges on the premolar, together forming a finely scr-

rated edge but no distinct anterior cuspid or posterolingual cuspid.

Although the molars are similar in size to those of *Kurrabi mahoueyi* (Flannery and Archer 1984) they differ in the development of precingulum and midlink, the size gradation of the teeth being less, and the tooth row straighter. The premolar P₃ is also much smaller.

***Protemnodon* Owen**
Species 4: *Protemnodon* sp.
(Fig. 18)

Four dentary fragments (SAM P24906, with P₃M₂; P26518 - partial M₄; P29899 - with M_{3,5}; P29900 - edentulous; P31796 - isolated M₄), a complete left maxilla (P31782), an isolated P³ (P31336), maxilla fragment with M² (P29861) and isolated M⁵s (P29914, P31789) belong to a small species of *Protemnodon* Owen (Table 7).

The cheek teeth generally fall at the low end of the size range of *P. chinchillaensis* Bartholomai and within those of *P. snewini* Bartholomai and *P. otibandus* Plane. P³ is just outside the range of all these species while P₃ is shorter and broader than those of *P. chinchillaensis* tabulated by Bartholomai (1973), and stouter than that of *P. snewini* (Bartholomai 1978). The P³ (P31336) is well preserved, though well worn and is almost a match for P³ of P31782. It is distinguished by being relatively narrow - the lingual cingulum being reduced in width - except for an abrupt expansion for the hypocone. The longitudinal crest has four cusps anterior to the worn metacone, as in *P. otibandus* and *P. snewini*, but fewer than described for *P. chinchillaensis*, and there is no fossette discernible posterior to the worn metacone-hypocone crest, unlike that in the above species. The M² resembles *P. chinchillaensis* also in form, but has a distinct

Table 6. Check tooth measurements in millimetres of the smaller macropodines cf. *Baringa* sp., *Baringa* sp. cf. *B. nelsonensis*, *Troposodon* sp. cf. *T. bowensis* from Corra Lynn Cave; u = unerupted a = approximate.

Specimen	Tooth	P2	P3	M1	M2	M3	M4	M5
cf. <i>Baringa</i> sp.								
SAM P31788	upper	-	7.1 x 3.3	-	5.8 x 4.7	8.5 x 5.0	7.3 x 5.6	-
P26547	lower	-	-	-	5.5 x 4.1	6.2 x 4.7	7.6 x 5.5	u
P26548	-	-	7.3 x 2.5	-	4.9 x 3.9	5.8 x 4.6	6.8 x 5.2	7.5 x 5.0
P26550	-	-	-	-	-	-	-	u
P29863	-	-	6.2 x 2.1	-	4.7 x 3.9	5.7 x 4.2	7.0 x 5.1	7.0 x 5.1
P29902	-	4.5 x 2.4	-	4.6 x 3.0	4.8 x 3.7	5.8ax 4.3	7.1 x 4.9	u
P29923	-	-	-	-	-	6.1 x 4.1	-	u
P31337	-	-	-	-	-	5.5 x 4.5	6.5 x 5.4	7.5 x 5.6
P31794	-	-	-	-	-	-	7.0 x 5.0	7.6 x 5.1
<i>Baringa</i> sp. cf.								
<i>B. nelsonensis</i>								
P24889	upper	-	8.1 x 4.0	-	5.9 x 5.2	6.8 x 5.4	-	-
P26510	-	-	8.8 x 4.5	-	6.2 x 5.2	6.8 x 6.0	7.6 x 6.5	-
P26511	-	6.3 x 3.8	9.0 x 4.0	6.2 x 5.2	7.2 x 6.1	-	-	-
P26551	-	-	-	-	7.2ax 6.5	9.5ax 6.7	8.8 x 6.7	-
P29869	-	-	-	-	5.8 x 5.2	6.8 x 5.5	7.7 x 6.0	-
P29903	-	-	-	-	7.0 x 5.6	7.4 x 6.0	-	-
P31338	-	-	-	5.6 x 4.3	6.0 x 4.9	-	-	-
P24887	lower	-	-	-	5.9 x 4.5	6.6 x 5.2	7.7 x 5.3	8.0 x 5.2
P26549	-	-	6.4 x 2.9	-	6.3 x 5.0	7.2 x 5.6	8.5 x 6.4	9.8 x 6.2
P29865	-	-	-	5.6 x 3.8	-	-	-	-
P29919	-	-	-	-	4.6	7.0 x 5.0	8.3 x 5.6	u
P29920	-	-	7.8 x 2.7	-	-	9.0 x 5.6	-	-
P29921	-	6.0 x 2.7	8.1u	6.0 x 4.1	6.8 x 5.0	8.5 x 5.4	-	-
P29922	-	6.7 x 2.2	6.9a,u x 2.8	-	6.2 x 4.8	7.6 x 5.2	8.0 x 5.4	-
P29927	-	-	-	-	-	-	-	8.7 x 5.3
P31789	-	-	-	-	-	-	7.9 x 5.3	-
<i>Troposodon</i> sp. cf.								
<i>T. bowensis</i>								
P22918	lower	-	-	-	-	10.0 x 7.0	11.5 x 8.0	-
P24888	-	7.2 x 3.3	u	-	-	-	-	-
P26546	-	-	9 a x 3.9	-	7.8a x 6.0	9 a x 7.0	10.2a x 8.0	11.8 x 8.2
P31793	-	-	9.0 x 3.5	-	7.8 x 5.8	-	-	-
P31795	-	-	-	-	-	-	-	11.0a,u

forelink which unequally divides the precingulum. In this feature it is like *Wallabia bicolor* (Desmarest) and unlike Pleistocene species of *Protemnodon*. Bartholomai's figure (1973, pl. 20, fig. 2) seems to indicate this structure but it is not specifically mentioned in the text.

Protemnodon sp. cf. *P. chinchillaensis* also occurs at Bow, N.S.W. (Flannery and Archer 1984), while *P. otibandus* is from the Pliocene Awe Fauna of Papua New Guinea (Plane 1967) and Kalimnan of Victoria (Plane 1972) and *P. snewini* is from the early Pliocene Allingham Local Fauna of north Queensland (Bartholomai 1978).

Simosthenurus Tedford

Species 5: *Simosthenurus cegsai* n. sp.

(Fig. 19)

Type Material. HOLOTYPE: SAM P31800, a left dentary lacking only the incisor.

Referred specimens. SAM P29917, a left maxilla fragment with M^{4-5} ; P30027 a right maxilla fragment with M^4 ; P30153, a possible M^1 ; P31335, a right dentary fragment with M_3 ; P29872, and P29891, isolated left lower incisors. Several upper incisors may also be ascribed to this species.

Type locality. Corra Lynn Cave (5YI), 3 km south of Curramulka, Yorke Peninsula, South Australia.

Diagnosis. A small sthenurine with relatively short, massive dentary, short diastema, low crowned molars: therefore, *Simosthenurus*. A *Simosthenurus* with massive jaw and small low crowned molars, with simple low midlinks and barely discernible cristids obliquae. Premolar P_3 long, narrow, rectangular; longitudinal crest central except in posterior third where it veers lingually; short posterobuccal crest tending diagonally (anterobuccally) and less than one third the tooth length; only slight increase in posterior

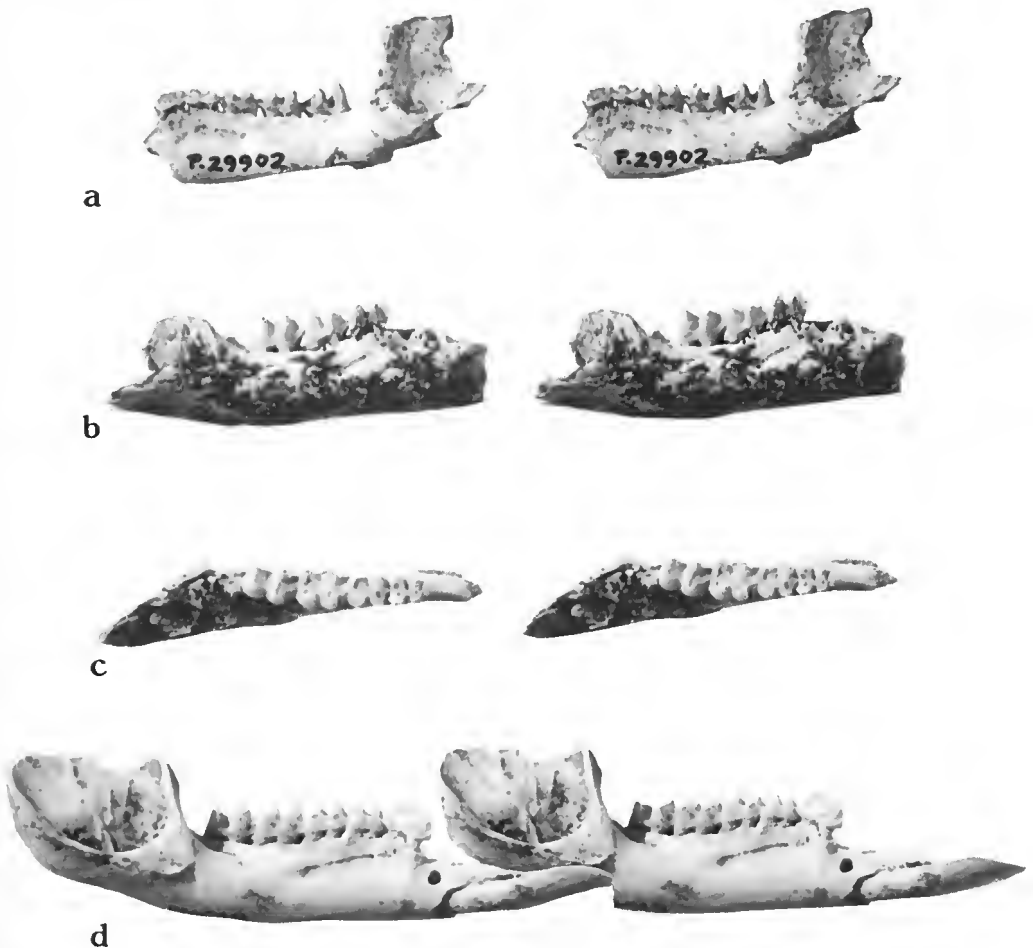
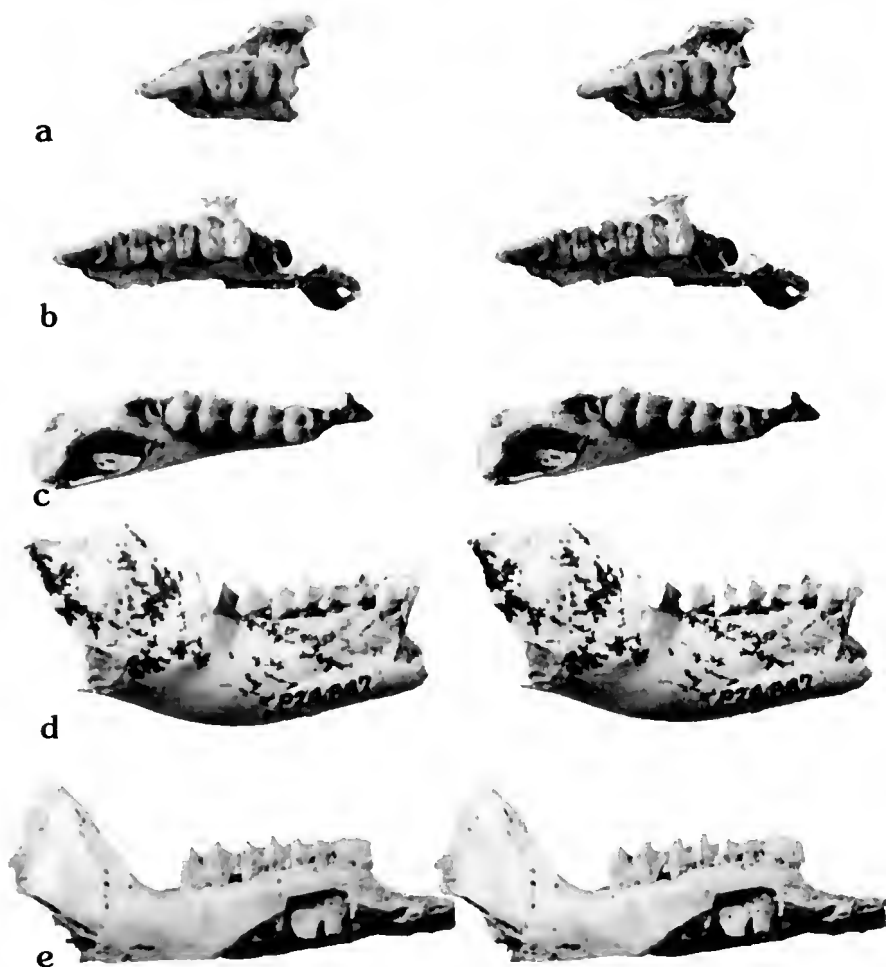


Fig. 15. cf. *Baringa* sp., dentaries in lateral and occlusal stereoview; a, P29902; b, P26547; c, P29863; d, P26548. Natural size.

Table 7. Cheek tooth dimensions (mm) of *Protomnodon* sp. from Corra Lynn Cave, compared with averages for other Pliocene species.

Specimen	P3	M2	M3	M4	M5
<i>Protomnodon</i> sp. (Corra Lynn)					
uppers					
SAM P31336	18.1 x 8.2	-	-	-	-
P31782	17.2 x 8.5	10.2 x 10.1	12.0 x 11.8	12.4 x 11.7	12.7 x 10.8
P29861	-	10.1 x 9.7	-	-	-
P29914	-	-	-	-	14.1 x 11.6
P31787	-	-	-	-	13.2 x 10.9
lowers					
P24906	15.1 x 6.5	-	-	-	-
P26518	-	11.3 x 8.4	-	-	-
P29899	-	-	13.9 x 9.0	13.6 x 10.2	13.5 x 9.8
P31796	-	-	-	13.9 x 10.0	-
<i>P. chinchillaensis</i>					
upper	19.5 x 8.7	11.0 x 10.3	12.5 x 11.7	14.2 x 12.3	14.3 x 12.1
lower	17.1 x 5.5	10.6 x 8.0	12.1 x 9.1	13.6 x 9.9	14.1 x 9.7
<i>P. otibandus</i>					
upper	19.0 x 8.8	10.8 x 10.8	12.1 x 11.6	13.4 x 11.7	13.5 x 10.5
lower	15.9 x 6.1	9.9 x 8.2	11.7 x 9.2	12.8 x 10.1	13.8 x 9.9
<i>P. snewini</i>					
upper	15.8 x 6.6	10.4 x 9.1	12.3 x 10.3	13.0 x 11.2	13.9 x 11.2
lower	15.0 x 5.0	9.9 x 6.8	12.3 x 8.3	13.1 x 8.8	13.8 x 9.1

**Fig. 16.** cf. *Baringa nelsonensis*, stereopairs; a, maxilla P24889; b, maxilla P31788; c, dentary P29919; d, dentary P24887; e, dentary P29921. a-c in occlusal view, d, e in lateral view. Natural size.

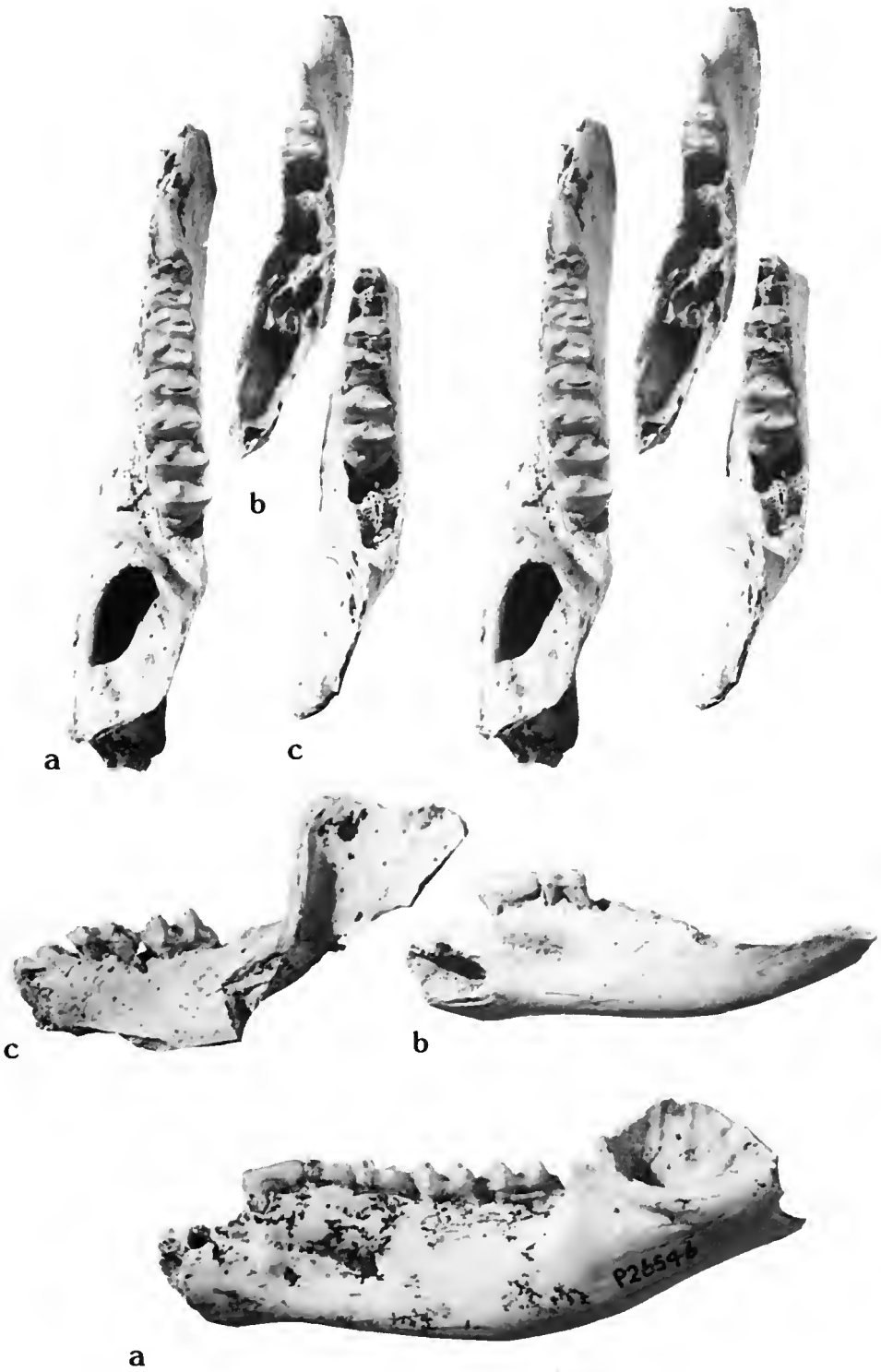


Fig. 17. *Troposodon* sp. cf. *T. bowensis*, dentaries in occlusal (stereopair) and lateral views; a, P26546; b, P31793; c, P29918. Natural size.

width; four pairs of transverse grooves on longitudinal crest. Differs from Chinchilla local fauna (Pliocene) taxa *Simosthenurus antiquus* (Bartholomai) and *Sthenurus notabilis* (Bartholomai) and most Pleistocene species in being much smaller. Differs from *Sthenurus gilli* Merrilees and *Simosthenurus maddocki* (Wells and Murray) in having larger molars, and more massive dentary. Differs from all other *Simosthenurus* species in having dentary only slightly deeper at M_3 than at P_3 ; in narrow rectangular shape of P_3 ; in central position of longitudinal crest on P_3 ; in having short, rather diagonal, posterobuccal crest on P_3 ; in having only four pairs of transverse grooves on longitu-

dinal crest of P_3 ; in showing little expansion of the posterior third of P_3 .

Description. The species is smaller than the Pliocene (Chinchilla L.F.) taxa *Simosthenurus antiquus* and *Sthenurus notabilis*, and most Pleistocene species. The teeth are larger than those of *Sthenurus gilli* and *Simosthenurus maddocki* but smaller than those of *Simosthenurus occidentalis* (Glauert) from Naracoorte, S.A., from which they differ only slightly morphologically, notably in simpler, less developed crenulations of the enamel and lower crown height. (Table 8).

The molars are roughly the size of those of *Sthenurus atlas* (Owen) except for being very



Fig. 18. *Protomnodon* sp.; a. P31782, left maxilla in occlusal view, stereopair; b, c. dentary fragments in lateral view; b, P29899; c, P24906. Natural size.

low-crowned, and the molar tooth row length approximates that of *Sthenurus atlas*. Morphologically the lower molars are simple with low midlinks and barely discernible cristids obliquae. There are also no obvious crenulations on the faces of the lophids. However, the premolar P₃ is the most striking feature. Its characters seem to be plesiomorphic for the subfamily; long narrow rectangular shape, longitudinal crest central except in the posterior third where it veers lingually, short posterobuccal crest trending diagonally (anterobuccally) and less than one third the tooth length. Only a slight increase in posterior width. Only four pairs of transverse grooves on the longitudinal crest. All Pleistocene species show a massive posterior expansion at the buccal crest with a developing longitudinal valley and with many ridges, often irregular, crossing it. The almost perfect dentary, P31800, sheds more light on this taxon. The jaw is slightly larger than that of *Sthenurus gilii* but quite massive - as much as *Simosthenurus gilii* - although only slightly deeper at M₃ than at P₃, unlike later *Simosthenurus* species. Pleistocene species of *Simosthenurus* also show a posterior deepening of the dental ramus, and are not so robust, whereas *Sthenurus* species (of this tooth size) have elongate gracile jaws.

Although the upper molars resemble those of *P. chinchillaensis* in size (Table 8), they display the (albeit barely discernible) overlap of the postmetacrista and posthypocrista on the hypoloph, a character which Flannery (1983) asserts as helping to define the Sthenurinae. The feature is better seen on P30153 (but in this writer's experience is not seen on all Sthenurine specimens).

It appears that this is the earliest species of *Simosthenurus* yet recorded (see discussion on age of the deposit, below).

Etymology. In recognition of the help of members of the Cave Exploration Group of South Australia, Inc. (CEGSA).

DISCUSSION AND CONCLUSION

It is difficult, with so many species only tentatively identified or apparently new, to make definite statements about the fauna. The overall aspect of the assemblage, with its particular combination of species, suggests considerable antiquity for a cave deposit, most of which in Australia seem restricted in age to the Late Pleistocene. Certain species (e.g. cf. *Baringa nelsonensis*) suggest an early Pleistocene date. Others (*Palorchestes* sp. cf. *P. painei*, *Troposodon* sp. cf. *T. bowensis*, *Protomodon* sp.) indicate a Pliocene age, while a few (cf. *Ibandornis* sp., zygomaticurine indet.) hint at a late Miocene age.

The evidence of age afforded by the dromornithid bones, referred to *Ibandornis* sp., is admittedly weak. These bones are not particularly diagnostic, or, in the case of the atlas, well known. *Ibandornis* is described only from the late Miocene Alcoota Fauna, so its range and evolution is unknown. The diprotodontoid teeth provide only slightly stronger evidence for age. The *Palorchestes* molars (Pledge 1991) show a greater similarity to those of *P. painei* from Alcoota - particularly in their relatively low crowns - than to the younger *P. parvus* which have higher-crowned molars. The zygomaticurine premolar shows a mixture of characters and, while not referable to *Kolopsis* species, does not fit *Zygomaturus* species either. In the form of its parastyle, this tooth shows a slight similarity to undescribed Miocene species from Riversleigh (Qld) and Bullock Creek (N.T.) (S. Hand, pers. comm. 1991).

The Curramulka faunal list is rather similar in general composition to that of the Hamilton Local Fauna (Turnbull and Lundelius 1970, Rieh 1991), and therefore suggests a similar environmental niche dominated by forest and woodland species. The similarities between these faunas are as interesting as the differences. Notable similarities are the presence of a species of

Table 8. Cheek tooth dimensions of *Simosthenurus cegsai* from Corra Lynn Cave.

Specimen	P3	M1	M2	M3	M4	M5
Upper						
SAM						
P29917(1)	-	-	-	-	12.5 x 11.9	12.0 x 11.3
P30027(r)	-	-	-	-	13.2 x 12.3	-
P30153	-	9.7 x 9.7	-	-	-	-
Lowers						
P31335(r)	-	-	-	13.8 x 11.2	-	-
P31800(1)	14.6 x 7.4	-	10.8 x 10.3a	12.8 x 11.1	13.2 x 11.5	11.8 x 10.7

Palorchestes nearer to *P. painei* than to *P. parvus*, a giant ringtail (*Pseudokoala erlita* at Hamilton), and the total absence of rodents. Among the possible differences are the identity of the Ham-

ilton macropodids, which include several large and small species, the latter being originally referred to modern genera. Unfortunately, nearly all Hamilton specimens are isolated teeth which



Fig. 19. *Simothenurus cegsai* sp. nov.: a, P31800, holotype left dentary in lateral view; b, P31800 holotype dentary; c, P30027, right maxillary fragment; d, P29917, left maxillary fragment. b, c stereopairs in occlusal view. Natural size.

makes identification more difficult. However, none of the small Hamilton wallabies show affinities with those from Curramulka, where no modern macropodid genera are recognised. The larger Hamilton macropodids, which include

Simosthenurus (Rich 1991), have not been described and/or identified and therefore cannot be compared with the Curramulka species. However, it appears that the Curramulka Local Fauna is at least as old as, and probably older

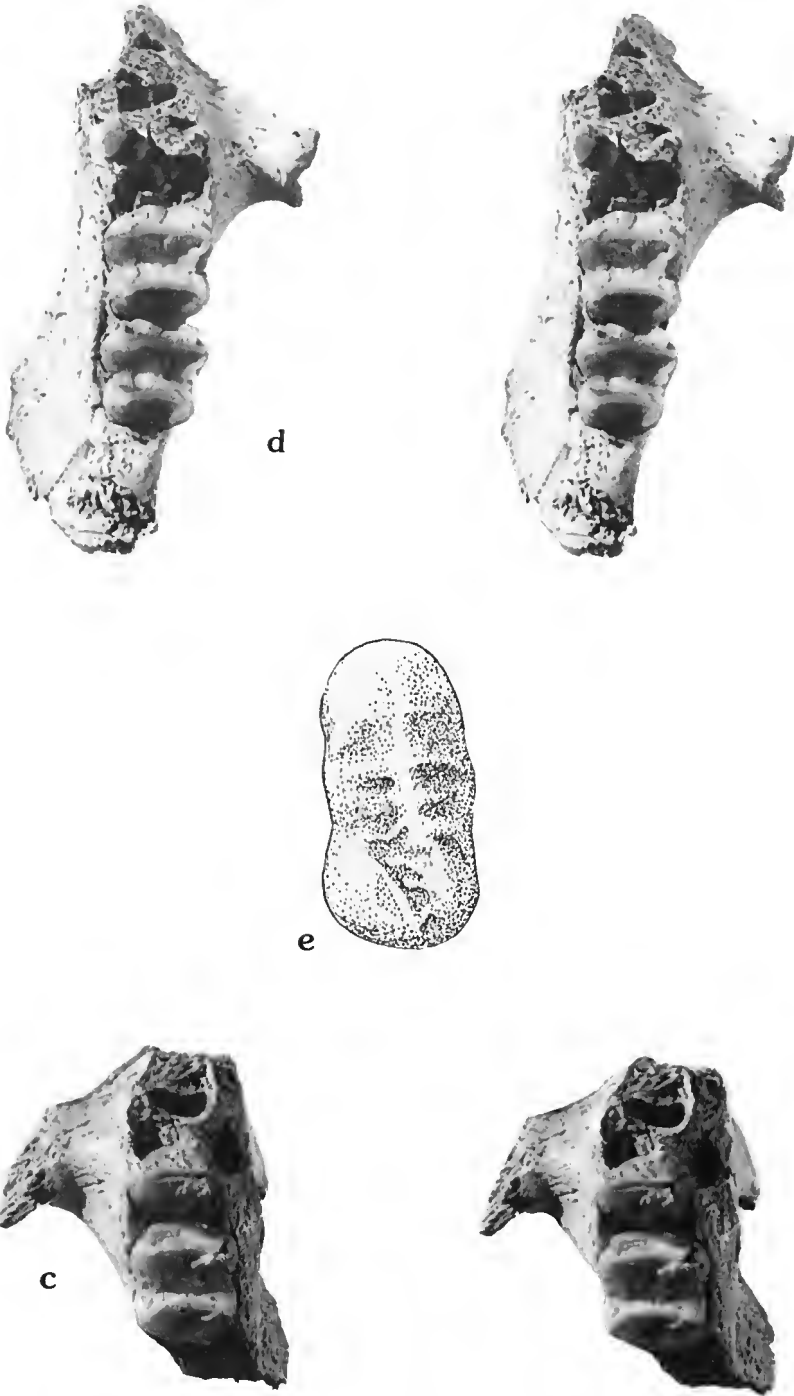


Fig. 19. (cont.): *Simosthenurus cegsai* sp. nov.; d, P29917, left maxillary fragment, stereopair in occlusal view; e, detail of premolar (x2.5 approx.). Natural size except e.

than, the Hamilton Local Fauna's 4.46 million years.

Conversely, comparison with the estimated early to mid Pliocene Bluff Downs and Bow Local Faunas indicates few faunal resemblances. These assemblages both contain macropodids of more modern, hypsodont morphology, often referred to modern genera, and are therefore considered to be younger than the Curramulka Local Fauna.

The rather abundant small Curramulka macropodines referred to *Baringa* are anomalous. *Baringa nelsonensis* is regarded as an early Pleistocene species (Flannery and Hann 1984) and is associated, *inter alia*, with a small *Palorchestes* and a giant pseudocheirid, both undescribed. It is therefore possible that the Curramulka Local Fauna is only as old as early Pleistocene - refuted by the presence of acknowledged Pliocene species and the lack of modern genera - or is a mixed assemblage, a common and frustrating problem in cave deposits (e.g. Archer 1974). The latter hypothesis must also explain the lack of modern macropodine genera as well as the absence of bandicoots and rodents. It is inconceivable that the mixing and sorting processes that can occur in a cave situation could preferentially remove such distinctive items as rodent jaws (and particularly incisors) and limb bones and bandicoot jaws while leaving small potoroid and dasyurid jaws, *Baringa* teeth, *Wonambi* teeth, elapid vertebrae and frog bones, especially when bandicoots and rodents are so abundant in Pleistocene cave deposits (e.g. Pledge 1990). Despite fine screen sieving of the Corra Lynn sediments no bandicoot or rodent remains have been found. The absence of bandicoots is puzzling, since they are so abundant in Miocene Riversleigh deposits (Archer *et al.* 1989) and in Pleistocene cave deposits (e.g. Pledge 1990) and are not uncommon in the Lake Eyre Basin deposits which are close to being biocoenoses. They are uncommon in the Alcoota deposit (Woodburne 1967b) which tends to be more of a megafaunal thanatocoenosis.

The absence of rodents, on the other hand, may be significant. They may not yet have arrived in southern Australia when the cave assemblage lived. Even the date of rodents' arrival in northern Australia - at Bluff Downs and Rackham's Roost (Riversleigh) - is subject to scrutiny, being based on long distance faunal and geological correlation (Rich 1991). The oldest published Australasian rodent occurrences are in

the Awe Local Fauna (Plane 1967), Bluff Downs Local Fauna (Archer and Wade 1976), Chin-chilla Local Fauna (Hand 1984, Godthelp 1990), and Rackham's Roost Local Fauna (Godthelp 1988). The Awe specimen, with a revised age of 2.5 to 3.3 million years (Hoeh and Holm 1986), is a mere sliver of enamel of uncertain identity (Plane 1967). The Bluff Downs material is a single upper incisor around 4 to 4.5 million years old, a date that is somewhat doubtful since it derives from a lava flow about 10 km away from the fossil site. Only Rackham's Roost has yielded a rich and diverse rodent fauna, and its age is inferred as being possibly early Pliocene on the basis of single species correlation with Bluff Downs (Rich 1991). Of the Pliocene terrestrial vertebrate faunas in Australia, only the Hamilton Local Fauna is securely dated and it contains no rodents. The absence, therefore, of murids from the Curramulka Local Fauna supports an early Pliocene age for the deposit.

Further support for a considerable antiquity of the deposit is seen in the total absence of hypsodont kangaroos. All the macropodids have low-crowned, simple teeth, as do the diprotodontoids, suggesting a browsing diet and a lack of extensive grasslands in the area of the cave. This does not necessarily indicate a pre-grassland age for the deposit, but Martin (1990) indicates that while grasslands were increasing in southeastern Australia during the late Miocene and Pliocene, they did not become widespread until late Pliocene times. The absence of grazers is typical of pre-Pliocene faunas in Australia.

It is apparent that Yorke Peninsula, now largely cleared for farming and at the time of settlement supporting only a scrubby sclerophyll forest at best (Griffiths 1988, Tate 1890, Tepper 1880), was rather heavily forested, enough to support at least four arboreal mammal species - three of them obligate folivores.

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A PLEISTOCENE MARSUPIAL FAUNA FROM LIMEBURNER'S POINT, VICTORIA, AUSTRALIA.

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ABSTRACT

A collection of fossil marsupials, recovered from freshwater limestones at Limeburner's Point near Geelong, Victoria, Australia, is described. The fauna, here named the Limeburner's Point Local Fauna, contains two species of *Sarcophilus* Boitard, one near *S. harrisii* (Boitard) and *S. lanarius* (Owen), and another large species; a large vombatid near *Lasiorchinus medius* (Owen); a new species of *Simosthenurus* Tedford, *S. mccoysi*, intermediate in size between *S. orientalis* (Tedford) and *S. pales* (De Vis); two wallabies, one near *Macropus (Notomacropus) parryi* Bennett, the other cf. *Wallabia bicolor* (Desmarest); a large indeterminate macropod; two diprotodontids, *Diprotodon "longiceps"* McCoy that is here referred to *D. optatum* Owen; and an indeterminate species of *Zygomaturus* Macleay. Most of these taxa belong to extinct lineages. The faunal assemblage indicates a mid-Pleistocene age which is in accordance with recent conclusions based on magnetic polarity stratigraphic analysis and earlier stratigraphic correlations.

KEYWORDS: Limeburner's Point Local Fauna, Geelong, Victoria, Pleistocene marsupials.

INTRODUCTION

Limeburner's Point, formerly known as Point Galena, is located on the east edge of Geelong, Victoria, Australia (38° 10' S, 144° 23' E) (Fig. 1). Approximately 50 specimens, registered in the collections of the Museum of Victoria, are designated the Limeburner's Point Local Fauna. This material was collected over a period of years from the mid 19th to early 20th century when the lime kilns were active. McCoy (1876), Keble (1945) and most recently Whitelaw (1991; in press) have mentioned the fauna or various elements of it. No prior systematic treatment has been given although Gill (1964) referred to the *Diprotodon "longiceps"* McCoy specimen in a paper in the Basalt Plains Symposium.

The dental enumeration follows Archer (1978). Abbreviations used in the text are: LBP,

Limeburners Point; AMNH, American Museum of Natural History; AM, Australian Museum; BMNH, British Museum Natural History; FMNH, Field Museum of Natural History; NMV, Museum of Victoria; QM, Queensland Museum; TMM, Texas Memorial Museum; UT, University of Texas.

STRATIGRAPHY AND AGE

The limestone and associated deposits at this locality were first recorded by Daintree (1863, *vide* Keble 1945) in his report on the survey of Quarter Sheet 24 S. E. where it was called Galena Point. Located on the south side of the Inner Harbour of Corio Bay, a western arm of Port Philip Bay, Galena Point rises rather steeply from the sea to about 21 m (70 feet). Keble quotes from the Daintree report:

“The section afforded in the thickest part of the limestone deposit at Limeburner’s Point is:

7 feet	Marly clay	} Marine shells
10 feet	Ferruginous sandy clay with marine shells	
3 feet 6 inches	Rubbly limestone	
3 feet 6 inches	Thin bedded lime-stone	} Freshwater shells, <i>Planorbis</i> , <i>Lymnea</i> , etc.”
7 feet	very compact limestone principal bed used for lime	
6 feet	Rubbly thin-bedded ferruginous-limestone resting on Miocene tertiary marl	

At this point Keble, without closing the quote, adds the comment: “This closely agrees with Note 3 printed on the margin of the sheet.” He then goes on to state: “It will be noted that the freshwater shells are identical with those obtained in the well (p. 30) in the Duck Ponds limestone.” He continues: “at Limeburner’s Point *Diprotodon longiceps* was obtained in situ in the 7 foot bed of ‘very compact limestone’”. Both McCoy (1876) and Pritchard (1895) had previously mentioned the *D. longiceps* specimen.

McCoy (1876) apparently, and Keble (1945) certainly, assumed that the *Diprotodon longiceps* specimen in the Duck Ponds Local Fauna came from the Lara Limestone unit contained within the stratigraphic section at the nearby Duck Ponds site. The Lara and Limeburner’s Point limestones have long been considered equivalent, either as extensions of the same limestone (Lara), or as independent, but time equivalent, deposits. The presence of *D. longiceps* recovered in situ at Limeburner’s Point doubtless reinforced that assumption. However Wilkinson (1972) has demonstrated conclusively that while the two limestones are indeed laterally equivalent deposits, at Duck Ponds, the *D. longiceps*

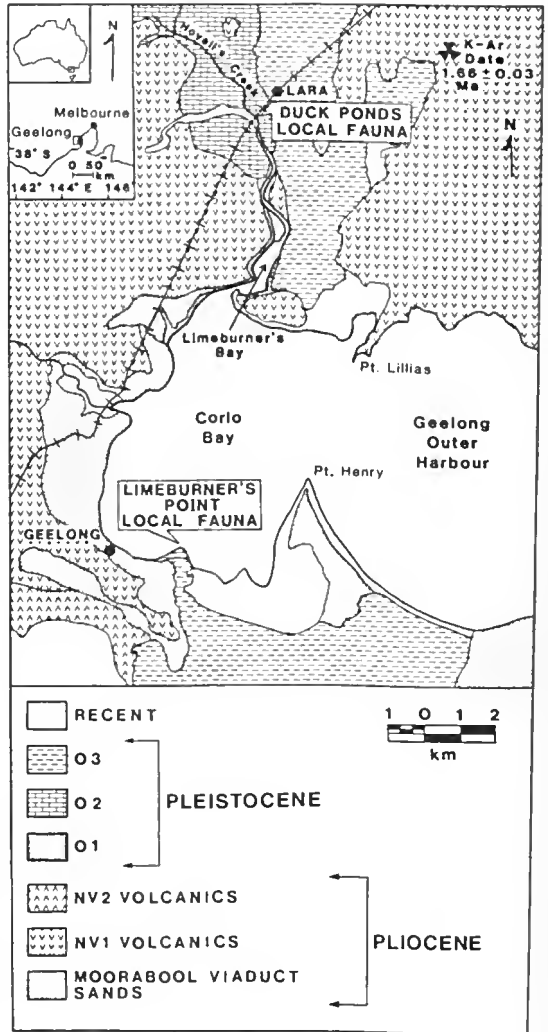


Fig. 1. Geological map showing the location of Limeburner’s Point near Geelong, Victoria, the source of the Limeburner’s Point Local Fauna. Map courtesy of M. J. Whitelaw and by permission of *Quaternary Research*.

material came not from the limestone itself, but from the underlying fluviatile sediments.

Recent studies by Whitelaw (1991; in press) of the magnetic stratigraphy of the Limeburner’s Point section has clarified the age relationships of this sequence and its correlates at the Duck Ponds site. Stratigraphic data show that the sediments containing the Duck Ponds Local Fauna lie above a basalt that has been correlated with one 7 km ENE. dated at 1.66 Ma (Wilkinson 1972; Aziz-ur-Rahman and McDougal 1972; Woodburne *et al.* 1985). This basalt has reversed polarity indicating that it is younger than the normal Olduvai Subchron (1.86-1.66 Ma) and

within the younger part of the Matuyama Chron. The Limeburner's Point sediments are also younger than 1.66 Ma and because they have normal magnetic polarity, they must fall into one of the normal magnetic chrons younger than 1.66 Ma, either the Jaramillo Subchron of the Matuyama Chron (0.98-0.91 Ma) or the Brunhes Chron (0.73-0 Ma). The sediments containing the Duck Ponds Local Fauna lie below the Lara limestone correlative with the fossiliferous limestone at Limeburner's Point and hence are older than the latter, but are unconstrained by magnetostratigraphy.

The preservation of the specimens from the thin-bedded or compact Limeburner's Point limestone is good. Some of the specimens were in partial articulation (NMV P-23267-70, 23274, 23276 and 23285) but most were isolated pieces. Evidence from bone fragments and tooth chips suggests preburial breakage, possibly from trampling (NMV P-23252, 23267-70, 23285). Those specimens from the rubbly limestone units show the same solution destruction seen in the Coimadai material reported by Turnbull *et al.* (1990). In one case the bone was dissolved away leaving a natural mold. This was filled with epoxy providing a cast that was identified as a crushed, obliquely distorted, distal portion of a ?macropodid femur, comparable in size to one of the living large kangaroos. One specimen is unique in being partially enveloped in calcite crystals and a black mineral that appears to be manganese oxide. The latter material also occurs as irregular blebs within the otherwise dense limestone matrix.

SYSTEMATIC PALEONTOLOGY

Class Mammalia
Subclass Theria
Infraclass Metatheria (Marsupialia)
Order Marsupicarnivora
Family Dasyuridae
Sarcophilus sp. 1
[near *S. harrisi* (Boitard, 1842)
and *S. lanarius* (Owen, 1838)].
(Figs 2-3; Tables 1-2)

Material. NMV P 23236-7, a left ramus with P_{2,3}, M_{2,5}.

Description. This specimen is clearly assignable to *Sarcophilus* Cuvier but specific assignment is less certain. The mandible of the LBP

specimen differs from that of the living species, *S. harrisi*, in that the horizontal ramus is slightly deeper (about 2.5 cm beneath M_{4,5} compared to about 2 cm for the living species; n=2) and the masseteric fossa is deeper and more open. The ridges defining the fossa anteriorly and ventrally form an angle of about 80° in the fossil compared to an angle of about 65° in the living form. The ascending ramus appears to be more upright and massive than in the living species. The flange that defines the ventral margin of the masseteric fossa is thicker in the fossil. The anteroposterior length of the ascending ramus taken slightly above the top of the condyle in *S. harrisi* is 2.08 cm (average of four FMNH specimens). The equivalent dimension of the LBP specimen is 2.6 cm. Although it is broken, it is clear that the coronoid process was higher in the fossil. Hence both the masseter and the temporalis portions of the masticatory musculature are proportionately more massive than in the modern species, and the insertion fields are more sharply defined.

The two lower premolars are crowded so that the anterior end of the P₂ and its anterior root labially overlap the posterior end and root of P₁. Both premolars are blunt, each consisting essentially of a swollen principal cusp fused with a broad and low "taloid" as in *S. harrisi*. The size relationships of the molars are M₂ < M₃ < M₄ <= M₅. All have the protoconid as the largest cusp. The paraconid is absent on M₂, small and almost joined to the protoconid in M₃ and is large in M_{4,5}. The latter two teeth have a well developed carnassial notch between the protoconid and paraconid. All molars possess hypoconids, grading from the largest on the M₂ to a vestige on M₅. The metaconids are small on all molars.

Discussion. Dental measurements of both LBP *Sarcophilus* species and other fossil species are given in Table 1; measurements of Recent *S. harrisi* are given in Table 2. The metric data and the bivariate scatter diagrams of premolars (length vs. width) and molars (length vs. anterior or posterior width) show the intermediate position of the LBP specimen of *Sarcophilus* sp. 1 between *S. harrisi* and *S. lanarius* (Fig. 3). This is particularly true for M₄ and M₅ in which the samples of *S. harrisi* and late Pleistocene *S. lanarius* show no overlap. In the case of M₂ and M₃, in which the clouds of points of the two samples overlap slightly or almost overlap, the fossil lies close to the mean of the *S. harrisi* sample. For the M₂ and P₂ where there is some or extensive overlap of the clouds, the fossil is also

Table 1. Measurements (mm) of fossil specimens of *Sarcophilus*: al = alveolar; u = unerupted; w = worn.

		<i>Sarcophilus laniarius</i>				<i>Sarcophilus</i> sp.	
		Topotype (Stirton, 1957)	Wellington Caves (Dawson, 1982)		LBP NMV 23236-7 Species 1	LBP NMV 23240 Species 2	
			N	Range	Mean	Left	Right
P ₁	L	-	-	-	-	7.13	al >8.8
	W	-	-	-	-	4.68	-
P ₂	L	-	17	6.3 - 7.8	7.0	7.19	al >9.1
	W	-	17	5.8 - 6.8	6.3	5.75	-
M ₂	L	10.6	52	8.9 - 11.2	9.9	9.14	al >10.6
	W	7.1	51	6.0 - 8.0	6.9	-	-
	AW	-	-	-	-	6.03	-
	PW	-	-	-	-	6.15	-
M ₃	L	-	56	10.6 - 12.5	11.6	~10.26	12.2
	W	-	54	6.5 - 8.0	7.2	-	-
	AW	-	-	-	-	~6.55	8.6
	PW	-	-	-	-	~6.75	8.4
M ₄	L	-	49	12.5 - 15.0	13.9	~11.95	al >14.4
	W	-	50	6.5 - 8.3	7.4	-	-
	AW	-	-	-	-	~7.55	-
	PW	-	-	-	-	~6.85	-
M ₅	L	15.0	33	12.7 - 15.1	13.9	>12.05	ant r >8.1
	W	8.2	32	7.0 - 8.5	7.8	-	-
	AW	-	-	-	-	~7.20	-
	PW	-	-	-	-	~6.25	-
Length anterior edge I ₁ to posterior end M ₃		72.5	-	-	-	>68.00	-
Length anterior edge P ₁ to posterior end M ₅		-	-	-	-	57.60	>60.8
Length molar series		49.4	-	-	-	44.20	45.4
Length between C and M ₂		13.8	-	-	-	~14.50	~13.5
Height of Prd of M ₅		15.2	-	-	-	10.20	-
Mandible depth below P ₂		23.7	-	-	-	18.10	>24.0
Mandible depth below M ₅		28.6	-	-	-	25.00	~20.0
Mandible thickness below M ₅		12.5	-	-	-	11.80	11.7

near the mean of *S. harrisi*. In all scatter diagrams the fossil is larger than the mean of *S. harrisi* in at least one dimension.

***Sarcophilus* sp. 2.**
(Figs 4-5; Table 1)

Material. NMV P 23240. A right ramus fragment with M₃, roots of C-P₁ and anterior root of P₂, and the alveoli of the rest of the cheek teeth.

This specimen represents a new species, but is not formally named here until the discovery of better material.

Description. The canine root is stout, oval in outline, slightly constricted lingually and is set vertically in the jaw. It measures 12.3 x 8.7mm. at the broken surface which is located just below the gumline. The two double-rooted premolars show the same crowding and en echelon arrangement seen in *S. laniarius* and *S. harrisi*. The M₂

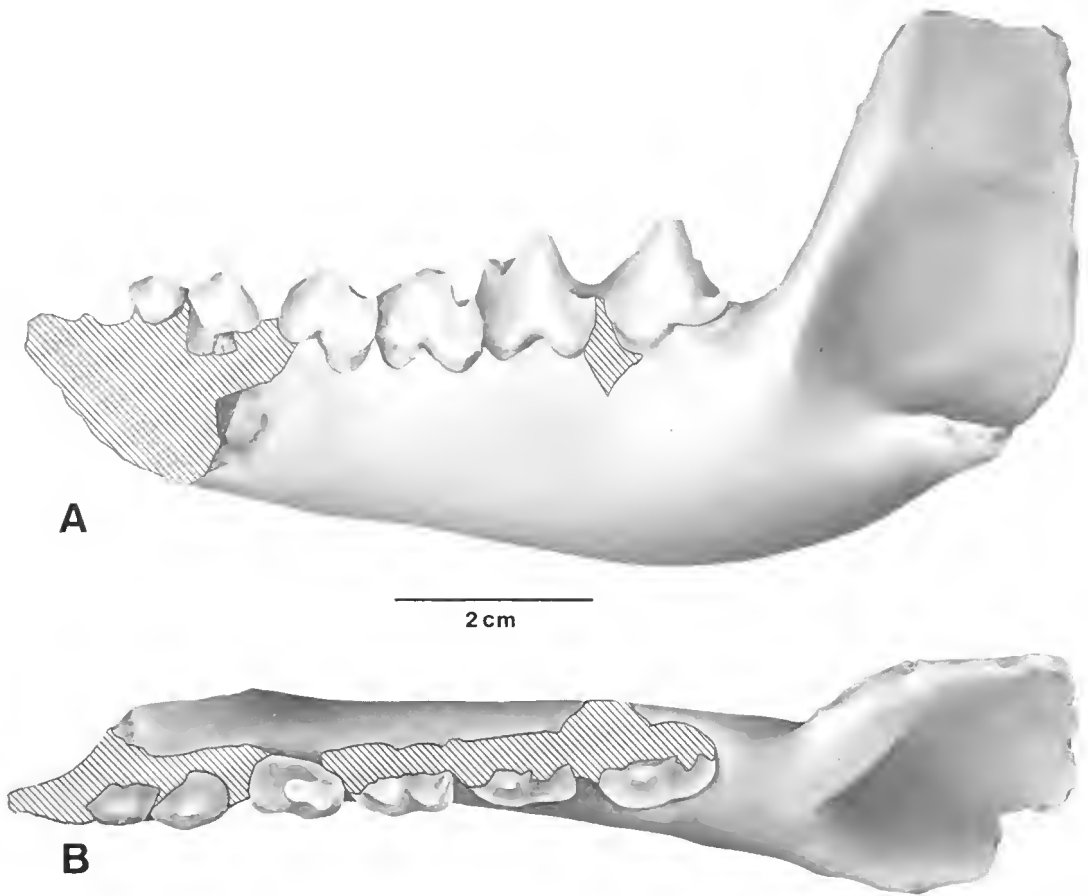


Fig. 2. *Sarcophilus* sp. 1 (near *S. lanarius* and *S. harrisi*) NMV P 23236-7, left mandibular ramus, shown in A, labial; and B, dorsal views.

appears to have been nearly equal in size and general proportions to the M_3 , judging from the alveoli and roots.

The M_3 is a stout, relatively broad tooth that is heavily worn. The protoconid is the dominant cusp. It is deeply truncated by wear. The paraconid is small, and has suffered minor damage to its lingual side. The hypoconid is low and stout, the metaconid small. Both cusps are worn. There is a small anterior cingulum that extends both lingually and labially from a small cuspid at its center, its highest point.

A minute dentine fragment located at the deeply abraded dorsal edge of the jaw at the rear of the tooth row appears to be the posterior root of M_5 . It is located 11 mm behind the back edge of the anterior root of M_5 . It lacks enamel and has what appears to be a pulp cavity perforation in its center. An X-ray of the specimen (Fig. 5) shows the roots and alveoli as indicated. If the questioned tooth fragment is the tip of the posterior root of M_5 (arrow on the X-ray), it indicates a

Table 2. Measurements (mm) of modern *Sarcophilus harrisi*: * = maximum width.

		N	FMNH Recent Mammal Collection		Bartholomai and Marshall (1973)		
			Range	Mean	N	Range	Mean
P_1	L	5	6.54 - 7.02	6.77	27	6.5 - 7.4	6.93
	W	5	4.31 - 4.71	4.48	27	4.0 - 5.0	4.50
P_2	L	5	6.68 - 6.99	6.89	27	6.5 - 7.6	7.19
	W	5	5.05 - 5.74	5.37	27	5.1 - 6.0	5.66
M_2	L	5	8.51 - 9.32	8.83	27	8.3 - 9.3	9.00
	W*	-	-	-	27	6.0 - 7.0	6.31
	AW	5	6.16 - 6.38	6.24	-	-	-
	PW	5	5.94 - 10.53	10.28	27	10.0 - 10.6	10.19
	W*	-	-	-	27	6.2 - 7.3	6.64
M_4	AW	5	6.26 - 6.97	6.74	-	-	-
	L	5	11.66 - 12.14	11.94	27	11.2 - 12.4	11.59
	W*	-	-	-	27	6.4 - 7.3	6.73
	AW	5	6.26 - 6.81	6.66	-	-	-
M_5	PW	5	6.03 - 6.93	6.60	-	-	-
	L	4	10.96 - 11.66	11.38	27	10.7 - 12.2	11.46
	W*	-	-	-	26	5.9 - 7.0	6.33
	AW	4	5.99 - 6.68	6.38	-	-	-
M_5	PW	4	5.00 - 5.94	5.52	-	-	-

rather elongate last molar for this specimen, more like that of *S. moornaensis* Crabb rather than an M_5 with a reduced talonid as in *S.*

laniarius or *S. harrisi*. Its more horizontal, oblique anchorage and higher position than the other root tips supports this interpretation.

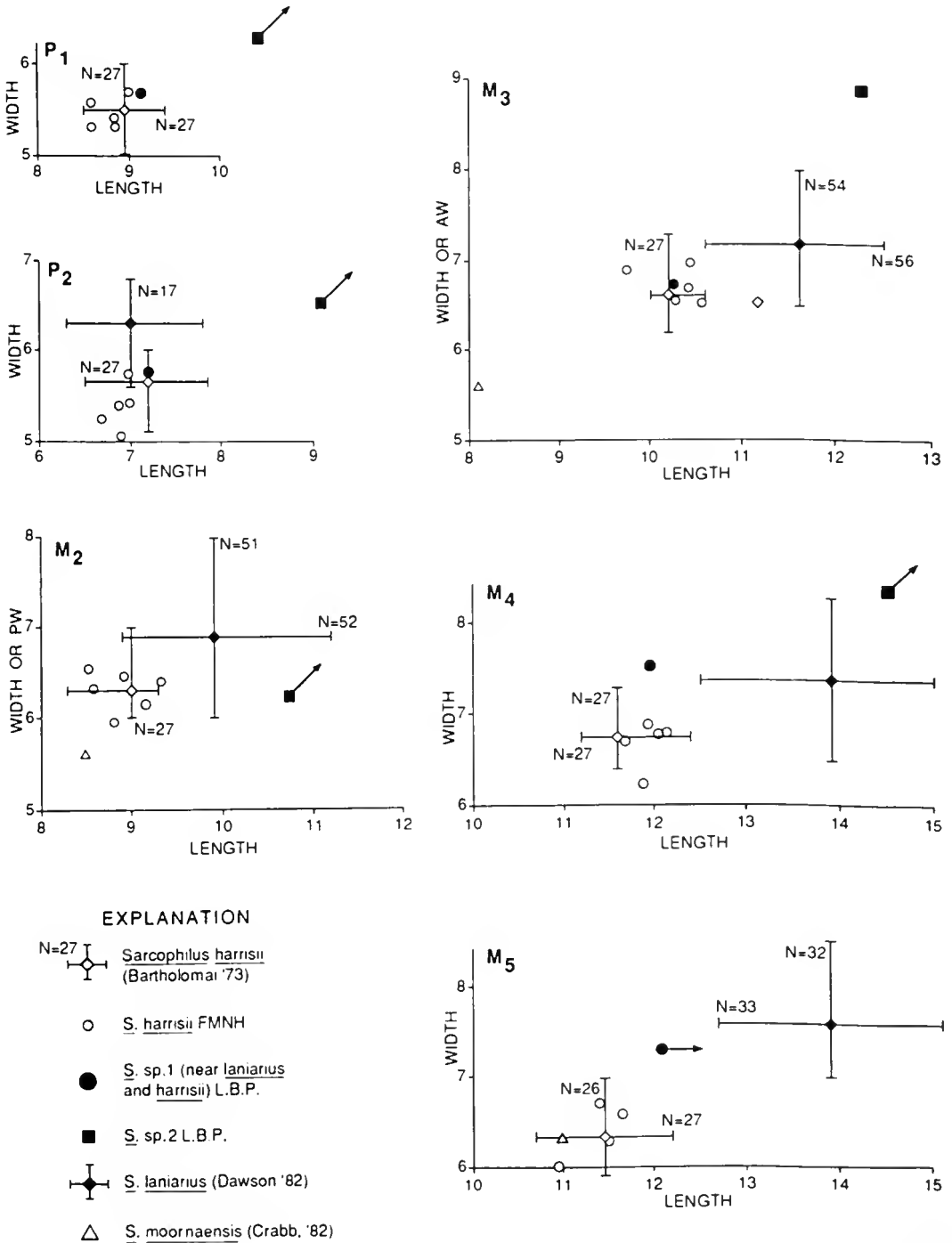


Fig. 3. Bivariate plots for each of the lower cheek teeth of the two LBP fossils, *Sarcophilus* sp. 1 (solid circle), and *S. sp. 2* (solid square) and other species of the genus. Abscissa and ordinate scales are in mm. Means, ranges and sample sizes are indicated for samples greater than 1.

There is little surface bone left on the jaw; a small patch remains in the center of the lower half of the lingual side where a 2 mm thick bit remains. As a result the positions of the mental foramen and the masseteric concavity cannot be determined.

Discussion. This specimen has been compared with the following dasyurids: *Dasyurus viverrinus* (Shaw), *Dasyurops maculatus* (Kerr),

Glaucodon ballaratensis Stirton, *Thylacinus cyuocephalus* (Harris), *Sarcophilus harrisii* (Boitard) and *S. laniarius* Crabb. In the apparent slenderness of the ramus this specimen resembles *Thylacinus* Temminck and *Glaucodon* Stirton but in the crowding of the premolars and the massiveness of the molars it is more like *Sarcophilus*. This specimen is not assignable to any known species of *Sarcophilus*. It is similar

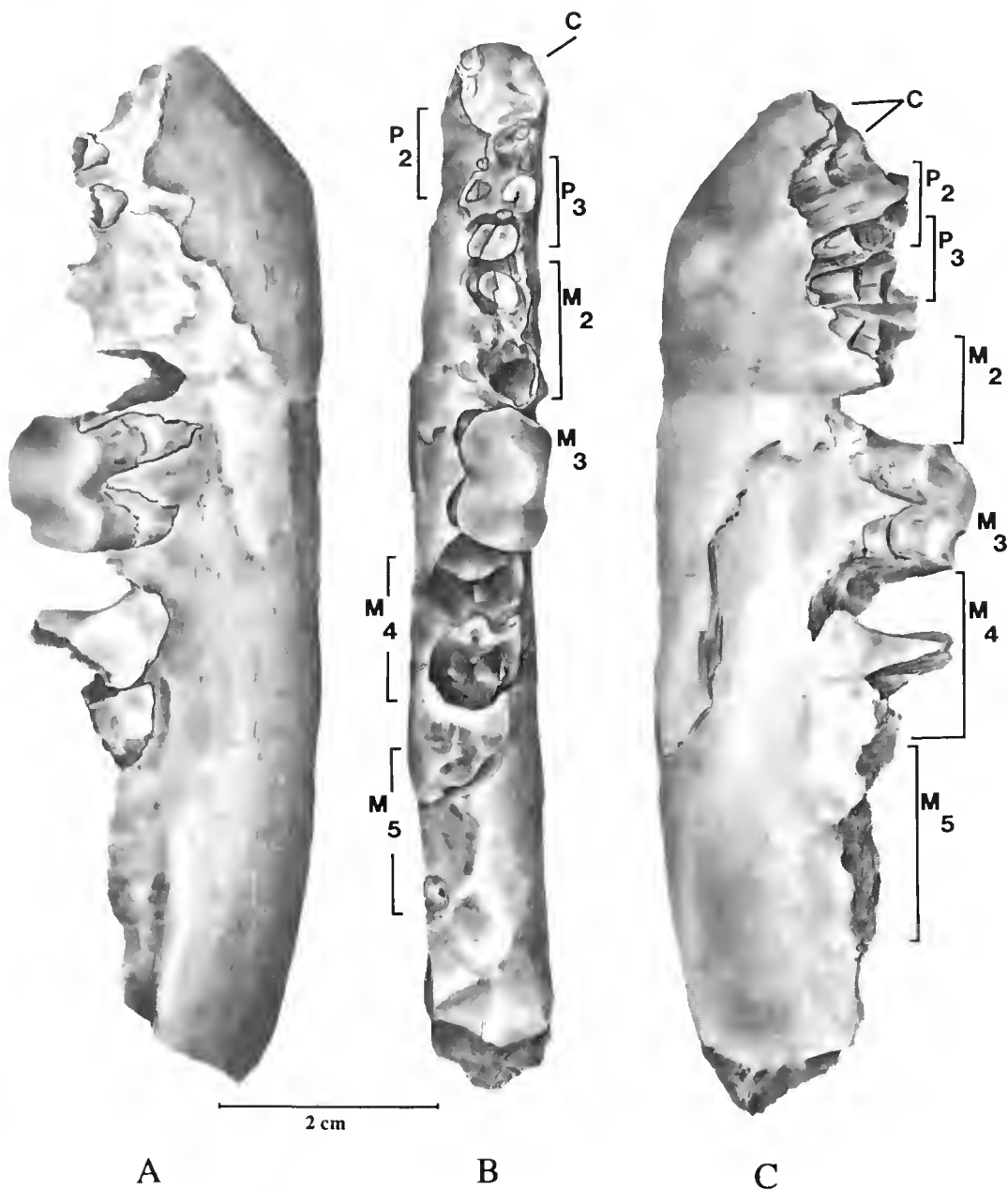


Fig. 4. *Sarcophilus* sp. 2, NMV P 23240, right ramus shown in: A, labial; B, occlusal; and C, lingual views. The specimen contains M₃ and roots and/or alveoli of the other teeth.

to, but larger than, *S. lanianus*. The extensive abrasion makes it impossible to determine its true proportions, but it appears to be more slender. The M_3 is more robust than in *Sarcophilus lanianus*.

Until recently, *S. lanianus*, which has been known only from late Pleistocene deposits, has been regarded as the ancestor of *S. harrisi* (Lydekker 1887; Ride 1964; Calaby and White 1966; Bartholomai and Marshall 1973). Dawson (1982) presented evidence from Wellington Caves materials that both validated the species *S. lanianus* and demonstrated its presence in late Pleistocene units older than had been recorded previously. The LBP sp. 1 specimen has a morphology intermediate between *S. harrisi* and *S. lanianus* and could be considered ancestral to both species. No morphological feature favors one notion of relationship over the other. The recognition by Crabb (1982) of *Sarcophilus moornaensis* from the Moorna Sands, considered to be early Pleistocene in age, further complicates the situation. The size of the dentition suggests that this species is decidedly smaller than either *S. harrisi* or *S. lanianus* and is much smaller than the LBP sp. 2 specimen.

In her study, Dawson (1982) reviewed the then known history of the late representatives of the genus *Sarcophilus*. She noted that in addition to *S. harrisi* and *S. lanianus*, at least one (perhaps more) much smaller unnamed species existed before about 20,000 years ago at Lakes Garnpung and Tandou, and at Dempsey's Lake. Further, she noted the presence of a large species of *Sarcophilus* (*S. lanianus*) at Laneefield and Buchan, also older than 20,000 BP. These new discoveries shed doubt on the dwarfing hypothesis (*S. lanianus*-*S. harrisi*) of Marshall (1973) and Marshall and Corruccini (1978).

The oldest record to date is of *S. moornaensis* reported by Crabb (1982) from the Moorna Sand estimated by him to be early Pleistocene in age or late Pliocene if the correlation of Woodburne *et al.* (1985) is accepted. Between this occurrence and the late Pleistocene to Recent record there is a very large temporal gap in *Sarcophilus* history. The LBP fossils appear to lie in this interval.

The presence of *Sarcophilus* sp. 2 in the LBP fauna adds a fourth species to the genus and further complicates the taxonomy. This is the largest species so far known. Dawson (1982) pointed out that temporal overlap of two species (a large one and a small) during the Pleistocene was possible but that no positive sympatry could

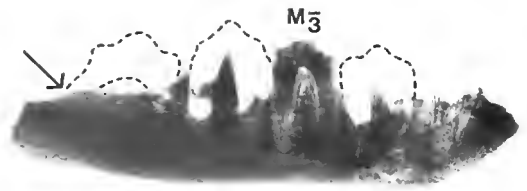


Fig. 5. *Sarcophilus* sp. 2, NMV P 23240, positive X-ray print of the right mandibular ramus showing the M_3 and roots of the other teeth. The dashed lines reconstruct the missing molars including the tip of the posterior root of M_2 (arrow).

be demonstrated. The presence of two species of *Sarcophilus* in the LBP Local Fauna is the first documented occurrence of two sympatric species (although not the same species pairs studied by Dawson). It is too early for a definite statement about the phylogenetic relationships of these taxa to be made. This must await the recovery of more material.

Order DIPROTODONTA
Suborder VOMBATIFORMES
Family Vombatidae
Lasiorhinus cf. *medius* (Owen, 1872)
 (Figs 6-8, Table 3)

Material. NMV P 14121, a well preserved pair of lower jaws with left and right incisors broken off near the alveolar edge, and with left $M_{2,5}$, right $M_{3,5}$.

Description. The P_3 's, now lost as a result of breakage during preparation, appear to have been relatively large, judging by the swollen labial side of the left horizontal ramus and from a photograph taken by WDT in 1964 which shows that both premolars were present at that time (Fig. 8A). The ascending ramus of each is incomplete. Each lacks the moiety which extends from slightly above the level of the occlusal surface of the molars to the tip. Also missing are the condyles and the rear parts of the inflected angular processes.

The symphysis is long and deep, extending posteriorly to the area at the front of M_3 . On the right ramus the deep masseteric fossa is well demarcated ventrally, anterodorsally and posteroventrally. At its deepest point an oval foramen, 5.5 mm x 4.0 mm, opens into the mandibular canal just ahead of the opening of the mandibular foramen on the medial side of the ramus where the broad inflected angle is preserved. The angular process forms an open, deep,

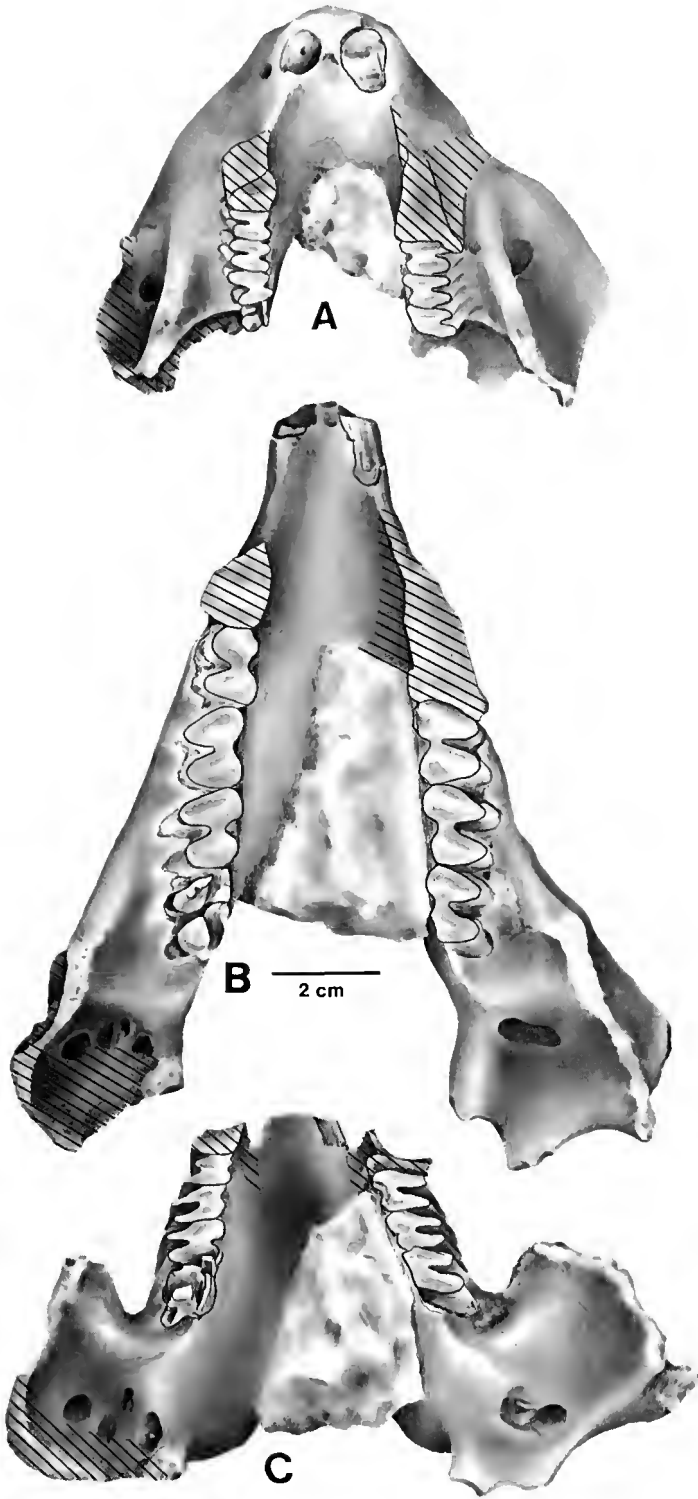


Fig. 6. *Lasiorhinus* cf. *L. medius* (Owen, 1872), mandible, NMV P 1412: A, 45° oblique view from the front showing incisors; B, dorsal (occlusal); and C, 45° oblique view from the back showing angular process and ascending ramus .

flat-bottomed pit for the insertion of the deep pterygoid muscle. The ventral margin of the horizontal ramus is convex downward and is evenly curved from the diastema to the angle. The labial side is slightly bulged but the lingual side is nearly flat, vertical and curves inwards towards the symphysis.

The lower incisors are broken away near the alveolar edge. They are oval in cross section at the break where they measure about 10.9 mm vertically by 7.3 mm horizontally (Figs 6A, 8C). On the left side at the break at the level between P_3 and M_2 , the section of the incisors is also oval and of about the same dimensions. On the right side where the break passed between the M_2 and M_3 (Fig. 8B) the section seems to be more circular (9.2 x 7.4 mm).

The cheek teeth are columnar and open at their bases (Fig. 8B) which reach near to the bottom of the ramus. The M_2 has its oval posterior moiety broader than its more rounded anterior one. In the other molars the relative widths of the moieties are reversed, and the size discrepancy between the M_2 and M_{3-4} increases. M_5 is about the size of M_2 , but its posterior moiety is much narrower. Mandibular and dental measurements are given in Table 3.

Discussion. McCoy (1876) and others, including Pritchard (1895), referred this specimen

to *Phascolomys pliocenens* McCoy, 1874, a taxon that Wilkinson (1978) has shown to be a synonym of the living species *Vombatus hirsutus* (Perry). A number of workers have identified characters that distinguish various taxa of wombats. These have been reviewed in Dawson (1981, 1983a, 1983b). The characters tabulated by Dawson (1983b: Table 1) are used here with modification. The LBP specimen is similar to *Lasiorhinus medius* (Owen, 1872: Plate 34) in size and general morphology. It differs primarily in having somewhat larger molars, especially in the molar widths. Other size differences are many but minor (Table 3). The jaw in the LBP specimen is deeper under all teeth than Owen's specimen, except the M_5 . The symphysis extends slightly farther back than in Owen's specimen, to the level of the anterior lobe of the M_3 rather than to the rear of the M_2 . The junction of the rami where they join at the symphysis is more rounded. The LBP specimen is more similar to *Lasiorhinus medius* than to any other taxon of wombats and consequently we assign it to *Lasiorhinus* cf. *medius*. The ascending ramus appears to have been much like that of *Warendja wakefieldi* from McEachern's Cave (Hope and Wilkinson 1982) in that the angle "a" seems to have been between 50° and 60° and angle "b" is estimated to have been between 16° and 20°. The LBP specimen is

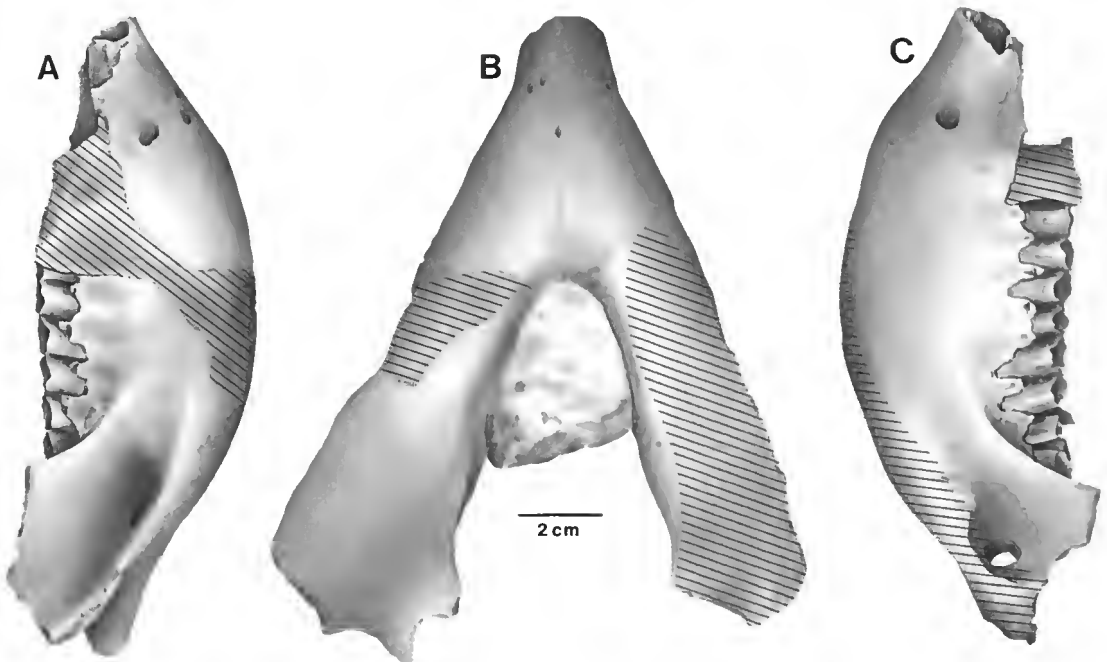


Fig. 7. *Lasiorhinus* cf. *L. medius* (Owen, 1872), mandible, NMV P 14121: A, lateral; B, ventral views of right ramus; and C, lateral view of left ramus.

Table 3. Dental and mandibular measurements (mm) of *Lasiorhinus medius*, *Ramsayia (P.) magna* and *Ramsayia lemleyi*: ¹ = dental measurements taken at wear surface whenever possible; ² = measured on Owen (1872; Plate 34); ³ = data from Dawson, (1981); **b** = broken; ~ = estimate.

		<i>Lasiorhinus</i> <i>cf medius</i>		<i>Ramsayia</i> <i>(P.) magna</i>		<i>Ramsayia</i> <i>lemleyi</i> ¹	
		NMV P 14121	Owen's Paratype ²	QM F 834	QM F 7350	QM F 7819	
P ₃	L	-	8.4	20.0	17.0	18.5	
	W	-	6.2	10.2	-	-	
M ₂	L	14.5	14.7	21.7	21.7	21.8	
	AW	8.6	7.4	-	-	-	
	PW	10.3	6.6	-	-	-	
M ₃	L	14.8	14.0	21.6	-	20.7	
	AW	11.1	7.1	-	-	-	
	PW	10.7	8.4	-	-	-	
M ₄	L	15.8	13.3	20.2	-	19.7	
	AW	11.5	7.2	12.7	-	12.5	
	PW	10.0	7.2	-	-	-	
M ₅	L	b 14.2	12.9	19.0	-	20.9	
	AW	>8.1	6.4	11.5	-	10.8	
	PW	7.2	6.0	-	-	8.3	
Width of I ₁		8.6	7.0	10.4	12.0	10.7	
Depth of I ₁		12.2	9.0	21.0	~24.0	22.7	
Ratio W/D		0.7	0.8	0.5	0.5	0.5	
P ₃ -M ₅	L	-	61.7	107.0	-	107.9	
	L	58.8	53.4	-	-	-	
Depth of jaw:							
below P ₃		38.4	33.3	-	-	-	
below M ₂		>44.2	41.1	83.5	-	82.0	
below M _{3,4}		-	45.1	80.0	-	78.0	
below M ₅		-	40.4	-	-	-	
Diastema:							
length		~31.5	~25.5	-	-	-	
depth I ₁ alveolar		~19.1	~22.0	-	-	-	

smaller than the other large wombats such as *Ramsayia magna* (Owen), *R. lemleyi* (Archer and Wade) and *Phascocolous gigas* (Owen).

Comparisons of the LBP specimen with modern *Lasiorhinus* Gray and *Vombatus* Geoffroy show that it resembles the former genus in the following ways:

- 1) the upper surface of the symphysis is flat and is bounded by low ridges,
- 2) the mental foramen is located away from the P₃,
- 3) the lower incisors are oval in cross section,
- 4) the pterygoid fossa is open, deep and not divided by a low ridge as in *Vombatus*,
- 5) the P₃ is subtriangular in cross section,
- 6) the maximum depth of the ramus is below M₃ and,
- 7) the posterior edge of the symphysis is more U shaped when viewed from below.

It resembles *Vombatus* in the depth of the masseteric fossa although the shape of the fossa is somewhat different. It is nearly 50% larger than either of the living taxa in the length of the cheek tooth row and 35% larger in the depth of the jaw. In general the LBP specimen and Owen's type of "*Phascocolouys*" *medius* are more similar to *Lasiorhinus* than to *Vombatus* which Owen (1872) noted and which led Marcus (1976) to place Owen's taxon in *Lasiorhinus*.

Superfamily Macropodoidea

Family Macropodidae

Subfamily Macropodinae

Macropus Shaw, 1790

Macropus (*Notomacropus*)

[near *M. parryi* Bennett]

(Figs. 9-10, 11A-B, Table 4)

Material. NMV P 23220, a right horizontal ramus of a juvenile individual with broken incisor root, P₂, P₃ (now exposed by fenestration of the labial side of the ramus), M_{1,4}; NMV P 23280, a left horizontal ramus of an adult with P₃, M_{2,5}, originally associated with a long bone (possibly a metatarsal V of some large macropod).

Description. The juvenile specimen, NMV P 23220 (Fig. 9; Table 4), has a small P₂ with a bulbous crown with a low crest made up of three unequal cusps. The anterior of these has weak labial and lingual ridges that extend down nearly to the crown base. The crest of the blade extends forward from this cuspid a short distance before bending sharply downwards and disappears as it approaches a small anterior cingulum prominence at crown midheight. The central cuspid of the crest is the smallest, and it too has weak rounded labial and lingual ridges. The posterior cuspid is the largest and most bulbous of the three, and it causes the crest to curve lingually. There is no cingulum on the labial or posterior sides, and only weak ones on the anterior and lingual sides. The crest has wear facets on the labial side, especially each cuspid and its ridge. However, anterior progression of the cheek teeth has already advanced enough to have brought the P₂ forwards out of any functional occlusion. It is inclined downwards on the thin anterior slope of the sigmoid dorsal alveolar edge of the jaw while M₁ is situated atop that curve.

M₁ and M₂ are worn with the transverse lophids breached down to the level of the interloph valley. In M₁ this wear also breaches half of the forelink. The molars show a size gradient, M₁ < M₂ < M₃ < M₄, and are elongate and

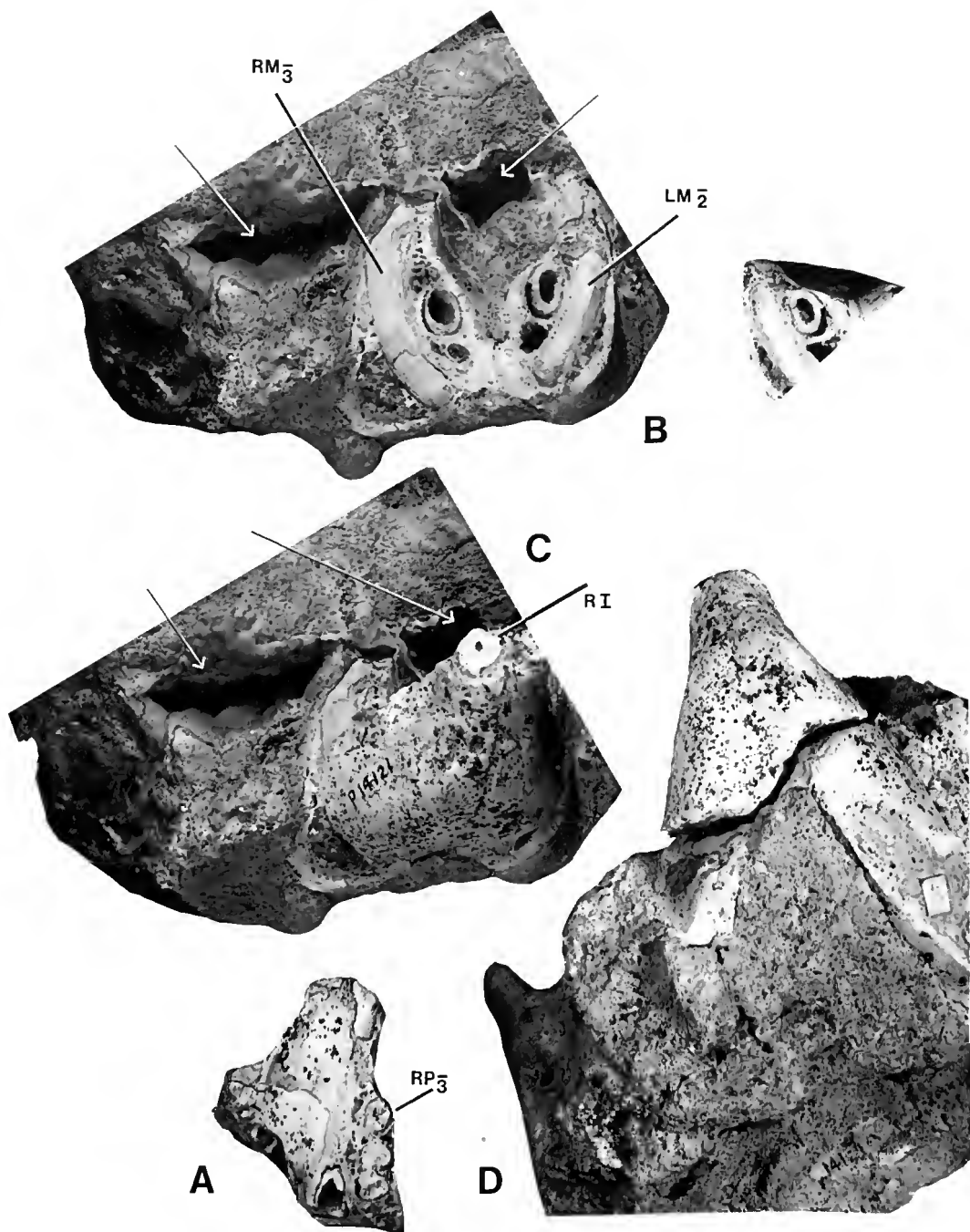


Fig. 8. Mandible of *Lasiorhinus* cf. *L. medius* (Owen, 1872) prior to preparation: **A**, dorsal view of symphyseal area showing P_3 s and right M_1 prior to their loss during preparation; **B**, views of the major break, on the left looking posteriorly showing the "roots" of both incisors and most of the left M_2 and right M_1 , and the calcite lined vug that overlaid the jaws and teeth (arrows). On the right looking anteriorly; **C**, the same as for the left side of (B), but with the symphyseal piece put into its position; **D**, ventral view of the jaws showing the major break.

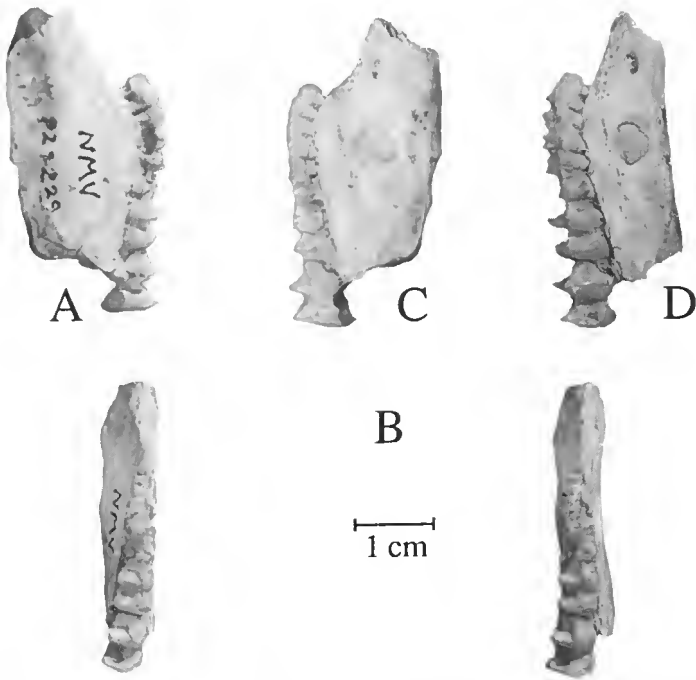


Fig. 9. *Macropus (Notamacropus)* near *M. parryi*. A juvenile right horizontal ramus (NMVP 23220): A, lingual; B, stereo-occlusal; C, labial; and D, dorso-labial views. The unerupted P_1 is shown in (C) and (D).

bunolophodont (Fig. 9, Table 4)) with pronounced broad procingulae. Cuspids and lophids are similar in each tooth and are of intermediate height. The lophids are only slightly convex posteriorly. Except for the M_1 , in which the anterior lophid is narrow, the lophids of each tooth are subequal. Fore- and mid-links are distinct, the latter being high, and located just slightly labial the midline of each tooth. No cingulum surrounds the teeth.

The replacement tooth, P_3 , not clearly shown in the X-ray (Fig. 11B), now exposed labially in its crypt (Figs 9C, D), is very like the P_2 in both size and morphology, with a crest comprised of three cuspids which are more nearly equal to one another in size than those of the P_2 . It has a rounded, weak cingulum labially which extends to an equally weak posterior cingular bulge, and anteriorly to a more substantial procingular one.

The dorsal edge of the horizontal ramus in addition to being sinuous, thins anteriorly, and a labial groove extends from the anterior end of the P_2 to the M_3 . The mental foramen lies 5.5 mm ahead of P_2 (Fig. 9C), and the broken end of the fragment of the incisor "root" is located just beneath and ahead of the foramen. At the break the incisor measures 6.8 mm vertically by 4.5 mm horizontally. The ramus thickens both

ventrally and posteriorly being 2.9 mm at the alveolar edge beneath P_2 and 7.2 mm just beneath the foramen, and 5.9 and 7.8 mm at the rear of M_3 at the alveolar edge and near the bottom of the ramus respectively. The ventral surface of the ramus is missing behind M_2 , but the margin appears to have been nearly straight.

The adult specimen, NMV P 23280, is the most complete of the three LBP macropodid jaws (Figs 10, 11B) consisting of almost all of the ascending and horizontal rami. The horizontal ramus was broken (postmortem) between M_2 and M_3 , the anterior portion being twisted down and labially. The ventral edge of the ramus appears to have been nearly straight for most of its length, but it is somewhat crushed and distorted. It is clear that the jaw was deepest beneath P_3 - M_2 and shallower but thicker below and behind M_5 . There is a very deep and elongated pterygoid fossa on the medial side of the inflected angular process (Fig. 10C) much like that of modern *Macropus irma* (Jourdan), but the posterior portion of the fossa and angular process could not be exposed without unduly risking the specimen. An X-ray (Fig. 11B) reveals details that can hardly be seen otherwise such as the condyle and the posterior edge from condyle to inflected

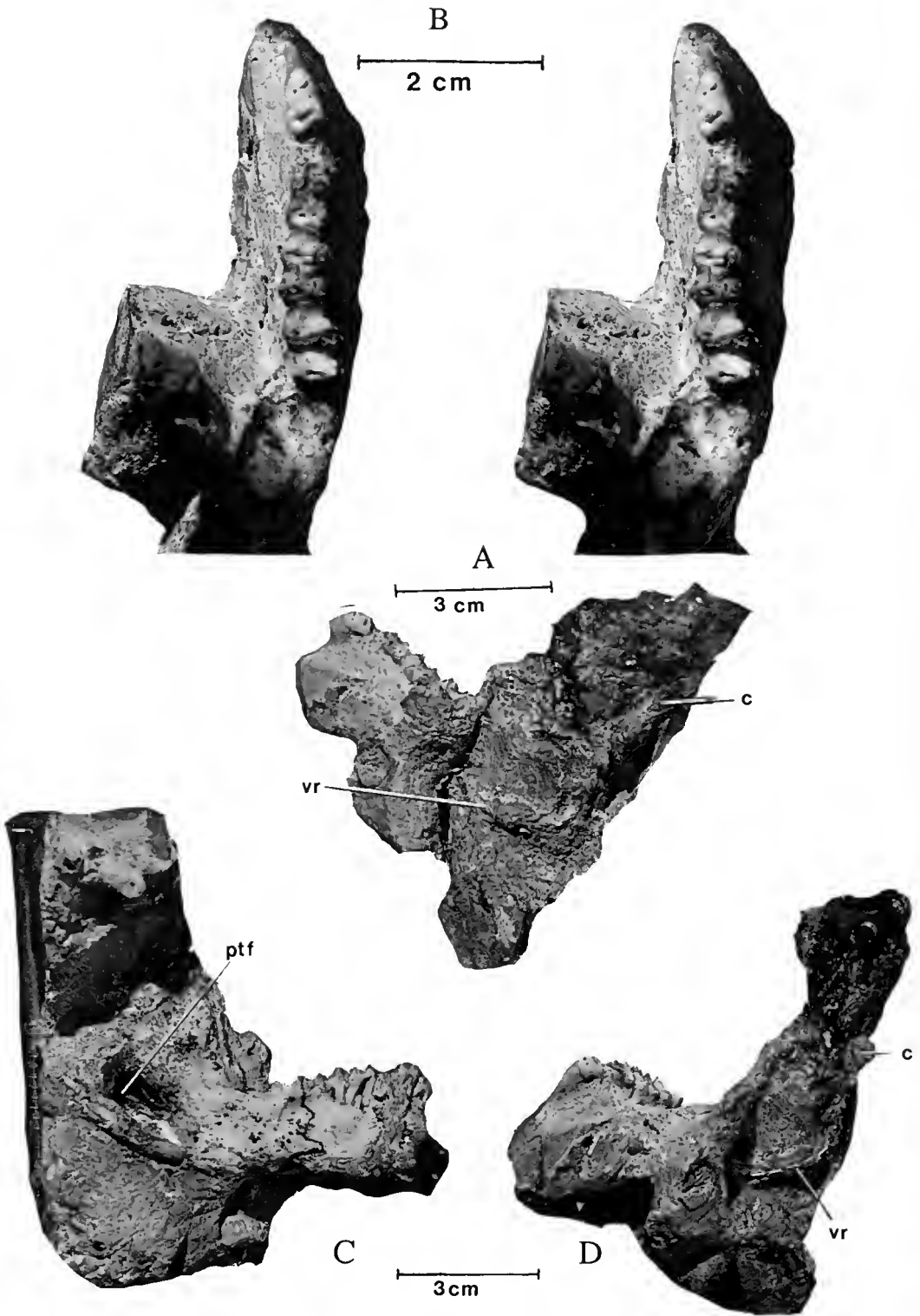


Fig. 10. *Macropus* (*Notamacropus*) near *M. parryi*. An adult left mandible, NMV P 23280: **A**, postero-dorso-lateral view of occlusal surface showing the condyle, and ventral ridge bordering the masseteric fossa; **B**, stereo-occlusal view of the cheek teeth; **C**, lingual view of the mandible showing pterygoid fossa; **D**, oblique view of labial side showing the ventral ridge of the masseteric fossa and the edge of the condyle. Abbreviations: **c**, condyle; **vr**, ventral ridge; **ptf**, pterygoid fossa.

angular process. On the lateral side, preparation beneath the ventral rim of the masseteric fossa and within the fossa was not possible so only the crest of this rim is seen (Fig. 10A, C, D)

The condyle and most of the ascending ramus remain encased in matrix because of poor preservation of the bone in these areas. The medial edge of the condyle and its neck have been exposed where the external pterygoid muscle originates. Just ahead of this, the bone margin leading to the coronoid can be seen, and behind and below the condyle the posterior descending strut that supports the condyle and leads down to the angle is clear, especially in the X-ray (Fig. 11). The antero-posterior dimension of the masseteric fossa of the ascending ramus is relatively greater than is common in most wallabies

(the distance from the vertical anterior edge of the ramus to the posterior edge of the strut beneath the condyle).

The P₃ is elongate and narrow in crown view. It has advanced and rotated forwards over the sigmoid hump of the alveolar edge of the jaw so that only its posterior cuspid shows a fresh wear facet: the other older facets are less distinct and sharp (Fig. 10 A, C, D). The tooth has a crest comprised of three cusps. The anterior one is more rounded than the others and has blunt labial and lingual ridges, and there is an anterior angular bulge at its base. It is separated from the central, smallest cuspid by a shallow U-shaped notch when viewed from the side. The middle cuspid has faint labial and lingual ridges that extend down to about midheight of the crown. The

Table 4. Dental measurements in mm of *Macropus*: **b** = broken; **w** = worn; **u** = unerupted; * = 3.5 subtracted for gap.

		<i>Macropus parryi</i>		<i>Macropus cf. parryi</i>		<i>Macropus irma</i>	<i>Macropus eugeni</i>
		FMNH 48301	FMNH 42090	LBP specimens		UT-TMM M2039	FMNH 49339
		Juvenile	Subadult	NMV P 23280	NMV P 23220	Adult	Adult
		Left	Right	Adult Left	Juvenile Right	Adult Left	Adult Right
P ₂	L	5.9	-	-	4.9	-	-
	AW	u ~2.5	-	-	2.4	-	-
	PW	3.1	-	-	2.5	-	-
P ₃ ^L	L	-	5.6	5.2	-	4.6	3.8
	AW	-	2.1	2.2	-	2.5	2.0
	PW	-	2.5	2.5	-	2.4	2.0
M ₁	L	6.4	-	-	6.0	-	-
	AW	4.0	-	-	3.4	-	-
	PW	4.5	-	-	4.1	-	-
M ₂	L	u ~7.4	6.8	6.4	6.3	w 6.2	w 5.0
	AW	u >4.7	4.2	3.9	b 4.1	w 4.1	w 3.3
	PW	u >5.2	b >4.1	4.5	b 4.0	w 4.6	w 3.7
M ₃	L	-	8.0	6.9	7.6	w 6.5	w 5.3
	AW	-	4.9	4.6	5.2	w 5.1	w 4.0
	PW	-	6.0	4.8	5.1	w 5.2	4.2
M ₄	L	-	9.3	8.3	9.3	7.3	6.0
	AW	-	5.4	5.9	5.6	5.2	4.7
	PW	-	5.3	5.6	5.4	5.2	4.8
M ₅	L	-	-	-	-	7.8	6.9
	AW	-	-	-	-	5.3	4.7
	PW	-	-	-	-	4.6	4.4
P ₂ -M ₄	L	-	-	-	31.0	-	-
P ₃ -M ₅	L	-	-	34.0*	-	31.2	w 24.8
M ₁₋₄	L	-	-	-	28.0	-	-
M ₁₋₃	L	-	-	-	19.1	-	-
M ₂₋₅	L	-	-	31.6*	-	27.5	22.2
M ₂₋₄	L	-	23.1	21.3*	22.9	19.2	16.1

posterior cuspid forms nearly half of the length of the crest which swings lingually at the rear of the tooth. Also at the rear the crest divides, the slightly greater part of its mass is located at the posterolabial corner, and the lesser, more pinched part descends towards a weak posterior lingual bulge. No ingulum is present labially and only weak rounded cingulae occur lingually, anteriorly and posteriorly.

The molars grade up in size from M_2 ($M_2 < M_3 < M_4 < M_5$) and are essentially of the same form as described for the juvenile. The measurements are given in Table 4.

Discussion. Direct comparisons were made with modern wallaby genera using specimens in the Recent mammal collections of the Field Museum and the Texas Memorial Museum (Appendix). The closest match is with two *Macropus parryi* specimens, FMNH 48301 a juvenile, and

42090 a subadult. Next closest resemblance is to *M. eugenii* (Desmarest), FMNH 48105, 48370 both juveniles and 49339 an adult, and to an adult *Macropus irma*, TMM M-2039. Other similarities are seen with *Petrogale inornata*, FMNH 64352 a juvenile, and 64435 a subadult. Inspection of the DeVis type materials of *Halmaturus indra, siva, thor* and *odiu* subsequently reported on by Bartholomai (1966, 1975, 1976) has allowed us to eliminate all of them from either this or the following taxon. Assignment to *Macropus*, near *M. parryi* is based on many close resemblances of dental and jaw features, most significantly the ratio of P_2 to P_3 lengths. The ratio of the P_2 of the juvenile and P_3 of the adult is 0.94. The ratio of the mean values of these two teeth in various species of *Macropus* is: *M. robustus* 0.872; *M. fuliginosus* (Desmarest) 1.02; *M. caugaru* 1.069; *M. antilopiinus* 1.005; *M. eugenii*

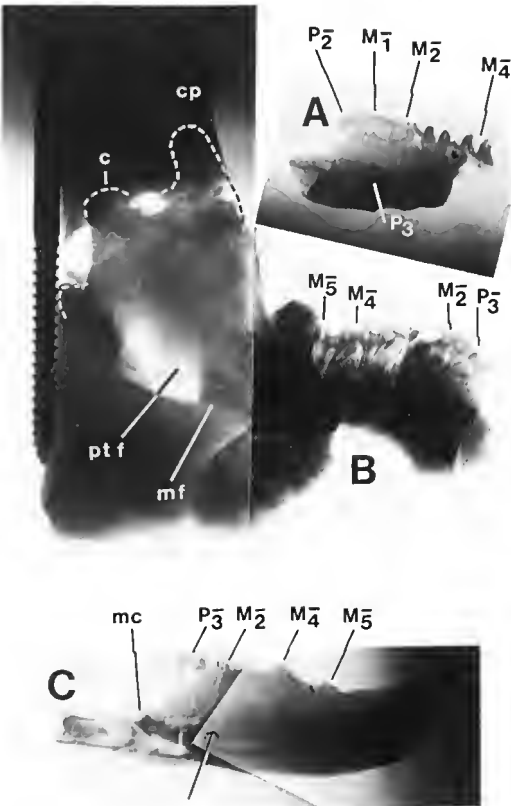


Fig. 11. Positive prints of X-ray photographs of the three wallaby specimens in the LBP Local Fauna: A, *Macropus* (*Notomacropus*) near *M. parryi*, NMV P 23220. The faint shadow of P_3 can be seen; B, *Macropus* (*Notomacropus*) near *M. parryi*, NMV P 23280; C, *Wallabia* cf. *W. bicolor*, NMV P 23221. Left ramus, arrow indicates a feature that resembles a P_3 ; Abbreviations: c, condyle; cp, coronoid process; mf, masseteric fossa; mc, masseteric canal; pif, pterygoid fossa.

Table 5. Dental measurements (mm) of *Wallabia bicolor*: al = alveolar; u = unerupted.

	LBP Specimen	Recent Specimens				
		NMV P 23221 Adult	FMNH 64365 Juvenile	FMNH 60892 Sub-adult	FMNH 64354 Adult	FMNH 48555 Subadult with pathology
		Left	Left	Right	Left	Right
P_2	L	-	5.6	-	-	6.1
	AW	-	2.6	-	-	2.9
	PW	-	2.7	-	-	3.5
P_3	L	7.5	-	7.5	7.8	u 7.4
	AW	2.7	-	2.3	2.3	u ~2.2
	PW	2.9	-	2.6	2.4	u
M_1	L	-	6.0	-	-	6.1
	AW	-	3.5	-	-	3.6
	PW	-	4.2	-	-	4.3
M_2	L	-	7.1	6.3	6.5	6.7
	AW	al 2.8	4.5	4.5	4.6	4.7
	PW	al 3.7	4.9	4.9	5.0	5.1
M_3	L	-	u ~8.0	7.3	7.2	7.5
	AW	al 3.2	5.5	5.3	5.3	5.5
	PW	al 3.6	u >5.6	5.5	5.5	5.6
M_4	L	-	-	8.7	8.2	8.8
	AW	al 3.4	-	6.0	6.1	5.9
	PW	al 4.3	-	5.9	6.2	5.7
M_5	L	-	-	u ~8.7	8.5	u >8.6
	AW	al 3.6	-	6.3	6.2	u >5.5
	PW	al 3.6	-	u ~5.6	6.1	u >4.9
P_2 - M_4	L	-	-	-	-	32.9
P_3 - M_5	L	~36.8	-	~36.2	36.2	~38.2
M_{1-4}	L	-	-	-	-	28.4
M_{1-3}	L	-	~20.4(R)	-	-	20.2
M_{2-5}	L	al 29.8	-	~29.4	29.0	~30.1
M_{2-4}	L	al 19.6	-	21.1	21.0	22.3

1.01; *M. parryi* 1.086. This ratio for *Thylogale* is: *T. billiardieri* (Desmarest) 0.752; *T. brunii* (Schreber) 0.710. Thus in this character the LBP specimens are closer to *Macropus* than to other genera of macropodids. The LBP specimens resemble *M. parryi* in the arched tooth row that is not so well marked in *M. eugenii*.

It is interesting and probably significant that another medial Pleistocene fauna, the Eastern Darling Downs, has a form, *M. thor* (De Vis), near the living *M. parryi* (Bartholomai 1975). Using a log-difference diagram, Bartholomai has shown that *M. thor*, which is about 1/3 larger than *M. parryi*, has a greater correspondence to it than to either *M. rufogriseus* (Desmarest) or *M. dorsalis* (Gray). He concluded "cheek teeth in *M. thor* have more in common with those of *M. parryi* than with other wallabies, and it may be that these species are related". Now, in the medial to early late Pleistocene LBP fauna we have another wallaby similar to, if not conspecific with, *M. parryi*. However, in this case the fossil is about 10% smaller than the living form.

Wallabia Trouessart, 1905

Wallabia cf. *W. bicolor* (Desmarest, 1804)

(Figs 11C, 12; Table 5)

Materials. NMV P 23221, a left horizontal ramus with broken I_1 (root), P_3 , the roots and alveoli of $M_{2,5}$, and the base of the buttress leading to the ascending ramus.

Description. Enough of the horizontal ramus is preserved to show these features:

- 1) the ventral margin is nearly straight,
- 2) the diastema is elongate, 21.0 mm from the front of the anterior root of P_3 to the approximate position of the incisor alveolar edge,
- 3) the mineralized fill of the canal shows that the mental foramen is single and that it exits about 8 mm ahead of the anterior edge of the P_3 ,
- 4) the lower incisor has an oval cross section at its broken surface (behind but near to the alveolar edge), being higher than wide (7.1 x 5.3 mm),
- 5) the dorsal edge of the ramus shows a typical macropodine sinuous upward anterior expansion, but the P_3 has not drifted out of occlusion and is well anchored in spite of considerable exposure of the top front of its anterior root,

6) there is a labial groove located very near to the alveolar margin that extends from beneath the P_3 to beneath M_3 where the ramus is broken, and

7) the ramus is rather massive ventrally with jaw depths being about 20.0 mm beneath P_3 and M_1 and 17.3 beneath M_4 .

The P_3 of NMV P 23221 is heavily worn, especially posteriorly. Its longitudinal crest, a pinched blade, has four cusps. The anterior and posterior ones are the larger two, the former is almost twinned by an anterior extension that carries the crest forwards onto the front edge of the tooth to a bulge in its base, and then on down to a small anterior circular prominence. The posterior cuspid is weakly bifid posteriorly, the lingual side being the posterior end of the blade. Its apex is separated from the more anterior part

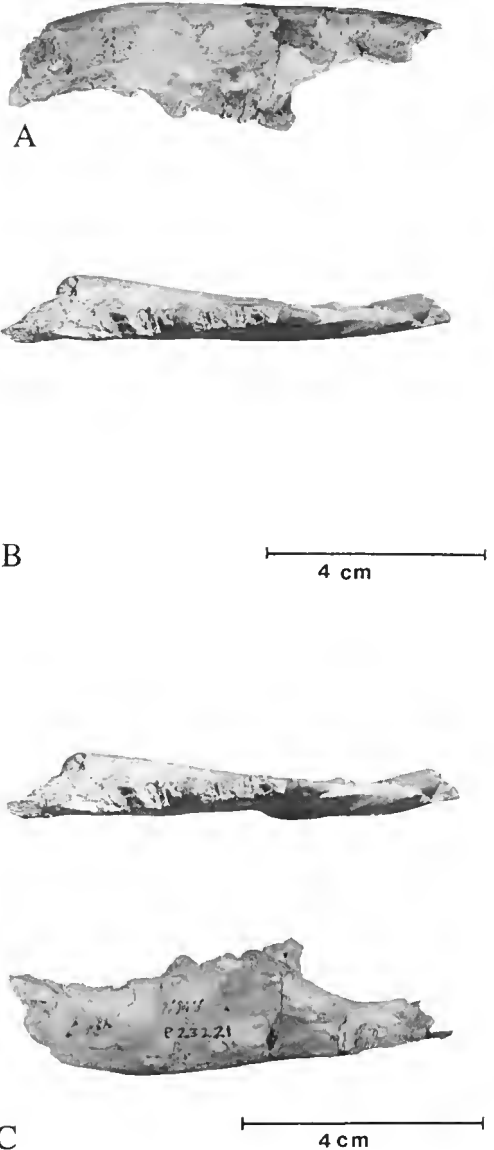


Fig. 12. *Wallabia* cf. *W. bicolor*, NMV P 23221: A, labial; B, stereo-occlusal; and C, lingual views.

of the crest by a cleft which has been nearly eliminated by wear, but which is still discernible in occlusal, lingual and labial views. The two intermediate cusps are small, especially the anterior one which has sharper, but short labial and lingual ridges. There is a weak, variably developed cingulum extending around the tooth base except for the rear of the tooth where it disappears.

The molars are missing and only alveolar dimensions can be obtained (Table 5). They were about the same size as those of the other LBP species whose P_3 is a much smaller tooth.

Discussion. This LBP specimen closely resembles modern specimens of *W. bicolor* in the Field Museum collection, particularly FMNH 60892 and 64354. The former is a subadult with the M_3 erupting, the latter with M_3 showing slight wear. These two modern specimens show variation within the species in the form of the P_3 s. The LBP specimen resembles the subadult more closely in that both show a clefted condition of the rear of the crest, just anterior to the posterior cuspid. The young adult and the fossil, partly because of greater wear, are closer in overall slenderness. However, the modern specimen lacks the deep cleft in the crest and its posterior cuspid is less prominent than in either the other modern, or the LBP specimens.

The narrow raised sigmoid curve of the alveolar edge of the jaw is higher in the fossil than in the two modern specimens, and the labial groove

is much higher and closer to the jaw margin. We attribute all of these differences to the different age stages represented, and if aligned from youngest to oldest, the groove is seen to migrate upwards with increasing age. In spite of the incomplete nature of this specimen, the characters of the one tooth and jaw and tooth proportions (alveolar) correspond more closely to *Wallabia bicolor* than to any other taxon we examined.

As with *Macropus parryi*, the LBP fauna has another taxon that is close to, if not conspecific with, a modern species, *Wallabia bicolor*. *Wallabia indra* (De Vis) from the Eastern Darling Downs, seems to belong to the *W. bicolor* lineage but differs in size from the modern species (Bartholomai 1976). As with the *M. parryi* material, the LBP specimen of *W. bicolor* is about 1/3 smaller than the material of *W. indra* from the Darling Downs. The closer size similarity of both taxa to their modern counterparts than to the Darling Downs material suggests a younger age for the LBP fauna.

Subfamily Sthenurinae ✓
Simosthenurus Tedford, 1966
Simosthenurus mccoysi n. sp.
 (Figs 13-15, Table 6)

Type material. HOLOTYPE: NMV P 23271-2, pair of lower jaws with left and right P_3 - M_3 .

Additional material: NMV P 23238-9, right ramus with broken P_3 , M_2 and $M_{3,5}$ (Fig. 14, Table

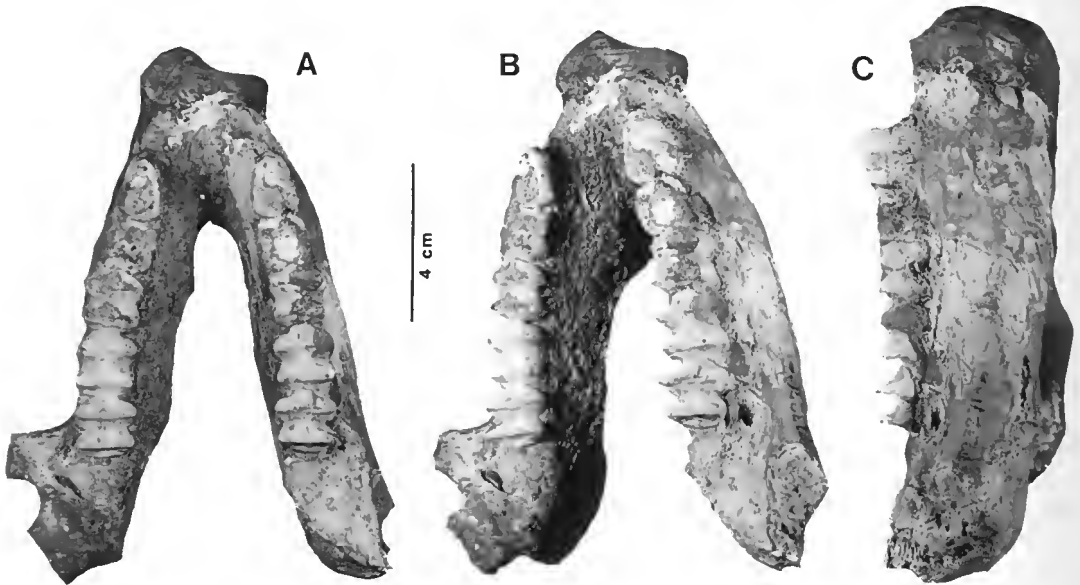


Fig. 13. *Simosthenurus mccoysi* n. sp. holotype, NMV P 23271-2: A, occlusal; B, right dorso-lateral oblique views; and C, labial view of right ramus.

Table 6. Dental and mandibular measurements (mm) of specimens assigned to *Simosthenurus*: b = broken; # = undesignated position; r = root measurement; * = measurement made on epoxy cast of natural mold; w = worn.

		<i>Simosthenurus mecoyi</i> LBP sp. nov.		<i>Simosthenurus oreas</i> De Vis		<i>Simosthenurus pales</i> de Vis (<i>Haluaturus</i>) Kreffit			<i>Simosthenurus orientalis</i>			
		NMV		Holotype		QM	AM	AM	Holotype			
		P 23271-2		P 23238-9		F2923	F812	41521	19653	F102201	40001	MF912
				(Bartholomai 1963)		(Bartholomai 1963)	(Tedford 1963)		(Tedford 1966)			
		Left	Right	Right	Left	Right						
P ₃	L	16.2	16.2	r 18.4	12.3	12.6	-	19.6	18.8	17.0	17.0	-
	AW	9.5	9.8	r 7.8	-	-	-	9.0	9.3	7.9	8.2	-
	PW	~11.4*	12.4	r 9.2	-	7.5	-	10.1	10.9	10.7	9.3	-
M ₂	L	w 13.6	w 13.2	-	12.7	12.6	18.5	16.4	17.0	14.0	12.1	-
	AW	~14.1*	>12.7	r 10.6	-	-	-	-	12.8	10.9	9.7	-
	PW	~13.9*	~13.7*	r~11.3	9.2	9.1	-	-	13.2	11.2	10.0	-
M ₃	L	16.1	16.2	16.6	14.6	14.5	21.0	18.9	-	15.0	13.7	14.3
	AW	15.9	>15.9	b 12.2	-	-	-	14.9	-	12.2	11.0	-
	PW	15.2	15.1*	b 13.8	10.8	10.7	17.5#	14.8	-	12.7	11.2	11.8
M ₄	L	17.4	17.4	17.8	15.8	15.5	22.4	19.4	-	15.2	16.4	15.3
	AW	16.6	15.8*	15.5	12.0	11.7	-	16.0	-	13.0	12.2	12.3
	PW	15.5	15.5	b 14.5	-	-	-	15.8	-	13.2	12.1	12.6
M ₅	L	17.2	17.3	16.9	14.8	14.9	-	18.1	-	14.6	-	-
	AW	16.4	16.4	15.2	11.6	11.6	-	16.0	-	12.7	-	-
	PW	14.6	14.7	13.7	-	-	-	14.2	-	12.1	-	-
P ₃ -M ₅	L	79.5	80.2	-	30.8	31.2	-	-	-	-	-	-
M ₂ -M ₅	L	62.4	62.6	-	20.4	-	-	-	-	-	-	-
M ₂ -M ₄	L	47.2	47.2	-	-	-	-	-	-	-	-	-

6). NMV P 23284, a right maxillary fragment consisting of the lateral wall of the bone in the area of the roots of the cheek teeth (Fig. 15). The teeth are broken away obliquely; from approximately the lingual alveolar border to the labial base of the crown. Portions of the roots of the cheek teeth can be seen. An approximate alveolar length of the molar series is 54 mm.

Diagnosis. Intermediate in size between *S. orientalis* (Tedford) and *S. pales* (De Vis). Differs from these and all other species of the genus in that P₃ is short relative to the lengths of M_{3,5} being equalled or exceeded in length by each of these molars, P₃ is wider for its length (77% of length), and the lower molars are nearly equidimensional in occlusal outline with their anterior widths 95-98% of length.

Description. These two well preserved specimens appear to belong to the same taxon. Dental measurements are given in Table 6, and although specimen P 23238-9 has suffered damage, making accurate width measurements of the molars and the lengths of the P₃ and M₂ impossible, it is possible to obtain reasonable measures for both lophids of M₄ and M₅. The massiveness and depth of the ramus show that this specimen is

comparable to the more complete type specimen, P 23271-2. The dimensions of the right mandibular rami of these two specimens are: NMV P23271-2, depth anterior to P₃ 30.0 mm, depth beneath M₅ >>28.0 mm, thickness beneath P₃ 24.9 mm, thickness posterior to M₄ 29.0 mm; NMV P23238-9, depth posterior to P₃ 35.4 mm, depth beneath M₅ 42.3 mm, thickness beneath P₃ 19.1 mm, posterior to M₄ 23.7 mm. In the type specimen the P₃s are worn so that their posterior moieties are truncated with near-circular dentine "lakes" exposed.

The molars (M_{2,5}) are subequal in bulk. In the M₂s all crown features are gone leaving dentine "lakes" with only very slight enamel surrounds. In the M₃s the transverse lophids are truncated by wear, but their form has not been erased, and the midlink, although breached, is still a raised feature, its bulk largely intact. The M₄s and M₅s are both only slightly worn, each has a slight beveled wear facet extending across the width on the posterior side of each lophid. The lophids are straight and both fore-and midlinks are present. There is a strong tendency for the links to be comprised of a double ridge, and, in the case of the forelink, several more enamel wrinkles par-

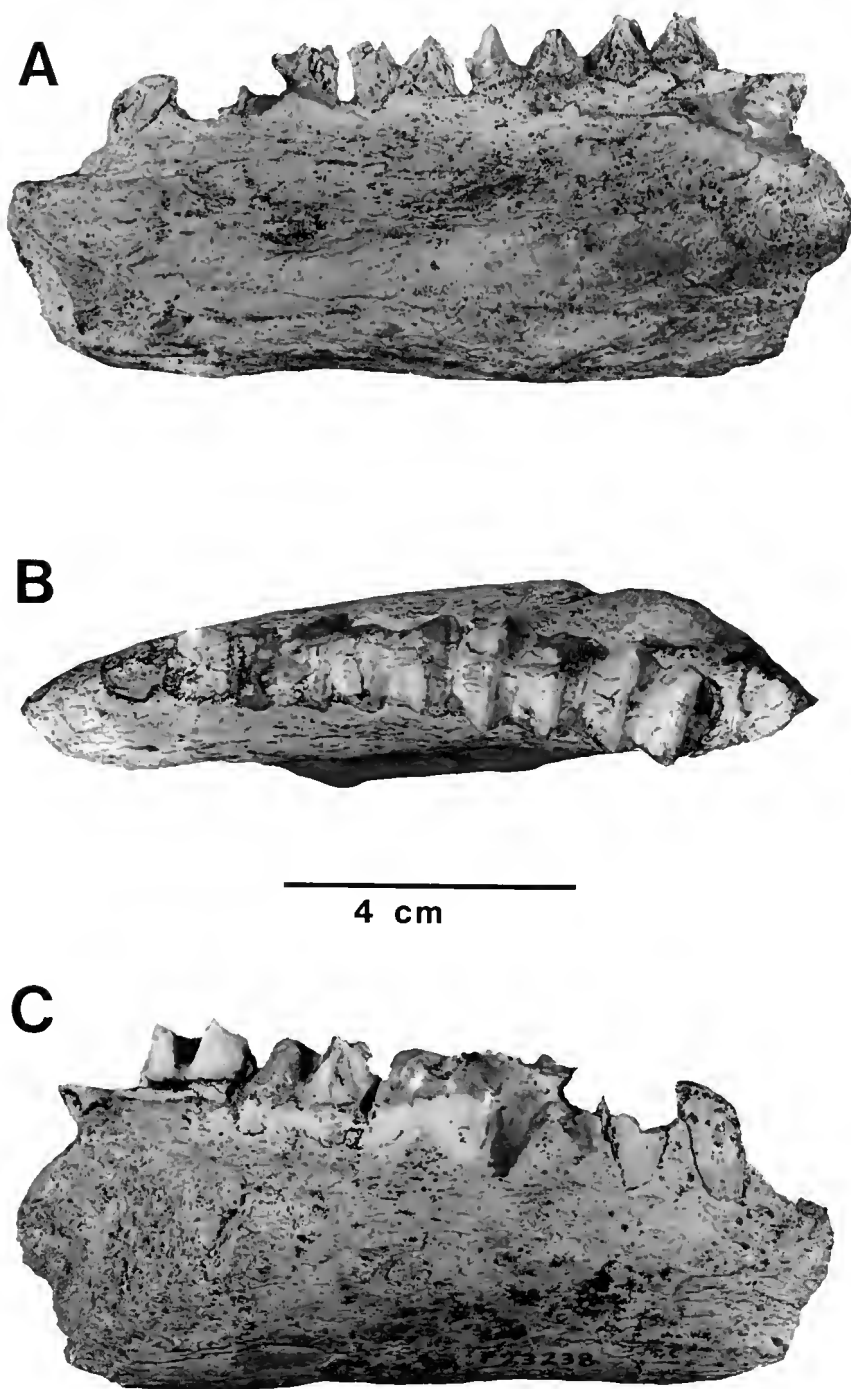


Fig. 14. *Simosthenurus mccoyi* n. sp., referred specimen, NMV P 23238-9, right horizontal ramus: A, labial; B, occlusal; and C, lingual views.

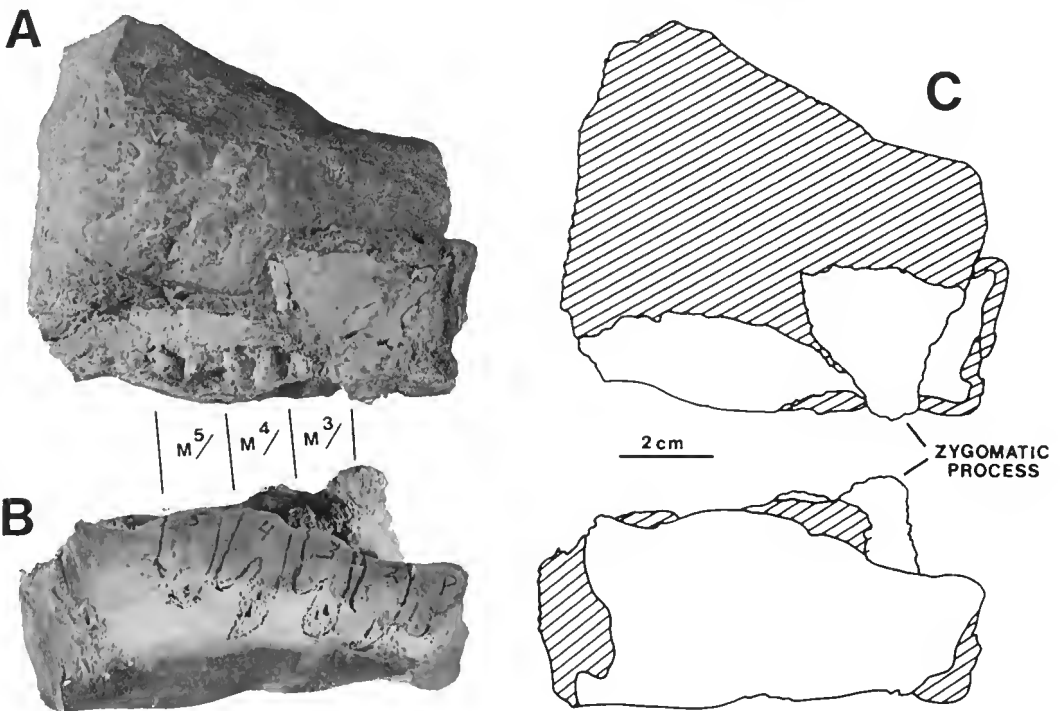
allel the link on the anterior face of the protolophid. Specimen P 23238-9 is at a slightly younger wear/age stage than the type specimen in that the crown of its M_3 shows a lesser degree of dentine exposure. Its protolophid is breached and the dentine exposure extends forwards along the forelink, but does not quite reach to the anterior border of the anterior cingulum. The enamel of the hypolophid has only been slightly breached, mostly on the postero-lateral edge of the crest at the hypoconid, and the midlink has not been involved at all. The crenulate ornamentation of the anterior faces of both lophids of M_4 and M_5 and the hypolophid of M_3 all show a somewhat greater degree of development than is seen in the type.

In the tentatively referred maxillary, the boss of the zygomatic process for attachment of the superficial masseter muscle descends steeply downwards, nearly vertically in front (Fig. 15C). There is a broad, open, relatively deep, anteriorly facing concavity anterior to this boss but no sign of the infraorbital foramen which would be expected to be located just ahead of the anterior edge of the preserved part of the specimen if it were in its usual position. The process itself is stout, tapers to a blunt point, and is set off 13 mm from the lateral wall of the maxillary. The bone

of the anterior part of the dorso-ventrally expanded zygomatic arch thins rapidly behind the process. In all of these features sthenurine proportions are seen, since the size is about right we tentatively assign it to the new species, *S. mccoysi*.

Discussion. The LBP specimens differ from other species of the genus *Simosthenurus* in the following ways: the ratio of the length to posterior width of the P_3 crown in NMV P 23271-2 is larger (0.77) than in any other described species. The crown of P_3 is shorter relative to molar length, being equaled or exceeded by M_4 and M_5 , rather than longer than all molars. Only the smaller *S. oreas* (De Vis) has a similar proportional relationship. In addition, the proportion of the length to anterior width of the $M_{3,5}$ is within the range 0.95-0.98, much closer to equidimensional than in other *Simosthenurus* in which the anterior molar width is usually 70-80% of length. In absolute length the LBP specimens have tooth dimensions intermediate between *S. orientalis* and *S. pales*. The posterolabial ridge of P_3 joins the lingual ridge near the mid-length, a distinct groove marking the junction, more like the condition in *S. orientalis* than in other taxa.

The lower molars have anteriorly short anterior cinguli, low but well developed links with an



✓ Fig. 15. *Simosthenurus mccoysi* n. sp., referred specimen, NMV P 23284, right maxillary fragment: A, lateral; B, ventral views; and C, an explanatory outline drawing of (A) and (B).

additional midlink, lophid erenulations are numerous and strong, especially lingual to the links, and the posterior eingulum forms a weak shelf. There is a mandibular foramen beneath the posterior root of M_3 , shown on NMV P 23238-9, and a shallow mandibular groove extending from beneath P_3 postero-ventrally to end in a pit beneath M_2 . The mental foramen lies well forward of the anterior root of P_3 and is inclined at about 45°.

The combination of size and proportional relationships of the dentition marks this as an unique taxon. The morphological features have resemblances to other species of *Simosthenurus*, but the combination in this taxon has not been recorded so far.

Etymology. Named for F. McCoy, pioneer paleontologist of Victoria, who first described fossils from Limeburner's Point.

Macropodidae
Genus and species indet.
(Fig. 16)

Material. NMV P 23241, right ramus with nearly all tooth material and compact bone lost, but with alveoli or root remnants of ? I_1 , ? P_3 , $M_{2,5}$. NMV P 23295, a ?right ramus fragment with

parts of roots of $M_{4,5}$ or a maxillary fragment with the impressions of the lingual side of the last two upper molars.

Description. Specimen NMV P 23241 has totally lost its external bone, and almost all of its dentition. There is no trace of any compact surface bone, or tooth enamel or dentine of the tooth crowns (Fig. 16A, C). There is left only the internal bone material and partial tooth roots or alveoli, similar to the mode of preservation seen in some specimens from Coimadai (Turnbull *et al.* 1990).

Discussion. From its overall size and proportions the specimen appears to be from a sthenurine macropodid but the wasted ramus appears to be far too shallow for that to be the case, or for it to be a *Macropus*. Perhaps it is a *Protomnodon* Owen.

Family Diprotodontidae
Subfamily Diprotodontinae
Diprotodon cf. *D. optatum* Owen, 1838
Diprotodon longiceps McCoy, 1865
Diprotodon longiceps Keble, 1945
(Fig. 17, Table 7)

Material. NMV P 13003 (and including one piece with the number P 2327_, probably 23277),

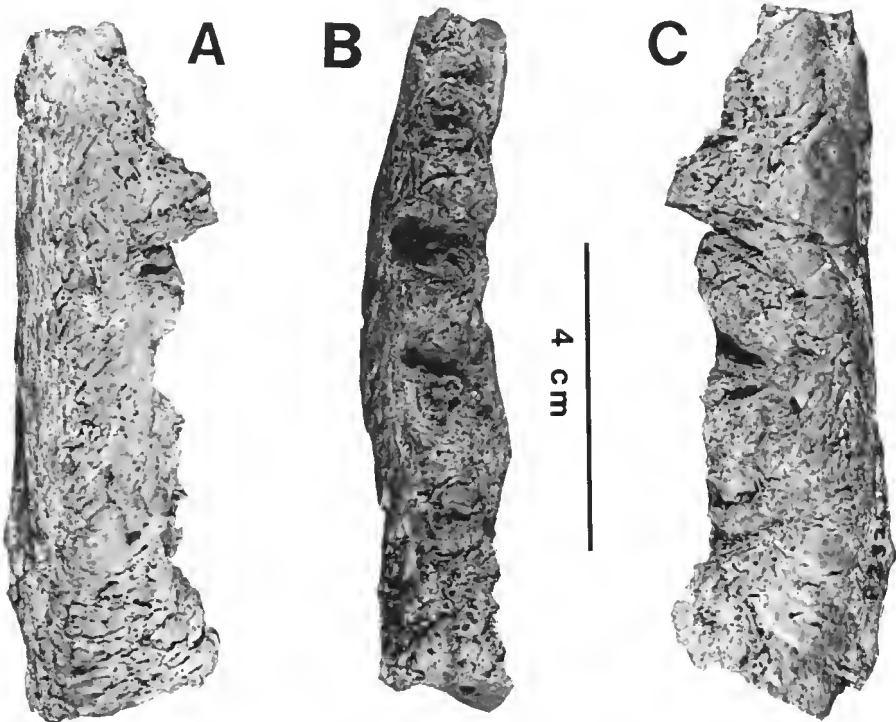


Fig. 16. Indeterminate macropodid left mandibular ramus, NMV P 23241: A, labial; B, dorsal; and C, lingual views. This specimen shows the unusual preservation seen in many of the Coimadai specimens.

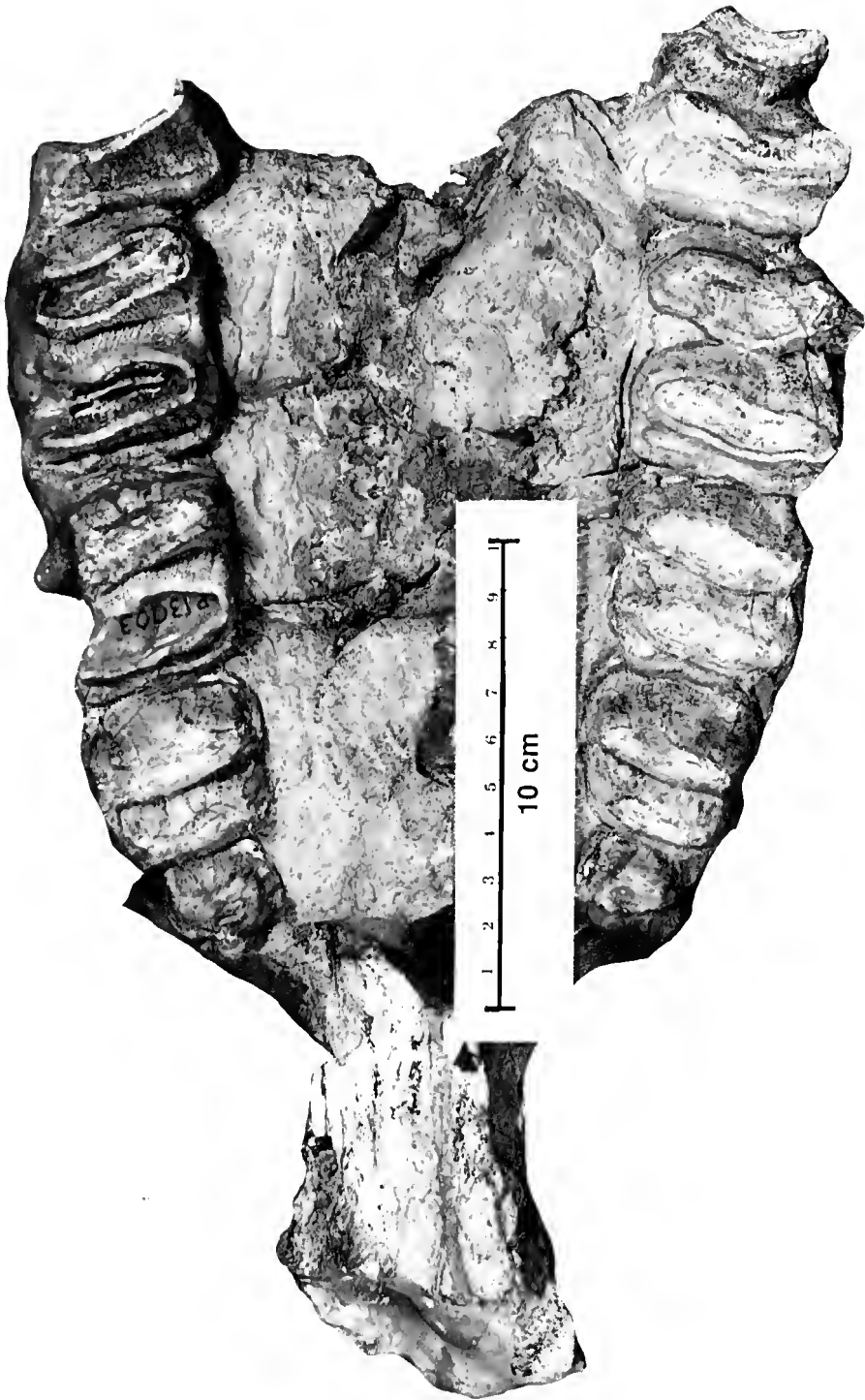


Fig. 17. *Diprotodon* cf. *D. optatum*, NMV P 13003 in palatal view.

palate with left and right P^3 - M^5 and alveoli of the I^2 s and I^3 s. Keble (1945) erroneously listed the specimen identified by McCoy (1876) as No 13303 when 13003 had been intended. It was originally in six pieces and could only be seen in sections along the breaks, the palate and teeth being covered by five or more centimeters of limestone. This must have been the condition when McCoy examined it. All of the pieces but one (P 2327_) bore the number 13003, none of them had the number 13303. (T. Rieh has verified 13003 as the correct number).

Description. The zygomatic process of the maxillary faces laterally and is located dorsal to

the posterior root of M^4 . The specimen shows the narrow anterior extension of the maxillary under the premaxillary. The alveolus for the right I^2 can be seen at the anterior end of the specimen just ahead of the presumed premaxillary-maxillary suture. Nowhere else can this suture be positively identified. The alveolus of the left I^2 is broken about 2 cm behind the anterior edge of the alveolar opening, to judge by that of the right I^2 . The premaxillary is broken away on the left side to expose nearly two cm of the root of the I^3 . At this point the remnant of the root is approximately parallel to the long axis of the premaxillary. Just anterior to this the alveolus

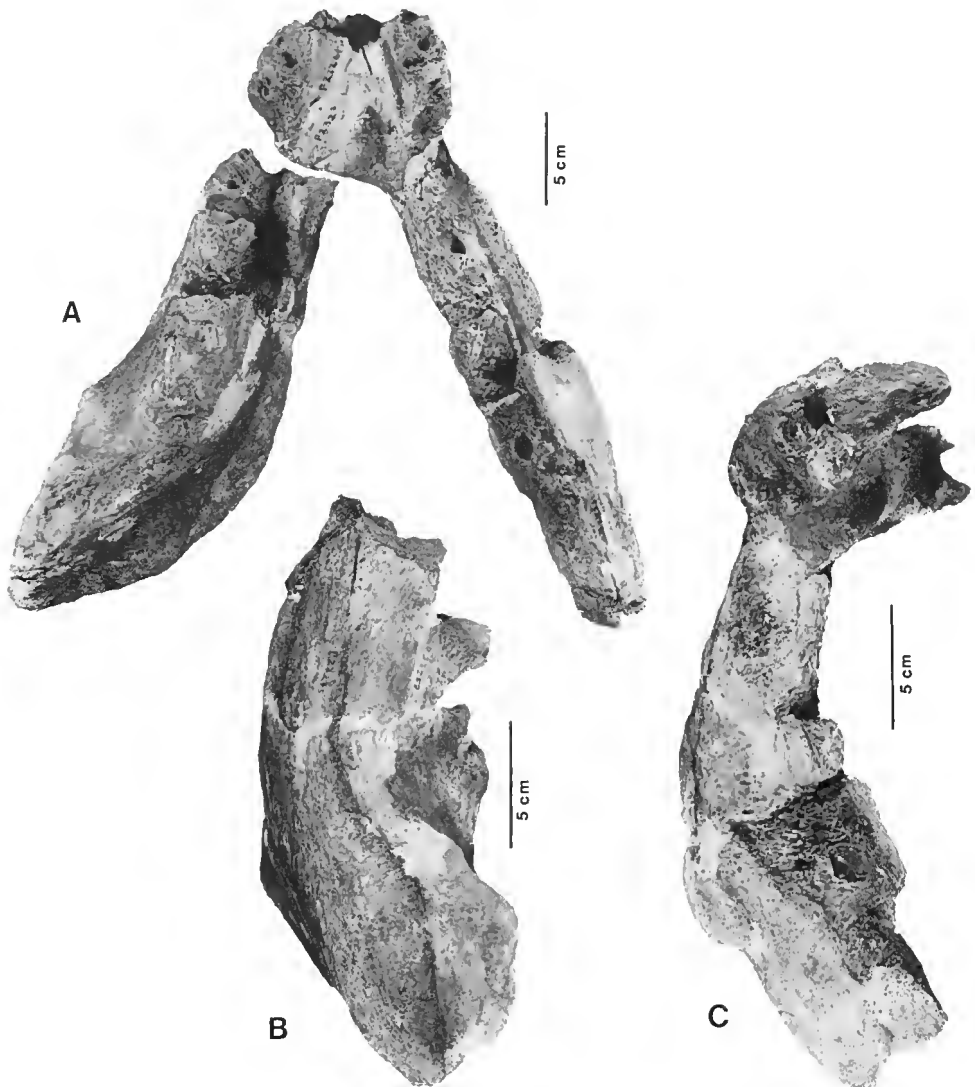


Fig. 18. *Zygomaturus* sp., NMV P 23235, 23242, edentulous mandibular rami: A, dorsal; B, lateral view of left ramus; and C, lingual view of right ramus.

turns outward about 15°. Part of the root of the right I³ is exposed in a window on the ventral side of the palate near its narrowest point. The antero-posterior diameter of the alveolus for the right I³ is 18.3 mm, its transverse diameter is 14.8 mm. What little remains of the poorly preserved palate seems to indicate that its posterior edges extended at least as far back as the rear of the M⁴s.

The left P³ is almost complete. It has the "horse shoe" crown morphology characteristic of *Diprotodon* (Stirton *et al.* 1967; Areher 1977) with distinct paracone and metacone, each joined to the protocone by a crest. A prominent ridge extends from the apex of the metacone to its base and forms the posterolingual corner of the tooth. There is no posterior cingulum. Breakage makes it impossible to determine whether or not there was an anterior cingulum.

The upper molars are bilophodont. The anterior loph is shorter than the posterior one on M², about equal to it on M³, and longer on M⁴⁻⁵. Prominent anterior cinguli are present on all molars. The posterior loph of M⁴ and both lophs of M⁵ are convex anteriorly. Each end of the posterior face of the anterior lophs of M²⁻³ has a low rounded ridge that extends into the interloph valley. On the M⁴ there is a broad bulge comparable to labial ridges on the M²⁻³. On M⁵ the condition is more like the condition on M². The enamel shows the punctate surface formed by fine crenulations mentioned by Areher (1977). Tooth dimensions are given in Table 7.

Discussion. This well preserved specimen was unprepared at the time McCoy (1876) referred it to his *D. longiceps* (McCoy 1865). The crowns of the cheek teeth are now revealed and these closely resemble in size and shape comparable teeth in the *D. optatum* Owen sample from Lake Callabonna. There seems no reason to refer this material to *D. longiceps* if that is indeed a valid taxon.

Subfamily Zygomaturinae

Zygomaturus sp.

(Figs 18-19, Table 7)

Material. Mandible (Fig. 18) consisting of left ramus (Fig. 18B) with alveoli of M_{3,4} and roots of M₅ (NMV P 23235 along with 23244, 23246, 23248-9, 23258, 23261-3 and 23266) and right ramus (Fig. 18C) including left and right symphyseal fragments and the partial alveoli of right I₁, P₂₋₃, M_{2,4,5} and left M_{3,5} (NMV P 23242 along with 23245, 23247, and one piece with its number lost [buried] in the assembly). NMV P

23243, left ramus fragment with roots of M_{4,5} (Fig. 19), probably same taxon as P 23235 and 23242 (Table 7). Missing numbers incorporated into one of the composites, most likely the pair of jaws of the *Zygomaturus* sp. specimen shown in Figure 17, without being recorded: NMV P 23254, 23264-5, 23277, 23289.

Description. Both of these rami have only the alveoli of M_{3,4} and some of the crown base of the M₅ (Fig. 18, Table 7). These poorly preserved fragments clearly pertain to a small diprotodontid, one that is most similar to *Zygomaturus* Macleay in size and what remains of the morphology. The ends of the oval incisor alveoli extend backwards beneath the M₂, the end of the symphysis to level of the posterior root of M₃, the inferior border of the horizontal ramus is strongly convex, and the anterior edge of the ascending ramus lies behind M₅ in NMV P 23235/P23242. In P 23243, presumably the younger specimen, the anterior edge of the ascending ramus lies labial the posterior root of M₅. These features together are typical of *Zygomaturus*. A form the size of *Z. trilobus* Macleay or *Z. victoriae* is indicated by the dimensions of the roots of the M₅.

Table 7. Measurements (mm) of the Limeburner's Point diprotodontids: b = broken.

	<i>Diprotodon</i> cf. <i>optatum</i>		<i>Zygomaturus</i> sp.		NMV P23243
	NMV P 13003		NMV P 23235/23242		
	Left	Right	Left	Right	
P ¹	L	26.0	b		
	AW	20.2	b		
	PW	25.4	24.3		
M ²	L	35.5	37.9		
	AW	b>33.5	35.4		
	PW	b>38.6	40.1		
M ³	L	46.6	40.9		
	AW	b>38.0	42.6		
	PW	b>44.7	43.6		
M ⁴	L	52.1	54.8		
	AW	b>44.4	50.4		
	PW	b>43.9	45.7		
M ⁵	L	b	54.6		
	AW	b>43.7	49.2		
	PW	-	b>40.5		
Symphysis	L		-	>80.0	-
Ramus	L		>145.0	~143.0	-
Ramus depth:					
symphysis rear			>55.0	-	-
beneath M ₅			98.0	>86.0	72.0
M ₁ alveolar	L		~48.0	-	~46.0
M ₅ alveolar	L		~44.0	~44.0	45.0

CONCLUSIONS

The LBP Local Fauna, collected mostly in the late 1880's from freshwater limestones, consists of nine taxa, all of which except two macropodids represent populations differing from known late Pleistocene to Recent species in significant ways. Six belong to extinct lineages. This strongly suggests a greater age, probably mid to early-late Pleistocene, for the fauna. This is in agreement with recent paleomagnetic data (Whitelaw, 1991; in press) wherein the strata containing the LBP Local Fauna were determined to be from one of the two normal polarity intervals younger than 1.66 Ma, either 0.98-0.91 Ma or 0.73 Ma. Unfortunately we have no firm basis for determining which of the two is the most likely. It seems most likely that the present normal (Brunhes) chron is

involved, as the LBP Local Fauna is composed of seven genera, three of which are common in better known late Pleistocene assemblages, with the distinctions being confined to the species level. In addition the small macropodid species seem most similar to living forms, further supporting a later Pleistocene age.

The Limeburner's Point Local Fauna consists of nine taxa comprising four species of macropodids, one *Macropus* near *M. parryi*, *Wallabia* cf. *W. bicolor*, a new sthenurine, *Simosthenurus mccoysi*, and an indeterminate large macropodid. There is one new large wombat that differs from, but is most similar to, *Lasiorhinus medius* (Owen). Two taxa of diprotodonts are represented, *Diprotodon "longiceps"* of McCoy which we believe is best referred to *D. optatum* since it is similar to the

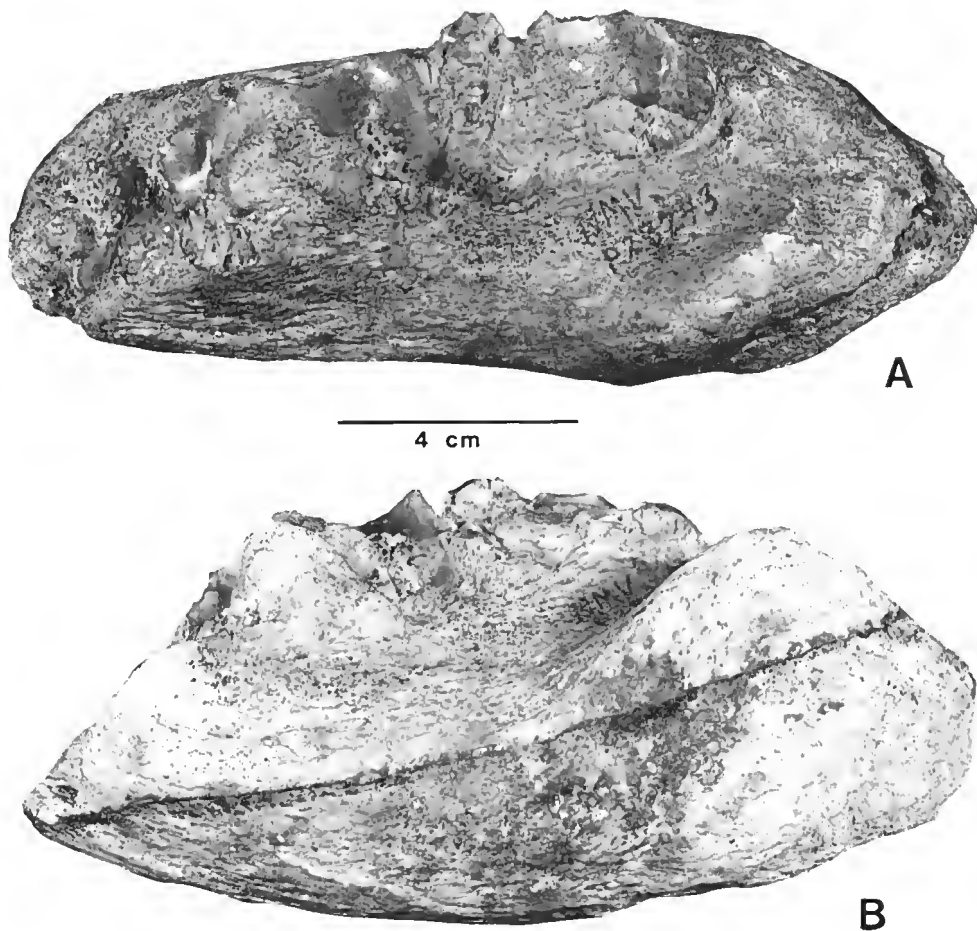


Fig. 19. *Zygomaturus* sp. NMV P 23243, left ramus fragment in: A, dorsal and B, lateral views.

Lake Callabonna sample of mid-Pleistocene age. The other is a *Zygomaturus* about the size of *Z. trilobus* or *Z. victoriae*. Finally there are two carnivorous forms both referable to *Sarcophilus*. One of these (sp. 1) is near to both modern *S. harrisi* and the extinct late-Pleistocene *S. lanianus*, and could be ancestral to both. The other (sp. 2) is decidedly different from any known sarcophiline species, being larger and of different proportions and morphology.

A lacustrine environment of deposition is indicated by the enclosing matrix of limestone with freshwater mollusks. Most of the fossils appear to be isolated pieces, but there is evidence for some partial articulation and also of trampling. Preservation is mostly fairly good, but the matrix is hard and tough and the bone is soft and fragile. The specimens from the more rubbly limestone units show poorer preservation similar to that of the Coimadai Fauna.

With such a small sample of taxa, comparisons to other mid to early late Pleistocene or later faunas are difficult. However the generic composition of the fauna agrees best with Pleistocene assemblages rather than Pliocene ones in accord with the stratigraphic evidence. Dated local faunas of this type are few, but the Duck Ponds Local Fauna, which is older than the LBP Local Fauna, possibly in the late Matuyama Chron, also contains taxa common to later Pleistocene assemblages. Evidence accumulated to date indicates rather uniform generic composition of Australian marsupial faunas during the time of rapid cycling of world climate (0.73-0 Ma).

ACKNOWLEDGEMENTS

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<i>Macropus</i>	<i>parryi</i>	FMNH 42090
		FMNH 48301
	<i>rufogrisea</i>	FMNH 58961
	sp.	FMNH 44874
	(juv. of <i>M. rufus</i> or <i>M. robustus</i>)	
<i>Petrogale</i>	<i>inornata</i>	FMNH 64352
		FMNH 64435
<i>Setonyx</i>	<i>brachyurus</i>	FMNH 67712
		FMNH 98787
<i>Thylogale</i>	<i>billiardieri</i>	FMNH 57798
		FMNH 98911
	<i>brunii keyseri</i>	FMNH 34207
		FMNH 60682
	<i>brunii brunii</i>	FMNH 31864
	<i>brunii</i>	FMNH 60777
	<i>stigmatica</i>	FMNH 60885
		FMNH 60886
		FMNH 64356
	sp.	AMNH 198047
<i>Wallabia</i>	<i>bicolor</i>	FMNH 64354
		FMNH 64365
		FMNH 64855
	<i>bicolor apicalis</i>	FMNH 60892
	<i>bicolor bicolor</i>	FMNH 48555

APPENDIX

Materials of extant macropodids examined in comparison with the LBP specimens assigned to *Macropus* near *M. parryi* and *Wallabia* cf. *bicolor*.

<i>Dendrolagus</i>	<i>goodfellowi</i>	FMNH 60238
		FMNH 104954
<i>Dorcopsis</i>	<i>liageni</i>	FMNH 31859
		FMNH 31860
	<i>luctuosa</i>	FMNH 8379
	<i>mulleri</i>	FMNH 104613
		FMNH 108014
<i>Macropus</i>	<i>eugenii</i>	FMNH 4810
		FMNH 48370
		FMNH 49339
	<i>irma</i>	UT TMM-M 2039

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TIRARI FORMATION AND CONTAINED FAUNAS, PLIOCENE OF THE LAKE EYRE BASIN, SOUTH AUSTRALIA.

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ABSTRACT

First recognized at Lake Palankarina, south-eastern Lake Eyre Basin, South Australia, the Tirari Formation has subsequently been traced northward to outcrops along the lower Warburton River. Unfossiliferous, red gypsiferous mudstone with interbedded cross-laminated gypsum sand is the most characteristic lithology. A basal stream-channel fill at Lake Palankarina, the Mampuwordu Member, contains the Palankarina Fauna, and a widespread nested sequence of channel fills at the top, the Pompapillina Member, produces the Toolapinna and Kanunka faunas. These faunas are dominated by extinct species and contain diprotodontid and macropodid genera not found in Pleistocene or Recent assemblages. They differ from older Tertiary faunas in that their taxa are more closely related to living or Pleistocene clades. The Kanunka and Toolapinna assemblages contain *Euryzygoma* Longman, *Prionotemnus* Stirton, *Kurrabi*, *Protomodon devisi* Bartholomai, and conilurine rodents in common with Pliocene faunas elsewhere in Australia. The presence of conilurine rodents suggests a maximum age of 4.5 Ma for the upper part of the Tirari Formation. Magnetostratigraphic studies indicate that the Tirari Formation is largely reversed in magnetic polarity, but contains normal intervals at and near the base at Lake Kanunka and the lower Warburton. Faunal evidence constrains correlation of the upper part of the Tirari Formation with the youngest reversed normal interval in the Gilbert Chron (3.9 - 3.4 Ma).

KEYWORDS: Lake Eyre Basin, Tirari Formation, lithostratigraphy, magnetostratigraphy, biostratigraphy, Palankarina fauna, Toolapinna fauna, Kanunka fauna.

INTRODUCTION

In their pioneer study of the Cainozoic deposits of the Lake Eyre Basin in South Australia, Stirton, Tedford and Miller (1961) coined the name Tirari Formation for the "flat lying brick red argillaceous sandstones and arenaceous claystones" that overlie the Etadunna Formation regionally, and the Mampuwordu Sand locally at Lake Palankarina, the type locality for all these lithostratigraphic units. The Tirari Formation rests with angular unconformity on the gently folded Etadunna Formation at Lake Palankarina. Its relationship with the fossiliferous channel-filling sands and clays of the Mampuwordu Sand were considered to be disconformable but there is no evidence of erosion or reworking of the Mampuwordu Sand into the overlying Tirari red

mudstones. We now believe that these units record aspects of a single basin-filling event, the Tirari Formation. The local channel fills at the base become the Mampuwordu Member of the Tirari Formation (Fig. 1).

In 1961, the Tirari Formation had been traced to outcrops on the lower Cooper (Katipiri Waterhole) and northward into the central Tirari Desert at Lakes Kanunka, Pitikanta and Ngapakaldi, where the stratigraphy showed the same general sequence as at the type locality. At that time, all supra-Tirari channel-filling sands and clays were grouped as the Katipiri Sand, although it was clearly recognized that the fossil assemblage from these rocks at Lake Kanunka was markedly different from the other local faunas from the Katipiri Sand. The Kanunka Fauna was considered early Pleistocene in age

by Stirton, Tedford and Woodburne (1968: Fig. 2).

In 1980 and 1983 the authors initiated field work to resolve questions about the latest Cainozoic (post-Etadunna) stratigraphy and paleontology east of Lake Eyre. All previously known outcrops were reinvestigated, new fossil collections were made, and outcrops along the lowest reaches of the Cooper and Warburton were examined, as well as those on the eastern shore of Madigan Gulf, Lake Eyre North. These field studies were guided and complemented by aerial reconnaissance, study of airphotos and LANDSAT imagery. The results of our work on the Pleistocene deposits and faunas were reported in 1986 (Tedford *et al.* 1986) and the present contribution summarizes the Pliocene deposits and their faunas. Some of our biochronological conclusions were incorporated into Woodburne *et al.* (1985), and a preliminary synthesis of the Pliocene and Pleistocene history of the Lake Eyre Basin was given by Tedford *et al.* (1986).

We have retained the serial identification of marsupial cheek-teeth as used by Stirton (1955), rather than that of Archer (1978). Abbreviations used: AM, Australian Museum, Sydney; AMNH, American Museum Natural History, New York;

SIAM, field catalogue of Smithsonian Institution, Washington - American Museum of Natural History collections; SAM, South Australian Museum, Adelaide; UCMP, University of California, Museum of Paleontology, Berkeley.

LITHOSTRATIGRAPHY

At its type locality, the exposures along the bluffs marginal to the western shore of Lake Palankarinna, the main body of the Tirari Formation shows a rather consistent stratigraphy and thickness. The unit can be characterized as red-brown (10R4/5-6 Munsell) claystones, clayey sands and sandy clays, thin-bedded to laminated where structure is visible. Although these rocks are locally cemented with gypsum, they do not contain abundant authigenic gypsum. The basal silty, very-fine to fine sands contain scattered coarser grains and intraformational clay clasts, but lack clasts from the adjacent silcreted older Cainozoic and Mesozoic rocks. A widely traceable bed of white, very-fine to medium quartz sand, 0.25 m thick, containing red-brown clay pellets and lenses, occurs about 1 m above the base of the unit throughout the Lake Palankarinna exposures.

<i>Stirton, Tedford, Miller: 1961</i>		<i>Tedford and Wells: 1990 & this paper</i>	
ROCKS	FAUNAS	ROCKS	FAUNAS
<i>Katipiri Sand</i>	<i>Malkuni</i>	<i>Katipiri Fm.</i>	<i>Malkuni</i>
	<i>Kanunka</i>	<i>Kutjitara Fm.</i>	<i>Lower Cooper</i>
<i>Tirari Fm.</i>		<i>Tirari Fm.</i>	<i>Kanunka Toolapinna</i>
			<i>Main Body</i>
<i>Mampuwordu Sand</i>	<i>Palankarinna</i>		<i>Mampuwordu Mbr.</i>
<i>Etadunna Fm.</i>	<i>Ngapakaldi</i>	<i>Etadunna Fm.</i>	<i>Ngapakaldi S.I.</i>

Fig. 1. Comparison of lithostratigraphic and biochronologic nomenclature, Pliocene and Pleistocene rocks and faunas, eastern Lake Eyre Basin, South Australia, over the past thirty years.

The upper quarter of the Tirari Formation contains shallow festoon cross-bedded, fine to medium quartz sands that pass upward into red-brown mudstones. Small celestite nodules occur in the mudstones beneath this sandy interval. Intense gypsum cementation characterizes the upper 2 m, indurating a widespread surface on which the Quaternary dunefield rests. This gypcrete represents a major morpho-stratigraphic

unit (Wopfner and Twidale 1967) in the Lake Eyre Basin.

The Mampuwodu Member has been recognized only in the northern part of the Lake Palankarinna escarpment where it is represented by the fill of perhaps a single stream channel excavated in places at least 5 m into the Etadunna Formation. The basal sands in the channel contain pebbles of the Etadunna Formation (green

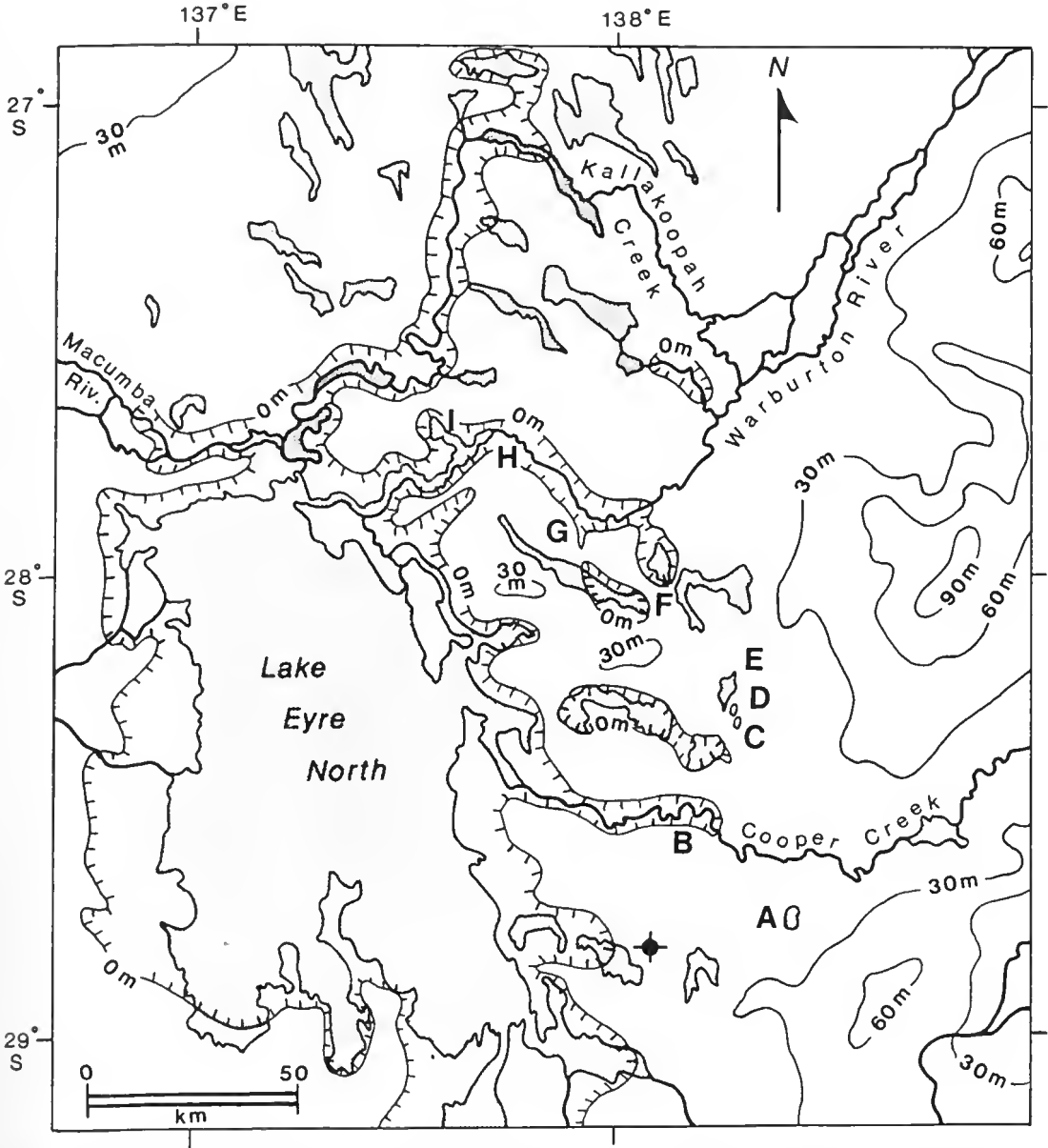


Fig. 2. Topographic map of the region east and northeast of Lake Eyre North. Contour interval 30 meters modified from Twidale and Wopfner (1990: fig. 2). Sites discussed in this paper: A, Lake Palankarinna; B, Katipiri Waterhole; C, Lake Kanunka; D, Lake Pitikanta; E, Lake Ngapakaldi; F, Lake Kittakiitooloo; G, Toolapinna Waterhole; H, Keekalanna Soakage; I, Lake Pompapillina. Symbol for exploratory well is Peachawarinna 2 and 2A.

mudstone and dolomite) and redeposited polished silcrete pebbles ultimately derived from the Paleogene Eyre Formation. The Mampuwordu channel-fill contains cross-laminated, fine, white quartz sands, green to black clay lenses and clayballs, and locally abundant vertebrate remains ranging from small fragments up to a 1 m wide diprotodontid pelvis. Observations of foreset bedding in the fossil excavations were few, but were of consistent orientation indicating northward transport along the trend of the exposed channel segments.

Outcrops of the Tirari Formation along lower Cooper Creek begin just west of Lake Tarlakupa and extend 6 km westward to Katipiri Waterhole and perhaps 5 km further west to "Red Bluff." These outcrops form the northern edge of the ancestral Cooper meander belt, which is incised into the Tirari and overlying Kutjitara Formations. Red-brown mudstones compose the lower part of the local Tirari sequence overlain by a plexus of internested, northward trending, stream channels filled with cross-bedded sands and interbedded mudstones. The upper part of these sands are heavily impregnated with gypsum, forming a gypcreted geomorphic surface beneath the dunes.

South of the Cooper, the Tirari Formation is buried beneath Quaternary fluvial deposits. This is indicated in the Peachawarinna 2 and 2A cores drilled by the Bureau of Mineral Resources about 34 km south of Katipiri Waterhole. In these drill holes, nearly 12 m of reddish sands and interbedded clays with a gypsum indurated cap lie on the Etadunna Formation. The gypcrete caprock is overlain by 13.5 m of Quaternary fluvial and aeolian deposits.

North of the Cooper, the Tirari Formation crops out in the escarpments along the western sides of Lakes Kanunka, Pitikanta and Ngapakaldi. At the first two sites the stratigraphy is identical. Lower red-brown and green mottled mudstones, up to 4 m thick, are disconformably overlain by fossiliferous, cross-bedded, white and ferruginous, medium grained sands with lenses of red-brown claystone, green and red clay balls and scattered pebbles of carbonate rock, silcrete and kaolinized sediments derived from the Etadunna Formation and the older rocks of the basin margin. The sands were deposited in a deeply dissected landscape cut into the red mudstones (and into the Etadunna Formation at Lake Kanunka) so that the thickness of the channel-fill varies from a meter or so to nearly 6

m. Gypsum concretions are common along the basal contact of the channel-fill, especially where it overlies the Etadunna Formation. Intensive gypsum cementation indurates the top of the section, holding up the sand-draped edge of a plateau that extends from Lakes Kanunka to Ngapakaldi.

A similar stratigraphy occurs farther north in the Tirari Desert along the western side of Lake Kittakitaooloo, where channel-sands overlie red brown mudstones that rest on silicified and ferruginized dark claystones referred to the Etadunna Formation.

Erosion during development of the Warburton meander belt in Quaternary time seems to have cut a broad swath into the Etadunna Formation, removing the Tirari Formation upstream from Toolapinna Waterhole. The long escarpment that borders the western side of the Warburton River from Toolapinna Waterhole nearly to Lake Pompapillina shows 15 m of Tirari Formation, the thickest in the region. In places, the escarpment has been undercut, giving rise to large slump blocks that have been rotated along curved slip-surfaces. Along this 30 km reach of the Warburton River, the Tirari Formation has a consistent stratigraphy that permits lithological correlation between outcrops. Contact with the Etadunna Formation can be seen at Toolapinna waterhole, and all traceable beds decline to the north-west at an angle greater than the present gradient of the river floor.

As in the south, the Tirari Formation along the lower Warburton can be divided into two units separated by a disconformity. The lower unit, or main body of the Tirari Formation, is red-brown gypsiferous mudstone that comprises about two-thirds the 15 metre maximum observed thickness. Sedimentary structures are difficult to observe, but those visible in the sandier units imply thin to laminated beds. A basal fine quartz sand contains limestone pebbles and reworked celestite nodules derived from the underlying Etadunna Formation. These sands fill fractures in the top of the Etadunna Formation. Above the basal metre, quartz is subordinate to authigenic gypsum seed-crystals as the coarsest clastic component in the red-brown claystone. At 4.5 m above the base, a widely traceable, bench-forming unit of horizontal to cross-laminated, medium gypsum sand occurs. Planar foreset laminae and ripple lamination indicate north to north-west transport of clastic gypsum. A more indurated ripple-laminated greenish gypsum sand occurs 8-9.5 m

above the base. This widely traceable unit bears rolled charophytes, disarticulated fish-bones, rare mammal bones and scattered limestone pebbles and granules. Above this distinctive bed, authigenic gypsum is rare and quartz dominates the coarser sand fraction. The upper third of the section is composed of interestered stream channels that cut as much as 3 m through the upper laminated gypsum sand into the underlying red mudstones. Celestite nodules frequently occur beneath this contact. These fluvialite deposits include festoon cross-laminated, medium to coarse quartz sand with red-brown claystone lenses that fine upward to climbing-ripple laminated fine sands and interbedded clays, and finally massive red-brown mudstone in the most completely preserved cycles. Occasional fossil mammal remains occur in the basal part of these channel deposits.

The consistent occurrence of such quartzose fluvialite deposits at the top of the Tirari Formation, from its type section to the Warburton River, encourages us to name this member to facilitate discussion of an important event in the history of the Lake Eyre Basin. We have chosen the name Pompapillina Member from the lake nearest the most northerly outcrop of the unit along the Warburton, but designate the type section at Toolapinna Waterhole.

We have not been able to recognize the Tirari Formation downstream from Lake Pompapillina, nor among the outcrops along the Kallakoopah to the north. Shallow drilling in the southern Simpson Desert north of the Kallakoopah, but south of the South Australia-Northern Territory border, has revealed nearly 100 m of red-brown fluvialite sediments overlying the Etadunna Formation that have been attributed to the Tirari

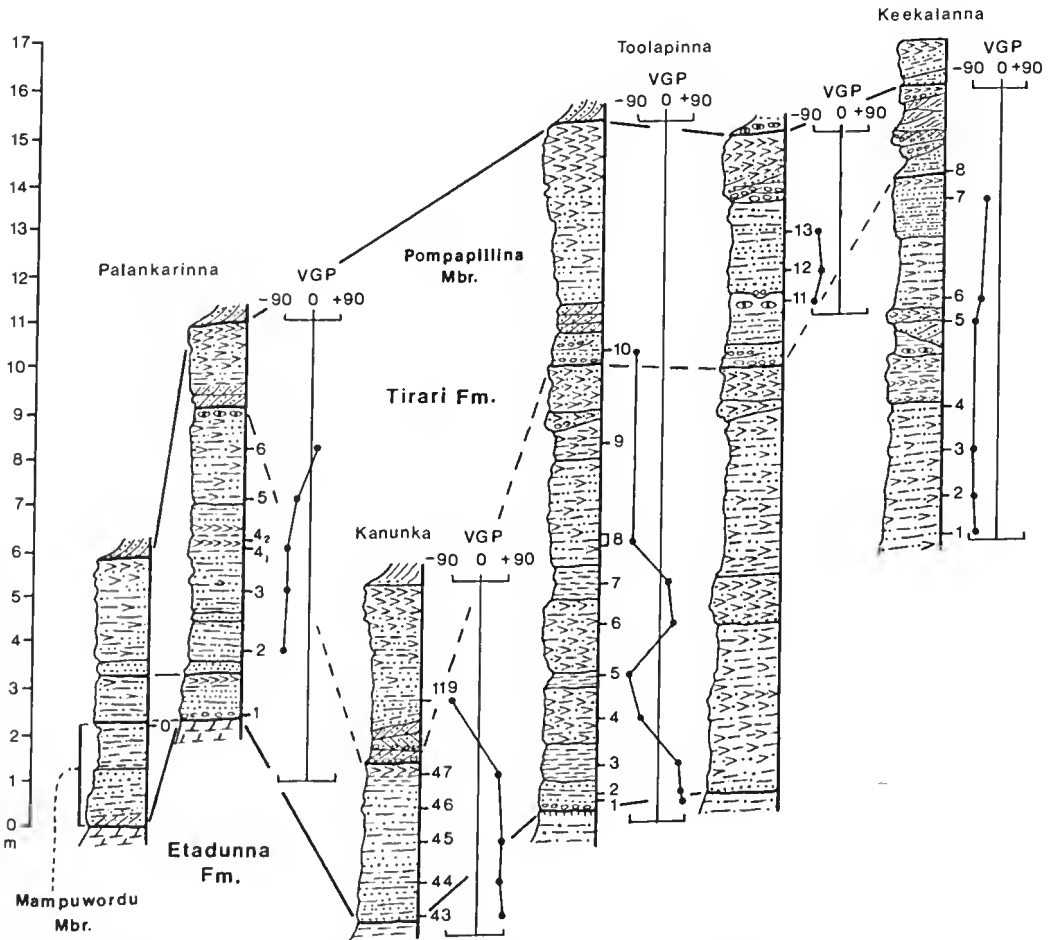


Fig. 3. Correlated stratigraphic columns of the Tirari Formation showing lithostratigraphy with conventional lithological symbols (">" denoting gypsum) and lithostratigraphic correlations. Magnetostatigraphy depicted by values for the Virtual Geomagnetic Pole (VGP).

Formation (Wasson 1983). This region also contains the thickest (subsurface) development of the Etadunna Formation, suggesting a stable depocenter from Miocene into medial Pleistocene time, based on the cited thicknesses and the presence there of Kutjitarra Formation prior stream deposits (Tedford and Wells 1990) as well. The persistent northward indications of transport provided by Tirari sedimentary structures and textural trends points to a depocenter north of Lake Eyre.

MAGNETOSTRATIGRAPHY

Thirty-three paleomagnetic sites were established in four local sections of the Tirari Formation. Eighteen of these sites gave site mean paleopositions which were statistically significant using minimum conventional criteria. We interpreted the remaining site mean paleopositions to have reversed or indeterminate polarities, based upon individual sample demagnetization behavior. Thus we concluded the Tirari Formation stratotype (Lake Palankarina) and local section at Keekalanna Soak to be uniformly of reverse polarity; the Toolapinna Waterhole reference section to be mixed polarity, but largely reversed; and the local section at Lake Kanunka to be of mixed but largely normal polarity (Fig. 3).

The behavior of samples during both alternating field and thermal step-wise demagnetization indicated the presence of a viscous component of Natural Remanent Magnetization (NRM) readily removed at low treatment levels (10 mT, 100° C). With increasing demagnetization, the remaining remanence did not appear to be consistently resolvable into components of distinct coercivity ranges or orientations. More complete step-wise removal of NRM was achieved with thermal demagnetization, and this was the preferred magnetic cleaning procedure. Nonetheless, magnetic cleaning was not sufficient to identify the polarity of all sites with respect to the simple geomagnetic dipole model.

Methods. *Collecting and Laboratory Procedure.* Stratigraphic site sampling interval was to average 1 m, but was adjusted to allow for outcrop exposure and lithologic type. Finer-grained lithologies were preferred: i.e. mudstones, silty mudstones, and finer-grained siltstones, although some medium to fine sandstones were also sampled. A minimum of

three samples was collected at each site, except at the Lake Kanunka local section where a large number of samples were taken. Lateral spacing of samples ranged from 1m to 8m, but was usually in the 3-4.6m range. Samples were extracted by hand tools from consolidated sediments beneath the surface weathered zone. As the stratotype section at Lake Palankarina is more severely weathered, it required deeper trenching. Bearing and dip data for each sample face was measured by Brunton Compass corrected for local declination.

In the laboratory, cube specimens (2.5cm) were cut from the oriented hand samples with a band saw, and cleaned to size with non-magnetic abrasive paper. Duplicate (contiguous) cubes were cut from a single sample wherever possible (labelled -i, -ii, etc.). Many of the samples from the Palankarina section cracked upon drying and it was not possible to cut them with the saw. Crumbly samples were consolidated by placing them face up in tailored aluminum foil boats and flooding them with liquid paraffin. The resulting block was then trimmed to size. Some of the more deeply cracked samples retained so much wax that thermal demagnetization treatment was not possible. Thermal demagnetisation was not possible for Keekalanna Site 4 (partially) and Palankarina Sites 1 (partially), 2 (partially), 3, 4 (partially), 5 and 6. Their mean palaeopositions were calculated from treatment in alternating fields only.

Specimen determinations were run on an ScT 3-axis Cryogenic Magnetometer. A custom plastic sample holder was used, which introduced an average moment intensity error of approximately $14 \times 10^{-9} \text{ A m}^{-1}$ over the course of the laboratory determinations. Alternating-field (af) demagnetizations was carried out on a Schoensted demagnetizer (non-tumbling), while thermal demagnetization was carried out in a Schoensted thermal demagnetizer.

Magnetic cleaning of all samples was achieved by step-wise demagnetization with the minimum of two, but usually six, treatment levels. For af treatment, vector and point diagrams were constructed at 10 mT increments up to 90 mT. For the thermal treatment, diagrams were plotted for 100°C increments up to 600°C; specimens were held at each temperature level for 40-45 minutes.

Demagnetization curves. Magnetic cleaning, or partial demagnetization by either alternating field or thermal procedures, serves to "strip"

portions of the initial sample NRM, leaving a smaller net magnetic moment after each step. Thus, decreasing net portions of the initial sample NRM are measured, i.e. those portions which are resistant to the randomizing effects of the elevated fields or temperatures, or in other words, those portions whose coercivity exceeds the randomizing energy of the peak treatment level at each successive step. The demagnetization behavior is analysed to identify discrete coercivities, or coercivity ranges (spectra), of

the components of the total NRM. NRM orientation and stability (coercivity) provide clues to the magnetic history of the rock. However, it is not always easy to relate the resolvable components of NRM to specific events in the postdepositional history of the rock. Using the conventions for the vector-end-point diagram (developed by Zijderfeld, 1967) used in Fig. 4, the magnetic moment vector of each determination is represented by two points which share a common abscissa value and whose disposition

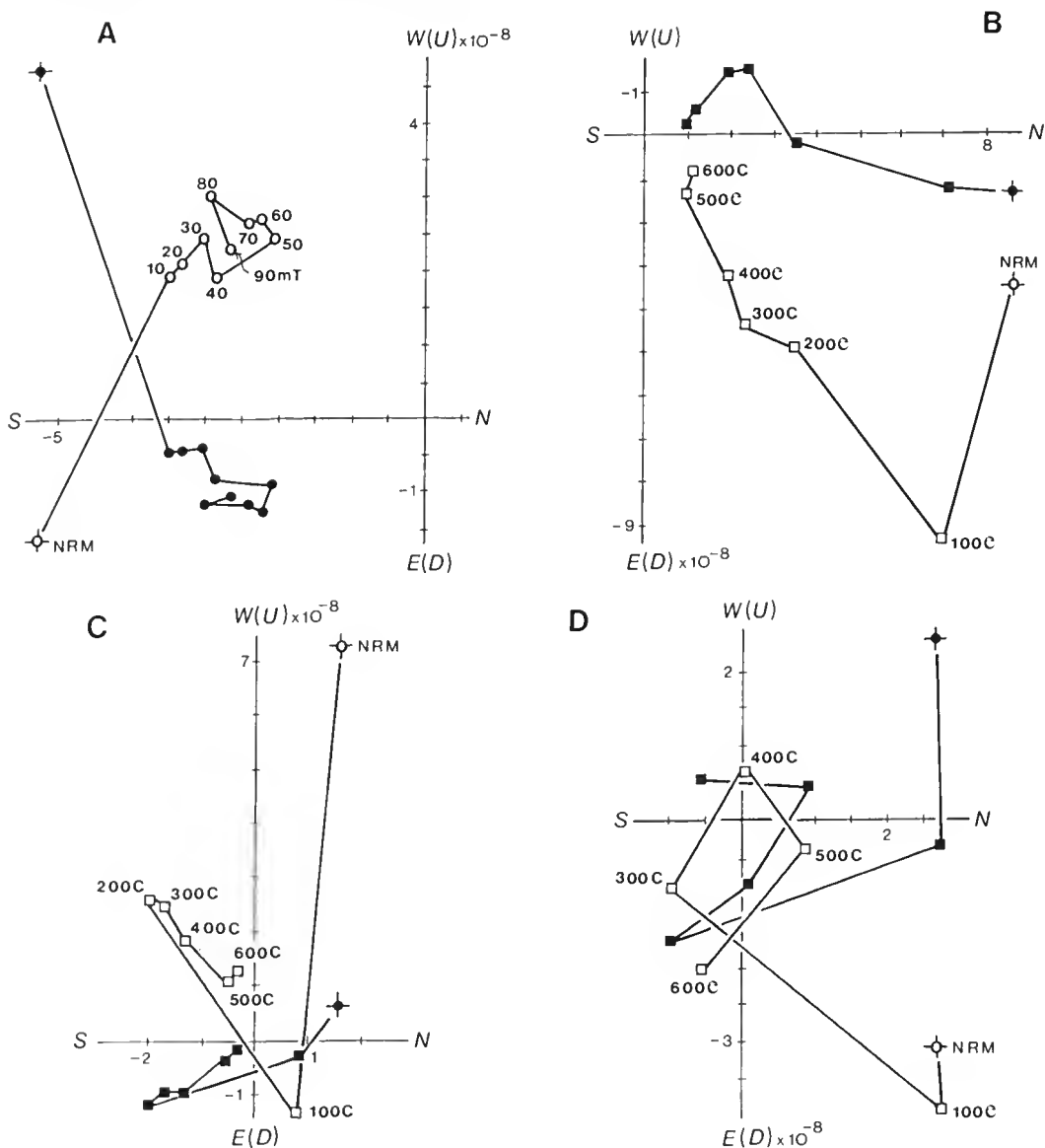


Fig. 4. Vector end-point (Zijderfeld) diagrams for four representative Tirari samples. A; sample PK-2c, B; sample KN-45c, C; sample KE-6a, D; sample KE-7b. Conventions: squares-thermal, circles-af, treatment; open symbols-inclination, closed symbols-declination, component of NRM vector. Intensities normalized to 10 cc sample volume, Am^{-1} .

together reflect the three-dimensional orientation of the measured NRM. The distance of the points from the origin reflects the length of the vector, and is a measure of the intensity of magnetization remaining. The removal of a given component of NRM after a certain demagnetization level may be followed by a distinct shift in orientation and/or intensity of the remnant signal. This results in either a more linear demagnetization curve, or distinct progression towards the origin. Overlapping coercivity spectra in multicomponent NRM signals will produce smoother curves if the component orientations are varied, or if all the components of NRM are parallel, a steady linear decay of the curves towards the origin. Alternatively, a wide scattering of points and no distinct progression of curves towards the origin may indicate unstable or unreliable magnetization, whose components cannot be clearly differentiated or explained, at least for the purposes of polarity stratigraphy. It may also be due to spurious signals introduced during the laboratory procedure.

Results. Figure 4 shows vector end-point diagrams for four specimens subject to step-wise demagnetization. These are representative of the behavior of Tirari samples. A variety of demagnetization curves was exhibited over the entire population of treated samples. These curves were segregated into several general categories, as explained below and with reference to Figure 4.

At lowest treatment levels, both af and thermal, all samples show the removal of a component of NRM with a substantial reorientation of net remanence. Usually this component comprises about 10% to 30% of the intensity of original NRM. Presumably this component consists of Viscous Remanent Magnetization (VRM) in part, and accounts for the variety of orientations observed. It is due to the procedures for handling and storage of the trimmed specimens. A portion of this lowest coercivity NRM may also be overprint from recent (normal) geomagnetic field acquired *in situ* and is a common source of VRM. No detailed study of this low-coercivity component was made to resolve these moieties. After removal of viscous component(s) at mid-range treatment levels (i.e., up to 400°C, 50 mT), most samples displayed a consistent range of orientations and more steady decay of intensity of net remanence. This mid-range component of NRM was used to derive site mean paleopositions. Alternating field cleaning to higher levels (up to

90 mT) did not prove to be effective in removing the remaining remanence. Higher thermal treatment (500°C to 600°C) often led to relative increases in intensity of magnetization, and substantial reorientation. However, the low strength of the remaining remanence, combined with the often widely divergent directions at these high temperature levels, led us to suspect laboratory contamination. These determinations were rejected in deriving polarity assessments.

Sample PK-2c (Fig. 4A) illustrates the incomplete effectiveness of af treatment. Stable orientation of net remanence is indicated at mid and high field levels, but there is incomplete progression to end-point (i.e., complete demagnetization or randomization of the NRM signal). This sample is interpreted to be of reversed polarity.

Sample KN-45e (Fig. 4B) shows satisfactory progression toward end-point with thermal cleaning, with more or less stable behavior of orientation over a broad range of coercivities. The increase of intensity with initial treatment may be due to removal of VRM acquired in the handling and storage of the specimen. The lack of intensity drop at the 600°C may reflect introduction of a spurious signal, although this is not substantial with this specimen. Samples with similar curves are considered to be stable samples, in this case of normal polarity.

Sample KE-6a (Fig. 4C) also shows satisfactory progression towards the end-point with thermal cleaning. In this case, it is possible that two moieties of low-coercivity remanence have been resolved by the determination at 100°C. The higher-temperature part is closely anti-parallel to the remaining net NRM. Again, a spurious signal appeared at the highest temperature. This sample is concluded to be reversed.

Sample KE-7b (Fig. 4D), in contrast KE-6a, shows no pattern of orientation of NRM at mid and high treatment levels, and no progression to end-point. It is considered to be unstable, and consequently polarity cannot be determined.

Table 1. Mean Intensity values for Tirari Formation samples. Intensity units: $\times 10^6$ A m³, normalized for 10cc sample volume.

Transect	NRM (M ₀)	Cleaned (M)	Ratio (M/M ₀)	No. of Samples
Toolapinna	0.891	0.305	0.342	39
Keekalanna	0.703	0.179	0.254	24
Palankarinna	2.012	0.728	0.362	24
Kanunka	1.719	0.620	0.361	41
Tirari Fm	1.331	0.462	0.347	128

Other Magnetic Characteristics. Table 1 lists means of sample intensities of magnetization, by section, before (M_0) and after (M) magnetic cleaning. Values for cleaned samples are from the ones used in determining the site means. The values for NRM intensity indicate that Tirari sediments were comparatively weakly magnetized. The mean intensity ratio for the entire sample population was $M/M_0=0.347$, indicating that the site mean paleopositions were based on the highest coercivity third of original remanence. This portion of the original NRM was presumably well above the coercivity spectrum of the viscous component(s). As discussed above, more deeply eroding the NRM with greater demagnetization may have lead to problems of weak or spurious signals.

Six samples were uniaxially magnetized to 5.0T, which introduced an artificial remanence known as the Isothermal Remanent Magnetization, or IRM. At such high applied fields, nearly all of the magnetic mineral domains were forced into alignment with the applied field (H); that is,

the sample is said to be saturated. These samples were then demagnetized stepwise to remove the IRM signal, by placing them in progressively higher fields oriented antiparallel to the saturating field ($-H$). The strength of the demagnetizing backfield required to totally remove all the IRM signal is the coercivity of isothermal remanent magnetization, or $-H_{cr}$.

The resulting IRM curves (Fig. 5) show that full saturation was not achieved for any of these samples at the peak field of 5.0T (Fig. 5, curves from origin at left). The back-curves (Fig. 5, right, plotted to the $-H$ axis) show a range of coercivities of IRM ($-H_{cr}$). Samples TP-7c and KE-2d both show very similar low intensities of IRM saturation and high values of $-H_{cr}$ (83 mT, 760 mT, respectively), which is consistent with hematite-borne remanence. These samples are from nearly equivalent levels of the Toolapinna and Keekalanna sections (qv. lithologic correlation Fig. 3). Sample PK-5e, in contrast, shows high saturation IRM intensity and low $-H_{cr}$ value (28 mT), a pattern more consistent for magnet-

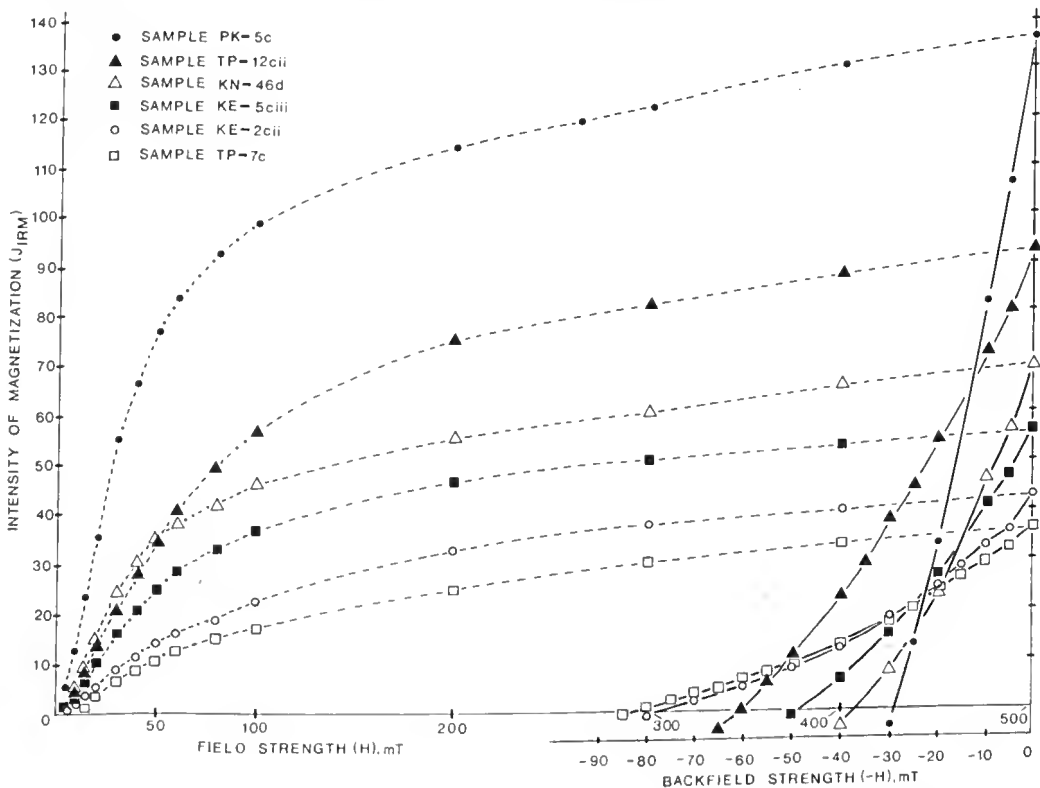


Fig. 5. IRM curves for six representative Tirari lithologies sampled. Sample TP-7c: red/green mudstone with minor silt; previously treated to 600°C. TP-12cii: medium fine sandstone with evaporites. KE-2cii: very fine-grained red/green mudstone. KE-5cii: medium-fine, well cemented, brown sandstone with gypsum. PK-5c: red mudstone/fine sandstone; previously treated to 60 mT. KN-46d: fine, well sorted brown sandstone, previously treated to 60 mT. Units: intensity of IRM, $\times 10^{-1}$; saturating and back field strengths, mT.

ite-borne remanence. The intermediate nature of the other samples, such as Sample TP-12c, indicate that the magnetic mineralogy of these sediments is more likely a combination of the two magnetic mineral groups, hematite and magnetite.

Mean Paleopositions for Sites. Site mean paleopositions were calculated from averaged sample paleopositions, before and after magnetic cleaning. The resulting paleopositions were selected from those treatment levels which appeared to reflect the stable spectrum of determinations (i.e. clustered orientations accompanied by directionally-steady or low-intensity declines of net remanence). In the vector-end-point diagram convention, those points group along straight-line or tightly flexured portions of the curves.

For our samples, the most effective cleaning temperature was 300°C (usually) or 400°C. In some cases where samples could not be cleaned thermally, an alternating field strength of 50 mT was most effective.

Figure 6A, B show site mean paleopositions for all sites, before and after cleaning. It is apparent that overprint component(s) of NRM before cleaning obscure any pattern of polarity stratigraphy. Sediments susceptible to overprinting gave reversed orientations before cleaning. The magnetic cleaning did, however, resolve nearly antiparallel polarities, with the emergence of two populations of site means (Fig. 6B), but left considerable scatter among the reversed sites.

Site mean results and statistics are listed in Table 2. Statistical significance is defined only by the minimum values for R (Fisher's Vector Sum) as conventionally applied (e.g., McElhinney, 1973). For each of the samples for a given site, the R value calculated for the mean must exceed the established minimum threshold R value to ensure a 95% probability that the mean has not been calculated from a population of randomly-oriented vectors. Three samples per site is the minimum required to achieve statistically meaningful R values. By these criteria, the site means of 18 of the 33 sites are statistically significant. Inference on polarity of other sites can be tentatively advanced, based on the following informal categorization of sites:

Class I - statistically significant site mean paleoposition, normal or reversed;

Class II - not statistically significant, but with sample paleopositions evenly scattered about the calculated mean, and/or R near threshold

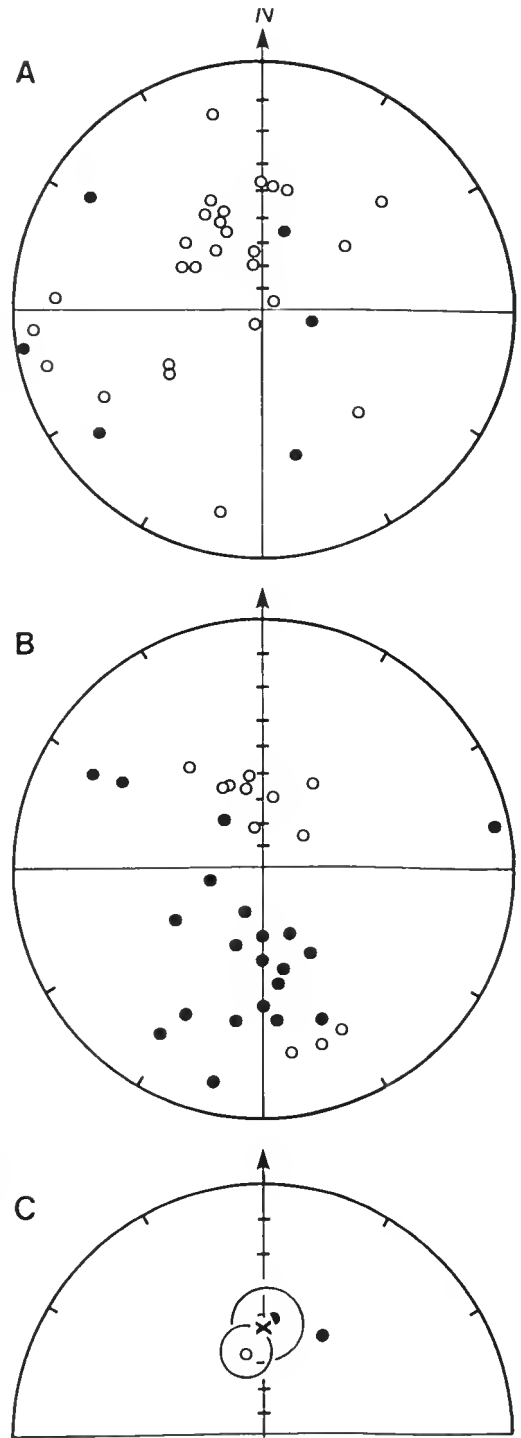


Fig. 6. Mean paleoposition of all sites, stereographic projection. A, before, B, after magnetic cleaning; C, reversal test for all statistically significant sites (reversed sites mean translated to northern hemisphere; circles of 95% confidence plotted). Open symbols=negative, closed symbols=positive, inclinations. "X"-present day geomagnetic dipole position for 28°S latitude.

Table 2. Tirari Formation Palaeomagnetic Site Means & Statistics; Columns: N= number of samples; k= precision parameter; Cof C=circle of 95% confidence; R= Fisher's Vector Sum; Pal'pos'n=Site mean paleoposition; P'lat. = Site palcolatitude; VGP=virtual geomagnetic pole. "Class", Pol.=Polarity - see text.

Site	N	k	CofC	R	Pal'pos'n		P'lat.	VGP Position		"Class"	Pol.
Toolapinna Waterhole											
1	3	42.1	12.5	2.9525	351.3	-50.2	31 S	72.2 E	81.8 N	I	N
2	3	6.6	31.5	2.6987	347.0	-55.6	36.1 S	88.1 E	76.2 N	I	N
3	3	8.2	28.2	2.7552	334.2	-51.8	32.4 S	65.8 E	67.3 N	I	N
4	3	11.9	23.4	2.8319	160.8	-17.0	8.7 S	167.6 E	49.0 S	IV	?R
5	3	2.0	57.2	1.9878	179.4	50.8	31.5 N	145.9 E	86.3 S	II	?R
6	3	44.0	12.2	2.9545	323.1	-38.0	21.3 S	50.7 E	56.0 N	I	N
7	3	6.6	31.5	2.6972	78.9	3.9	2.0 N	220.9 E	8.9 N	IV	?R
8	3	4.1	39.9	2.5100	189.0	27.3	14.5 N	104.1 E	74.2 S	III	?R
9	3	0.9	85.2	0.7630	50.6	-66.6	49.1 S	184.8 E	46.1 N	V	I
10	3	6.8	31.0	2.7077	174.7	28.9	15.4 N	160.5 E	76.6 S	I	R
11	3	4.2	39.4	2.5260	180.2	59.4	40.2 N	137.2 E	77.7 S	II	?R
12	3	5.6	34.2	2.6419	211.6	14.0	7.1 N	76.7 E	53.6 S	I	R
13	3	1.8	60.2	1.8910	193.3	8.2	4.1 N	106.5 E	62.8 S	III	?R
Keekalanna Soak											
1	3	13.0	22.4	2.8457	199.7	67.0	49.7 N	108.6 E	63.4 S	I	R
2	3	3.3	44.5	2.3955	156.4	59.1	39.9 N	189.6 E	67.0 S	II	?R
3	3	155.0	6.5	2.9871	170.6	-45.5	27.0 N	224.9 E	81.6 S	I	R
4	3	1.0	80.8	0.9144	170.4	-16.5	8.4 S	153.5 E	52.7 S	V	I
5	3	12.5	22.9	2.8406	172.6	-42.1	24.3 N	202.4 E	82.5 S	I	R
6	3	526.3	3.5	2.9962	150.8	48.2	29.2 N	217.4 E	64.3 S	I	R
7	3	2.7	49.2	2.2658	153.3	-19.2	9.9 S	176.0 E	44.4 S	IV	?R
8	3	0.9	85.2	0.8311	298.6	14.7	7.5 N	68.8 E	21.1 N	V	I
Lake Palankarinna											
1	7	1.4	44.7	2.5828	257.4	65.1	47.1 N	89.1 E	28.9 S	V	I
2	6	3.3	31.5	4.4745	200.0	55.1	35.6 N	75.6 E	71.8 S	I	R
3	3	2.3	53.3	2.1251	207.6	24.0	12.6 N	75.0 E	59.6 S	III	?R
4	3	9.4	26.4	2.7871	159.2	22.2	11.5 N	191.0 E	64.0 S	I	R
5	3	6.7	31.2	2.7024	239.0	45.4	26.9 N	61.3 E	38.3 S	I	R
6	2	3.4	53.7	1.7023	321.7	62.2	43.5 N	111.3 E	9.7 N	III	?R
Lake Kanunka											
43	3	5.7	33.9	2.6480	337.1	-51.7	32.3 S	65.3 E	69.9 N	I	N
44	9	5.3	20.3	7.4788	348.2	-71.7	56.5 S	125.0 E	60.6 N	I	N
45	9	2.6	28.9	5.9306	6.3	-59.4	40.2 S	160.3 E	77.1 N	I	N
46	8	1.2	45.2	1.9933	300.6	23.4	12.2 N	75.0 E	19.7 N	V	I
47	5	5.7	26.2	4.2968	31.6	-48.8	29.7 S	217.7 E	62.4 N	I	N
119	7	73.2	6.2	6.9180	179.2	33.1	18.1 N	142.5 E	79.6 S	I	R
Tirari/Formation Means, statistically significant ("Class I") sites only											
	8	25.0	9.9	7.7204	348.6	-55.2	35.7 S	91.2 E	77.1 N		N
	10	10.5	13.7	9.1459	184.1	42.9	24.9 N	77.9 E	85.7 S		R

value; mean paleoposition oriented as expected for normal or reversed polarity;

Class III - not statistically significant, two of three or three of four samples, however, consistent, and the remaining sample(s) divergent; polarity assigned from non-divergent samples;

Class IV - statistically significant or not, with sample paleopositions apparently consistently oriented in anomalous directions (e.g., south-seeking declinations and negative inclinations), or "intermediate" directions, not fully normal or reversed polarities. These sites possibly reflect

tracking of intermediate geomagnetic field positions, but are considered more likely to be the result of unsuccessful magnetic cleaning;

Class V - not statistically significant, with wide scatter of sample positions, reflecting no interpretable pattern of orientation, or magnetically unstable samples; polarity indeterminate.

Following this classification, the polarity of sites in Table 2 are concluded to fall in one of four categories: statistically significant normal (N); statistically significant reversed (R); tentatively reversed (?R); or indeterminate (I). Indetermi-

nate (Class V) sites were excluded from further consideration. All normal sites were Class I, and their samples gave consistently normal orientations, indicating that discernible, high-coercivity (stable) reversed overprint is not a major component of NRM. In contrast, cleaned samples of sites in Classes II-IV did not give normal orientations, but rather consistently reversed, scattered reversed, or incompletely reversed directions. Polarity assessment of these latter sites indicates that they are probably reversed, although affected by incomplete magnetic cleaning or introduction of spurious signals in weakly magnetized samples.

Summary means for all normal and the reversed sites for the Tirari Formation as a whole are included at the end of Table 2, based only on statistically significant means (Class 1 sites), and plotted in Figure 6C.

Paleomagnetic Stratigraphy. Paleomagnetic stratigraphy is indicated in Figure 3, expressed as tracking of Virtual Geomagnetic Pole (VGP) latitude and in Figure 7, as inferred normal (solid symbol) and reversed intervals. Accepting the tentative use of all but Class V sites, the main

body of the Tirari Formation at the Toolapinna reference section indicates the presence of four magnetozones, with most of the upper part of the sampled section of reversed polarity. The Keekalanna section is uniformly reversed, which is consistent with its lithologic correlation with the upper part of the Toolapinna section. On this basis, the Keekalanna results help to confirm the uniformly reversed character of the upper Toolapinna section, although we do not have the coverage we would prefer in the sandy 7 to 9m zone of the Toolapinna reference section. The main body of the Tirari Formation at the Lake Palankarina type section is also uniformly reversed. In contrast, the main body of the Tirari Formation at the Kanunka section is uniformly normal. The Pompapillina Member is uniformly of reversed polarity at all localities where it has been determined.

An indication of the reliability of the 1 m sampling interval is provided by the combined results from the Toolapinna and Keekalanna sections. Vertical site density is closer to twice the normal in the 5 to 6 m (main body) and 11 to 13 m (Pompapillina Member) ranges. Were the

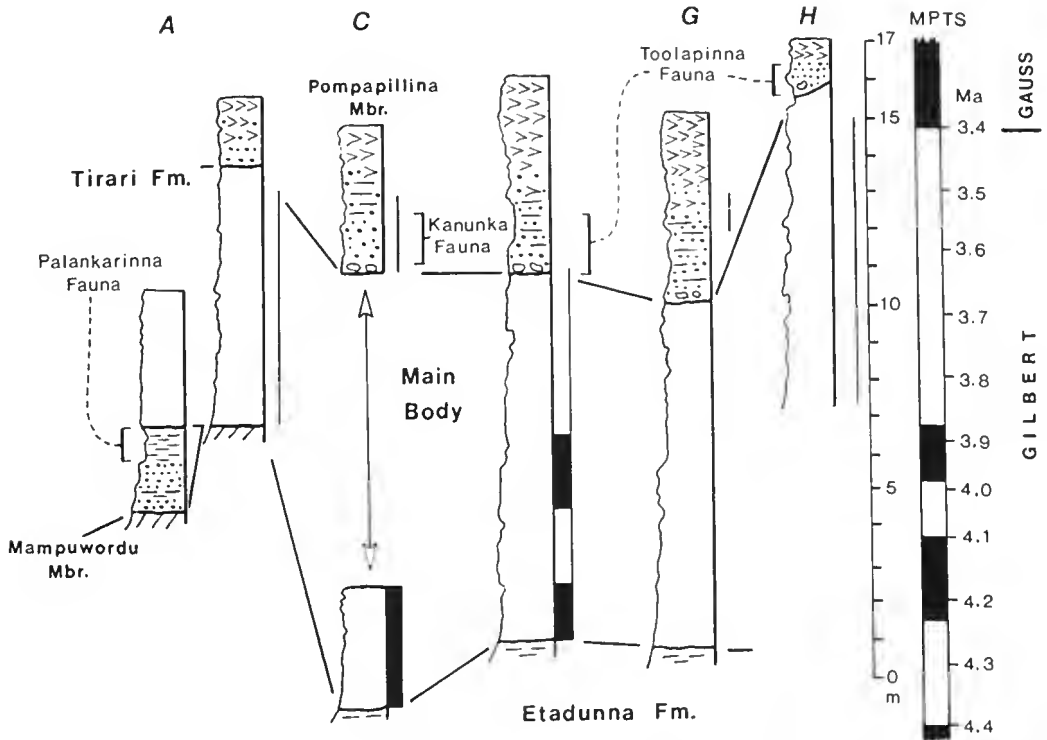


Fig. 7. Summary of litho-, magneto- and biostratigraphy depicted by a simplification of Fig. 2, adding stratigraphic position of fossil vertebrate assemblages discussed in the text. Magnetostratigraphy summarized to right of each lithological column (black indicates normal polarity), and favored correlation to the Magnetic Polarity timescale (MPS) indicated.

Tirari postulated to represent substantially more geologic time than we currently envisage, and our usual sampling interval were so broad as to detect only a fraction of polarity intervals actually recorded in the section, these two intervals might be expected to document more magnetic events. Such a pattern is not observed for either member of the Tirari formation, suggesting that our sampling interval is appropriate for the sedimentation rate(s) of these deposits, and therefore the amount of geologic time represented by the units.

The broad picture of this polarity stratigraphy is unchanged, albeit with considerably less resolution, with the exclusion of all sites which are not statistically significant. The primary magnetostratigraphic information indicated by inclusion of the additional sites in classes II-IV is the resolution of an additional reversed magnetozone in the lower part of the Toolapinna section (Sites 4 and 5), which implies greater time represented by the Tirari Formation in this reference section.

BIOSTRATIGRAPHY

When defined in 1961, the Tirari Formation was thought to be unfossiliferous, but as regional stratigraphic evidence began to build, it was recognized that the referred "Katipiri Sand" at Lake Kanunka should be referred to the Tirari Formation (Woodburne *et al.* 1985) as part of the plexus of stream channel-fills (now the Pompapillina Member) in the upper part of that unit at most other outcrops in the Tirari Desert. Although it could not be distinguished lithologically from Pleistocene channel-fills (Kujitara and Katipiri), it was everywhere involved in the episode of intensive groundwater gypsum cementation that typified the oldest gypcrete in the Lake Eyre Basin.

We have also incorporated the "Mampuwordu Sand" of Stirton, Tedford and Miller (1961) into the Tirari Formation as the basal member. These are local stream deposits filling shallow valleys at the base of the formation near the southern margin of the Lake Eyre Basin.

In the 1980s we discovered *in situ* fossil remains in the Tirari Formation along the lower Warburton River. Rare post-cranial elements of medium-sized macropodids were found in the upper part of the gypsiferous mudstones in the main body of the Tirari Formation and in the base of the uppermost gypsum sand beneath the

Pompapillina Member, but the majority of the remains were taken from the basal part of the Pompapillina Member at Toolapinna Waterhole, and from outcrops south of Camel Swamp Yard and east of Keekalanna Soakage. These local faunas from correlative stratigraphic positions have been united as the Toolapinna Fauna.

Palankarinna Fauna. The Palankarinna Fauna was obtained from the Mampuwordu Member at the base of the Tirari Formation. It was the first Tirari age fauna known and the only one completely described. The local fauna of the Woodard Quarry at Lake Palankarinna supplied the first sample, described by Stirton in 1955. Discovery of the Lawson-Daily Quarry in 1957, the Keane Quarry in 1962, and Mullet Locality in 1971 provided further local faunas, each different in composition or abundance. The Woodard Quarry yielded mostly *Prionotemnus* Stirton and the diprotodontine *Meniscoplus* Stirton, the Keane Quarry nearly exclusively *Zygomaturus* Meleay without other vertebrates, the Mullet Locality, near the Keane Quarry, yielded *Zygomaturus* and *Prionotemnus* whereas the Lawson-Daily Quarry had both diprotodontid genera plus ratite birds and abundant *Prionotemnus*. The Palankarinna Fauna as a whole is very limited in taxonomic diversity although rich in individuals of the forms present. Only the *Zygomaturus* from the later excavations was described (Stirton 1967). The large sample of *Prionotemnus palankarinnicus* Stirton now available at the University of California Museum of Paleontology (UCMP) would allow fuller description of the morphology of this otherwise rare macropodine. The holotypes of these species reside in the South Australian Museum (SAM).

The Palankarinna Fauna includes the following.

Pisces. Lungfish dental plates and disarticulated remains of unidentified teleost fish were found at the Woodard and Lawson-Daily Quarries.

Reptilia. Chelonia: Unidentified turtle remains are recorded from the Woodard Quarry (Stirton 1955).

Crocodylidae: Crocodile teeth are well represented at all sites. A right maxilla (UCMP 113956) and isolated teeth represents a ziphodont crocodylian thought to be either a eusuchian or sebecosuchian (Hecht and Archer 1977). Teeth of *Crocodylus* Gmelin are also present.

Aves. Two ratites are present, an extinct emu *Dromaius ocybus* Miller, 1963b, represented by a tibiotarsus and a dromornithid recorded by a

fragment of a synsacrum (UCMP 60613) identified by Miller (1963b) as *Genyornis* sp. (see comments in Rich, 1979:56). No other bird remains are recorded.

Mammalia. Peramelidae: The holotype and only known specimen of the extinct bilby *Ischnodon australis* Stirton, 1955, was collected at the Woodard Quarry.

Diprotodontidae: Stirton (1955) initially described the diprotodontine *Meniscolophus mawsoni* Stirton from the Woodard Quarry. This taxon is also the most abundant diprotodont in the Lawson-Daily Quarry, but it is rare in the Keane Quarry where *Zygomaturus keanei* Stirton, 1967, is the dominant form. *Zygomaturus keani* occurs at all the sites. Stirton (1967) described, but did not name, a smaller *Zygomaturus* from the Lawson-Daily Quarry that he thought was significantly different from *Z. keanei*.

Macropodidae: In all of the Palankarinna sites with macropodids, *Prionotemnus palankarinnicus* Stirton, 1955, is dominant.

There is evidence for two other taxa. A medium-sized sthenurine, possibly *Simosthenurus* Tedford, is represented by a lower incisor with typical short and deep crown (UCMP 45420) and a lumbar vertebra (57086). A larger macropodine, possibly *Protemnodon* Owen, is represented by a tibia (UCMP 57195) and an ulna (60909) of comparable size. These fragments give evidence of a more diverse fauna, including some of the larger kangaroo genera that occur in other Pliocene and Pleistocene sites.

Kanunka Fauna. This collection was obtained from the lower part of the fill of a single stream channel that crops out along a salient and associated isolated hill ("SAM Hill") in the north-western part of the dissected escarpment bordering the Lake Kanunka saltpan. This channel trends to the north-west and cuts through the lower Tirari Formation and into the top of the Etadunna formation. It has the stratigraphic, lithologic and diagenetic features of the Pompapillina Member of the Tirari Formation as seen at other sites, the only difference being the Tirari red-brown mudstones are thinner here than elsewhere, presumably because Lake Kanunka is nearer the basin margin.

The Kanunka Fauna was obtained mostly from Stirton Quarry on the escarpment salient, but also from prospect pits around SAM Hill and from float on the Etadunna Formation beneath these outcrops. The fauna is taxonomically diverse, but nearly all the remains are fragmentary,

as typical of an energetic fluvial environment, the holotype ramus of *Troposodon keuti* being one of the more complete specimens. The major collection from these sites resides at the Museum of Paleontology, University of California, Berkeley, but a few specimens are contained in the American Museum of Natural History, New York, the Australian Museum and Zoology Department of the University of New South Wales, Sydney and the South Australian Museum Type specimens are housed in the South Australian Museum, Adelaide.

The Kanunka Fauna contains:

Pisces. Lungfish dental plates and isolated teleost remains of unidentified species are abundantly present. Some teleost vertebrae imply the presence of large fish.

Reptilia. Chelonia: Gaffney (1981) described and figured chelid shell fragments that are part of the Kanunka Fauna.

Squamata: Hecht (1975) recorded the presence of *Megalania* Owen in the Kanunka Fauna.

Crocodylia: Isolated crocodile remains are abundant at the Kanunka sites, and most pertain to *Crocodylus* sp.

Aves. In addition to remains referable to the living emu, *Dromaius novaehollandiae* (Latham), described by Patterson and Rich (1987), Rich *et al.* (1982) record a diverse assemblage of water birds. Pelicans are represented by remains of the living *Pelecanus conspicillatus* Temminck and the extinct *P. cadimurka* Rich and Van Tets, 1981, and the anhingas by the extinct *Anhinga novaehollandiae* Miller, 1966. Rich *et al.* (1987) record three flamingos: one close to the living Greater Flamingo, *Phoenicopterus ruber* Linnaeus; an extinct form, *Xenorhynchopsis minor* (DeVis, 1905), similar in size to the living Lesser Flamingo, and a smaller extinct species *Ocyplanus proeses* (DeVis, 1905) with which Miller's (1963) *Phoeniconaias gracilis* can be equated. Other waterbirds include representatives of Ciconiidae, Ardeidae, Anatidae, and Gruidae (*Grus* sp.). The Rallidae, Otidae and passeriform birds are also represented. A giant eagle (*Aquila* Briss. sp.), larger than the living wedge-tail, is also present.

Mammalia, Marsupialia. Dasyuridae: At least two species are represented by fragmentary material. Two maxillary fragments (UCMP 56900), edentulous except for the last molar, are the size of the largest *Dasyurus* Goffroy. A right ramus with canine, P_{1,3} alveoli and well worn M_{1,4} (UCMP 60800) is the size of *Dasyercus*

cristacauda (Kreffit), but retains a P_1 crowded against the outside of the canine.

Vombatidae: Wombats are represented by three isolated teeth from Lake Kanunka, but at nearby Lake Pitikanta a palate of a large wombat was collected from the Pompapillina Member. The latter specimen is under study by Eric Wilkinson. The Kanunka teeth indicate the presence of *Phascolonus* Owen and a small wombat comparable to living forms.

Diprotodontidae: In contrast to other Tirari Formation sites, the Lake Kanunka locality produced few identifiable diprotodontid remains. Despite statements to the contrary in Stirton, Tedford and Miller (1961), *Diprotodou* sp. is represented by three incisor teeth: the tip of a lower incisor (UCMP 60810), a left I^3 (in the University of N.S.W. collection) and a right I^2 (UCMP 56916) all of which are well worn and could represent a single individual. *Zygomaturus* sp. (not *Euowenia* fide Stirton, Tedford and Miller, 1961) is represented by an unerupted left M^4 (UCMP 56917) and the posterior part of a lower molar (probably M_3 , UCMP 56918). These teeth are similar in size to *Z. keanei* although perhaps a little higher-crowned. There are fragments of the teeth of other, smaller, diprotodontines, but none is complete enough to verify the occurrence of *Euryzygoma* or other forms.

Thylacoleonidae: *Thylacoleo* sp. is represented by an isolated M^1 .

Macropodoidea: This is the most abundantly represented group, but specimens complete enough for identification are rare among the many isolated and broken teeth and post-erianal remains.

Potoroidae: *Bettongia* Quoy and Gaimard is represented by a new species similar in size to *B. leseur* Quoy and Gaimard but with bicuspid M_4 talonid, narrower molars, narrower and more recumbent ascending ramus. A right ramus (UCMP 56902) and right maxillary (UCMP 56915) pertain to this taxon. A larger potoroid is indicated by an isolated left M_4 about twice the length of the same tooth of *Bettongia*.

Maeropodinae: Smaller macropodine remains are more abundant than larger ones, and the group as a whole has a significant Kanunka representation.

One of the surprises in the Kanunka collection is a right maxillary fragment (AMNH field number SIAM 70) with the posterior alveolus for P^3 , the roots of M^1 , M^2 with labial face broken

away and M^3 with only the anterolabial part of the anterior cingulum preserved. The M^2 corresponds morphologically to that of *Deudrolagus* Muller and it is only about 10% larger than "cf. *Deudrolagus* sp. 2" from the Bow Fauna of northeastern New South Wales (Flannery and Archer 1984) and about twice the size of species of the living genus. A large dendrolagine, *Bohra paulae* Flannery and Szalay 1982, has been described from postcranial elements from the Wellington Caves, but no teeth referable to this taxon have been identified. The Kanunka and Bow fragments indicate that large tree kangaroos were also present in the Pliocene of Australia.

Two species of *Lagorchestes* Gould are present, the smaller is the most completely represented by a right ramus of an old individual with complete cheek tooth dentition (UCMP 60809) appears to be a new form about the size of *L. leporides* Gould. The larger form is represented by two jaw fragments (UCMP 56922 and unnumbered) that show $M_{1,2}$, M_3 erupting and dP_3 - M_1 respectively. This taxon is slightly larger than living *L. conspicillatus* Gould.

Two species of genus *Protenuodou* are present. The best represented is a small species closely similar in size and morphology to *P. devisi* Bartholomai, 1973a. A nearly complete left ramus (UCMP 56894) allows full comparison with topotypes. Fragmentary maxillae, teeth and metapodials of appropriate size can also be referred to this form. There is also a larger species indicated by an isolated M_4 (UCMP 56904) the size and crown height of *P. brehus* Owen.

The presence of *Priodontemnus* is suggested by fragmentary material, none of which show the diagnostic dP_3 . Among the most likely remains is a left ramal fragment with M_1 , M_2 erupting (UCMP 129197) which differs from topotypic *P. palaukarinunicus* in slightly greater tooth dimensions, height of crown and wider anterior cingulum, but is otherwise morphologically similar to the topotypic sample. An isolated M_4 is within the dimensions of *P. palaukarinunicus*.

Another left-ramal fragment with broken M_1 and erupted little worn M_2 (UCMP 56912) is the size of *Kurrabi mahoueyi* Flannery and Archer with which it agrees in morphology particularly in replacement of the posterior cingulum by a pit on M_2 .

A small wallaby is represented by several ramal and maxillary fragments. Although not demonstrably conspecific, they all agree best in

morphology and size with species of the pademelon *Thylogale* Gray, especially with *T. stigmatica* (Gould) which has relatively large upper and lower third premolars.

Larger macropodines are very rare in the Kanunka collections. Flannery and Archer (1982) report the occurrence of *Macropus* (*Macropus*) *pearsoni* (Bartholomai, 1973b) collected by the University of New South Wales from the type locality (AM F 64000). There is also a smaller *Macropus*, represented by a left ramus with lower incisor, P_3 , dP_3 , $M_{1,2}$, M_3 unerupted (UCMP 60777) that closely matches *M. (M.) woodsi* Bartholomai, 1975, in size and morphology. The lower incisor in this specimen shows the long crown and extensive distribution of enamel onto the ventrolabial face that Dawson and Flannery (1985) held diagnostic of *Macropus* (*Macropus*) species. Isolated upper molars, designated paratypes of *Troposodon kenti* Campbell, by Campbell (1973), UCMP 56907 and 60825, are also referable to *M. (M.) woodsi*.

Sthenurinae: Relatively primitive sthenurines are present in the Kanunka fauna including two species of *Troposodon* Owen, and a new genus. Campbell (1973) based *Troposodon kenti*, the largest known species of the genus, on the holotype left ramus (SAM P14507) and a group of isolated teeth as paratypes, some of which pertain to other taxa (*Macropus* and *Protemnodon* Owen). There is another, smaller, species in the Kanunka Fauna close to *T. bowensis* Flannery and Archer in size and morphology. This is most completely represented by a fragment of a right ramus with broken dP_3 and complete $M_{1,2}$ (UCMP 60747) that shows this species to be a small low-crowned form whose molars have posterior cinguli.

A new sthenurine genus is present, almost the size of *Sthenurus tindalei* Tedford with a short (equal to length of M_1) P_3 blade, lacking posterolabial crest, whose posterior end turns lingually like *Troposodon*. The high-crowned lower molars have rectilinear lophids like *Sthenurus* Owen, but they lack the premetacristid characteristic of *Troposodon*, the links are more sharply defined than in *Sthenurus* and the anterior lophid surfaces lack crenulations. There is a mandibular foramen characteristic of *Sthenurus* and *Procoptodon* Owen.

A right maxillary fragment (UCMP 56928) with $M^{1,2}$ alveoli and a complete high-crowned M^3 more clearly represents a large *Sthenurus*, about the size of *S. tindalei*.

Additional tooth and limb-bone fragments indicate that there are other sthenurines in the Kanunka fauna, but none can be clearly identified as either *Sthenurus* or *Procoptodon*.

Mammalia, Eutheria, Rodentia, Muridae: There are several isolated incisors, permineralized reddish-tan like the larger mammal material so there is no doubt about the presence of rodents in the Kanunka Fauna. Two specimens represent different taxa. A fragment of a right ramus with $M_{1,2}$ (UCMP 60781) represents a small conulurine and a right M_1 pertains to a larger member of this group.

Toolapinna Fauna. This composite is assembled from local faunas collected from the vicinity of Toolapinna Waterhole, and from outcrops near Camel Swamp Yard and Keekalanna Soakage along the lower reach of the Warburton River. All of these sites occur in the upper fluvial deposits of the Tirari Formation, the Pompapillina Member. As is typical of fluvial environments, the fossil remains are very fragmentary and relatively rare in these deposits resulting in a lower diversity of taxa and uncertainties in taxonomic assignment. All the collections are part of the South Australian Museum holdings.

Lower Vertebrates. Unidentified fish, turtle, crocodile and bird remains were collected at these sites.

Mammalia, Marsupialia, Diprotodontidae: Remains of *Euryzygoma* sp. are the most abundant diprotodontid in the Toolapinna Fauna. This is a larger form than *E. duiense* (De Vis) (especially in the dimensions of the posterior molars) but not as large as the teeth in the Bluff Downs cranium (Archer and Wade 1976, plate 58). *Zygomaturus* is also represented by single specimen, a badly weathered skeleton that had been mired in Tirari red claystone near Keekalanna. The lower cheek teeth indicate a form larger and proportionately different from *Z. keani*, and closer to *Z. victoriae* (Owen) or *Z. trilobus* Mcleay. Fragments of teeth suggest other, smaller, diprotodontids in this fauna, but not *Diprotodon* Owen.

Palorchestidae: Fragments of associated lower molars (SAM P 250437) indicate the presence of *Palorchestes* cf. *azeal*.

Vombatidae (?): A broad upper incisor fragment, with flattened, enamel-covered anterior surface and broadly grooved posterior surface may represent a *Plascolonus*-like large wombat.

Potoroidae: A right ramus with broken P_3 and

M_{1,3} complete and the incisor base (SAM P 250500) appears to represent a new genus with short (about as long as length M₁), ungrooved premolar. *Bettongia*-like molars (lower crowned than in living species of that genus), and very long crowned lower incisor whose enamel reaches nearly to the open root beneath M₂.

Macropodidae: Macropodinae: There are a number of fragmentary remains that represent small macropodines of uncertain generic reference. Large macropodines are best represented by metatarsals that indicate *Protemnodon* as large as *P. brehus*, and large *Macropus* (*Macropus*) cf. *titan* or *ferragus* are present. A short fifth metatarsal (SAM P 250487), with laterally curved slender shaft (79 mm in length), lacks the strong plantar process of *Protemnodon* and resembles *Dendrolagus*. A similar short fourth metatarsal (SAM P 250486) could represent the same form.

Sthenurinae: An edentulous fragment of a left ramus (SAM P 25048) indicates a species of *Sthenurus* about the size of *S. tindalei* with mandibular features of that specific taxon. There is another sthenurine represented by a left maxillary fragment with dP³, M¹⁻³ (SAM P 25504) that is similar in size to *Troposodon minor* (Owen), but differs in a number of significant ways: the presence of a forelink, well developed pre- and, particularly, post-paracristae, strong midlink, a premetacrista, distally tapering lophs, and a large, wide P³ indicated by its crypt. In these features this apparently new taxon resembles *Procoptodon* and the new sthenurine.

DISCUSSION

Geological history. Widely scattered outcrops and limited subsurface information hinder reconstruction of the areal extent and regional sedimentology of the Tirari Formation. However, the consistent stratigraphy throughout the Tirari Desert does facilitate lithological correlation and subdivision of the unit into a basal channel filling member (Mampuwordu Member, only at Lake Palankarinna) developed in a higher gradient basin margin setting, passing upward and presumably laterally into red-brown gypsiferous mudstones characteristic of the main body of the Tirari Formation which in turn is truncated by a widespread fluvial unit (Pompapillina Member) that includes nested channel-fills and overbank red mudstone facies.

About two-thirds of Tirari deposition took place in an evaporitic environment of predominantly fine-grained clastic supply, the largest grains being reworked authigenic gypsum seed-crystals. The indications are that the depositional setting was a broad shallow basin in an arid climate with ephemeral saline lake(s) and marginal mud flats at, or just above, groundwater level.

A major change in sedimentary environment to widespread fluvial deposition is implied by the Pompapillina Member which represents a return to more mesic conditions and a higher watertable during deposition of the final third of the thickness of the Tirari Formation. In basin marginal settings, such as at Lake Kanunka, relatively deep dissection preceded deposition of the Pompapillina stream deposits. At all other sites this contact is also a disconformity, suggesting a hiatus of unknown magnitude that preceded the introduction of quartz sand-filled channels that blanketed all older rocks.

The depocenter for the Tirari Formation was evidently in the southern Simpson Desert as indicated by thickness increases in that direction and limited observations of directional sedimentary structures. The uplifts of Paleogene and Cretaceous rocks now followed by the Birdsville Track formed the eastern basin margin and provided centripetal drainage.

At the close of Tirari deposition the climate returned to at least seasonal aridity. The saline groundwater level remained high in the basin, eventually precipitating the gypcrete carapace that indurated the upper part of the Pompapillina Member.

Vertebrate history. Three faunas have been described from fluvial sands of the Tirari Formation. The oldest is the Palankarinna Fauna from the basal Mampuwordu Member at Lake Palankarinna, and the youngest are both from the Pompapillina Member, the Kanunka Fauna at Lake Kanunka, and the newly recognized Toolapinna Fauna from the Warburton River (Fig. 7). Remarkably, these faunas share few taxa, each has its own characteristic composition, and dominance of certain forms. The Palankarinna Fauna is particularly noteworthy in this regard, as it is represented by a large collection of relatively well preserved remains yet it is composed essentially of species of three mammalian genera, the diprotodontids *Zygomaturus* and *Meniscolophus* and the macropodid *Prionotemnus*. The taphonomic factors leading to such narrow samples of the biota

in a fluvial setting are perplexing, but could reflect an arid environment with limited resources. The Mampuwordu Member does contain aquatic vertebrates including teleost fish and lungfish indicating freshwater environments of deposition for these fluvial deposits, but distally these channels are very likely interbedded with red mudstones and they are succeeded vertically by gypsiferous red mudstones. Such facies relationships indicate an evaporative environment in which saline surface waters became widespread, suggesting climatic conditions that may have limited many Pliocene mammals. Bones of any kind, including those of aquatic vertebrates, are rare in the main body of the Tirari Formation.

The widespread fluvial environment of the Pompapillina Member contains abundant aquatic vertebrates and more diverse mammal faunas than the Mampuwordu Member. These facts imply a major interval of high water table and mesic environments followed the arid interval in which the main body of the Tirari Formation was deposited. The Kanunka Fauna shares *Zygomaturus* and *Prionotemnus* with the Palankarina Fauna. The Toolapinna Fauna, less diverse taxonomically because it is a smaller

sample, is dominated by remains of the diprotodontid *Euryzygoma* with rare *Zygomaturus*.

These striking compositional differences make comparison among the younger Tirari faunas difficult, but they do not refute the lithological correlations that arrange them in relative temporal order. The occurrences and phylogenetic relationships of the diprotodontids provide stage-in-evolution correlations. The three diprotodontines have relative stratigraphic occurrences that agree with their cladistic relationships, namely *Meniscophus* as the sister taxon of *Euryzygoma* and *Diprotodon*. The coeval occurrence of *Euryzygoma* and *Diprotodon* is also predicted by this phyletic relationship. The species of *Zygomaturus* also show change from *Z. keani* and the relatively primitive *Z. sp.* at Palankarina, to forms more like *Z. trilobus* or *Z. victoriae* in the youngest part of the Tirari.

Comparison with eastern Australian Pliocene faunas containing a diverse large marsupial component, such as Bluff Downs, Chinchilla and Bow, shows considerable similarity at the generic level. There are also some important alliances at the specific level, particularly when the central Australian material permits such identi-

Table 3. Occurrences of Pliocene vombatoid and macropodoid marsupials: "*" denotes the type locality of the species.

	Palankarina	Kanunka Toolapinna	Bluff Downs	Chinchilla	Bow
PALORCHESTIDAE					
<i>Palorchestes</i>	-	cf. <i>azeal</i>	-	<i>parvus</i>	<i>parvus</i>
DIPROTODONTIDAE					
<i>Euowenia</i>	-	-	cf. <i>grata</i>	<i>grata</i> *	?
<i>Meniscophus</i>	<i>mawsoni</i> *	-	-	-	?
<i>Euryzygoma</i>	-	sp. large	cf. <i>dunense</i> , sp. large	<i>dunense</i> *	?
<i>Diprotodon</i>	-	sp.	-	cf. <i>optatum</i>	?
<i>Zygomaturus</i>	<i>keani</i> *	cf. <i>trilobus</i>	cf. <i>trilobus</i>	cf. <i>trilobus</i>	?
MACROPODIDAE					
<i>Lagorchestes</i>	-	n. sp., sp.	-	-	-
<i>Thylagale</i>	-	sp.	-	-	-
<i>Prionotemnus</i>	<i>palankarinnicus</i> *	cf. <i>palankarinnicus</i>	-	<i>palankarinnicus</i>	-
<i>Kurrabi</i>	-	cf. <i>mahoneyi</i>	-	-	<i>mahoneyi</i> *, <i>merrivuanensis</i> *, <i>chinchillaensis</i>
<i>Protemnodon</i>	?	<i>devisi</i> , sp.	<i>snewini</i>	<i>devisi</i> *, <i>chinchillaensis</i> *	-
<i>Macropus (M.)</i>	-	<i>pearsoni</i> , <i>woodsii</i>	-	<i>pan</i> *, <i>woodsii</i> *	-
<i>Macropus (O.)</i>	-	-	<i>pavana</i> *	-	<i>pavana</i>
<i>Macropus</i>	-	sp.	<i>naranda</i> *, cf. <i>dryas</i>	<i>dryas</i> *	<i>dryas</i>
<i>Dendrolagus</i>	-	cf.	-	?	cf.
<i>Troposodon</i>	-	<i>kenti</i> *, cf. <i>bowensis</i>	<i>bluffensis</i> *, <i>minor</i>	<i>minor</i> , <i>kenti</i>	<i>bowensis</i> *
<i>Sthenurus</i>	-	sp.	sp.	<i>notabilis</i> *	-
<i>Simosthenurus</i>	?	-	-	<i>antiquus</i> *	sp.

fication (Table 3). *Prionotemnus palankarinnicus* has been identified at Chinchilla (*vide* Bartholomai, 1975), but the Chinchilla diprotodontines *Euryzygoma* and *Diprotodon* are more derived than *Meniscoplus*, and the *Zygomaturus* is larger than *Z. keani* and more like the Toolapinna form, suggesting that Palankarina is older than Chinchilla.

Diprotodon does occur at Chinchilla, as Woods (1962) and Stirton (in Stirton *et al.* 1968) believed. It is represented by a large mandible, the size of *D. optatum* (QM F 5580) collected at Chinchilla by K. Broadbent on 2 Feb. 1887 (data written on specimen). There is another mandible, QM F 10293, with Chinchilla preservation but without provenance data. Woods' (1960:396) geological study of the Chinchilla area found no evidence of fossils in the younger terraces incised into the Chinchilla Sand.

The combined diprotodontid fauna of Toolapinna and Kanunka strongly resembles that of Chinchilla. The Bluff Downs Fauna also contains *Zygomaturus* sp. and a large *Euryzygoma* sp. in addition to *Enowena* cf. *grata* ("Nototheriinae, genus indet." of Archer and Wade 1976), the latter shared with Chinchilla but not recognized in central Australia. The Bow diprotodontids have not yet been identified but apparently both diprotodontines and zygomaturines are present.

Comparison of the macropodids again reveals the greatest similarity with Chinchilla at the generic level (Table 3) and some specific similarities of the combined Toolapinna and Kanunka assemblages, particularly *Prionotemnus palankarinnicus*, *Protemnodon devisi*, *Macropus* (*M.*) *woodsii*, and *Troposodon kenti*. There is less similarity with the Bluff Downs and Bow Faunas which may be older assemblages than Chinchilla as concluded by Archer and Wade (1976).

Geochronology. Having established the relative age relationships and correlations of the Tirari faunas with assemblages in eastern Australia, we are in a position to calibrate this succession using geochronological information derived from isotope dating and magnetostratigraphy.

The age of the Bluff Downs Fauna is constrained by radioisotopic ages on the overlying Allensleigh basalt. Whole rock dates range from 4.1-4.6 Ma based on samples from different parts of the outcrop but these may not be significantly different from one another. Archer and Wade (1976) believed the minimum age for the basalt

was 4.00 ± 0.12 Ma based on standard error estimates. The occurrence of murid rodent remains at Bluff Downs and not at Hamilton where the fauna lies beneath basalt flows of 4.47 Ma suggest that 4.0 Ma maybe a minimum estimate for the Bluff Downs Fauna as well as the first occurrence of rodents in Australia.

Additional data bearing on the calibration of the Kanunka and Chinchilla faunas can be determined from the paleomagnetic signature of the Tirari Formation. As discussed above, the Tirari Formation falls within a predominantly reversely magnetized interval that is paleontologically constrained to represent the later part of the early Pliocene Gilbert Chron. Placement within the Gilbert (Fig. 7) is limited by the occurrence of rodents in the Pompapillina Member which constrain the maximum age for the long reversed interval in the upper part of the Tirari Formation to be 3.9 Ma and a minimum age to be 3.4 Ma at the end of the Gilbert (Fig. 7). The age of the base of the Tirari Formation is more problematic depending on the span of the hiatus beneath the Pompapillina Member. If this is short at the 10^5 yr scale then the normal events at the base of the Tirari Formation in the Warburton outcrops probably represent the normally polarized subchrons in mid-Gilbert, but if 10^6 yr or greater, Chron 5 or older normal intervals might be indicated. In this synthesis we have chosen the former alternative and thus correlate the long reversed interval containing the Pompapillina Member to the late part of the Gilbert Chron. The Mampuwordu Member, one site at the top of which is apparently reversed, would lie near the beginning of this interval, the Pompapillina toward the end. This calibration does no violence to the paleontological relationships and, although the data does not constrain it as much as we would prefer, we accept it as a working hypothesis.

In conclusion, the geochronological age of the Tirari Formation outcrops seems most parsimoniously attributed to the late Gilbert Chron when all the evidence both paleontological and physical is considered. In this hypothesis the Mampuwordu Member with its Palankarina Fauna would be approximately 3.9 Ma, the Pompapillina Member with the Kanunka and Toolapinna faunas would be approximately 3.4 Ma. At a minimum these faunal levels are separated by about 0.5 Ma, probably sufficient time to account for the biological changes implied in the comparisons made among them.

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CONTINUITY AND CONTRAST IN MIDDLE AND LATE MIOCENE VERTEBRATE COMMUNITIES FROM THE NORTHERN TERRITORY.

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ABSTRACT

Comparisons of the the late Miocene Alcoota Local Fauna and the middle Miocene Bullock Creek Local Fauna reveal fundamental similarities in faunal composition and in the structure of the terrestrial component of their respective communities. The Bullock Creek palaeocommunity contains an abundance of aquatic and stream-bank species. Few aquatic species are present in the Alcoota palaeocommunity. The taxonomic succession is predominantly at the level of generic rank. The temporal succession by closely related ecomorphic species suggests continued integrity of the basic community structure. The Alcoota LF expresses an increase in species diversity and an increase in the body sizes of diprotodontids and macropodids that occurred during the approximately three million year long interval between the two local faunas. Biological, taphonomic and geological data indicate that both communities were intermittently subject to environmental stresses due to periods of low precipitation and high evaporation. The Bullock Creek Local Fauna shows evidence of seasonal aridity. The Alcoota Local Fauna shows evidence of one or more event-based mass mortalities due to regional drought.

KEYWORDS: Alcoota Local Fauna, Bullock Creek Local Fauna, Miocene, palaeocommunities, taphonomy, palaeoenvironment, succession.

INTRODUCTION

Since 1983, the Northern Territory Museum has been collecting vertebrate fossil material from the Alcoota Locality (22°52'S, 134°27'E), Alcoota Station, central Australia and the Bullock Creek Locality (17°7'S, 131°31'E), Camfield Station, northern Australia. Although certain Alcoota and Bullock Creek Local Fauna taxa have been widely compared on a systematic basis with related forms from other Australian Tertiary localities (e.g. Archer and Rich 1982, Murray and Megirian 1990), there have been no serious attempts to compare the whole faunas in terms of community structure, taphonomy, succession or inferred palaeoenvironments.

By way of a progress report we compare the species composition and taphonomy of the middle Miocene Bullock Creek Local Fauna (LF)

with those of the late Miocene Alcoota LF. The comparison is designed to examine the pattern of succession, the factors of mortality, the similarities and differences in community structure, the shared and contrasting palaeoenvironmental factors and the implications of the results in relation to other Australian Neogene local faunas. A brief and selective summary of the palaeontology of both localities is presented below.

Camfield locality. Fossils were discovered in the Camfield Beds at Bullock Creek by the Bureau of Mineral Resources (BMR) geologist C.G. Gatehouse in 1966 (Randal and Brown 1967, Plane and Gatehouse 1968). M.D. Plane of the BMR and associates undertook the first systematic collection, preparation and study of the Bullock Creek Local Fauna. Primary palaeontological publications resulting from BMR activities at Bullock Creek include Clemens and

Plane (1974), Rich (1979), Flannery *et al.* (1982), Smith and Plane (1985) and Murray *et al.* (1987).

Although other palaeontological parties visited the Bullock Creek fossil localities from time to time, further systematic collection recommenced with a survey by T.H. Rich (Museum of Victoria: NMV) and P.F. Murray (Northern Territory Museum: NTM), in 1983. Substantial collections of Bullock Creek material are now lodged with the BMR, NTM and NMV. The preliminary interpretations of the Bullock Creek Local Fauna presented here are based primarily on the NTM collection.

The Camfield Beds, which contain the Bullock Creek Local Fauna, consist of light coloured calcareous sandstone, siltstone and limestone with ferruginous mottling at the base and chalcidonic silification at the top (Plane and Gatehouse 1968) (Fig. 1). The most comprehensive account of the geology of the Camfield Beds is that of Randal and Brown (1967). The stratigraphy of the formation, based on a composite section measured by Randal and Brown (1967) along Bullock Creek, is shown in Figure 2.

Randal and Brown (1967:49) give the following interpretation of the environment of deposition: "The presence of algae and stromatolites indicate the sediments were deposited in shallow water. A near-shore environment is supported by fragmentation of fossil material, the conglomeratic material in the sequence, and the topographic situation of the unit. Deposition may have been in waters normally saline as indicated by the gypsum and barytes, but subject to freshwater flooding which brought in the gastropods. The environment may have been lacustrine, or associated with lagoons or estuaries frequently flooded by freshwater."

Because no marine animals are preserved in the Camfield Beds, (nor has any other organic evidence for a marine influence been identified), we interpret the presence of evaporites and lithoclastic carbonate deposits to be of non-marine origin and therefore indicative of periods of relatively dry, perhaps semi-arid, climatic conditions in the region (Megirian 1992). The inference of freshwater sedimentation producing the Camfield limestones is further supported by the abundant fish fauna which includes obli-

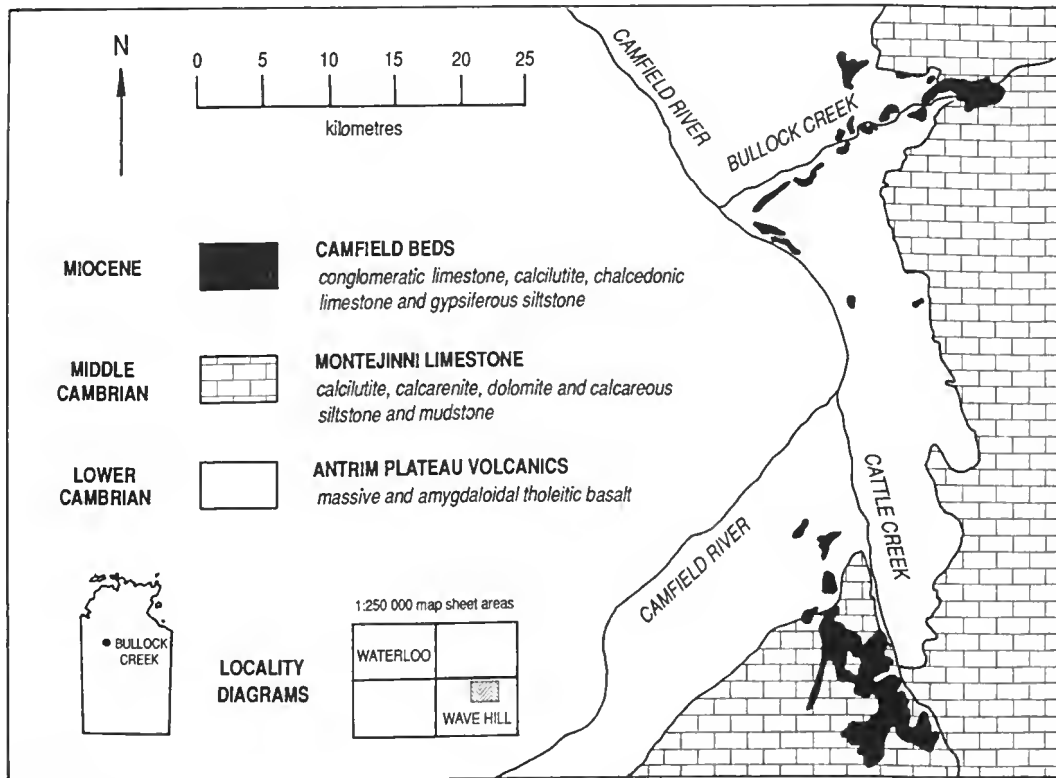


Fig. 1. Simplified geology of the Bullock Creek region showing the relationship of the Camfield Beds to basement formations and Recent drainage (after Bultitude 1973). Sweet *et al.* (1971) and Sweet (1973) identified a massive limestone cropping out in the southeastern part of the Waterloo map sheet area as Camfield Beds. No fossils are known to occur in these outcrops.

gate freshwater forms (eg. saratogas), all of which are relatively small-sized. Judging from the size of the remains, the largest teleost had a body-length of perhaps 20cm, and the largest lungfish is estimated to have been about 80cm body-length (A. Kemp, written communication). The palaeoenvironmental significance of the small size of the fish is explained below.

The NTM material was quarried from two distinct lithologies: conglomeratic limestone (Blast Site, Pebble Site, Far Site, Dromornithid Mountain, Top Site) and massive calcilutite (Site X and Site Y), interpreted to represent stream-channel and lacustrine facies respectively (Fig. 3). Siliceous pebbles and cobbles in the conglomeratic limestone are typically well-rounded, as are the limestone elasts. Some elasts in the Blast Site are composed of chalcidonic limestone in which fossil gastropods are preserved. These elasts are presumably derived from ancient weathered surfaces, suggesting that the Camfield Beds are diachronous, though no clear biostratigraphic evidence for this is available. Fragmented fossils in the conglomerates are typically sharp-edged and have not been transported far, though a few well-rounded bone fragments are also present. The latter may be reworked, indurated specimens of older age. The lithostratigraphic relationship of the quarried units is unclear; Site X and Site Y are probably within the same bed. The Blast Site is topographically low in the fossiliferous sequence (Fig. 3), but its stratigraphic relationship to other fossiliferous units is not known.

Much less material has been processed so far from the lacustrine sediments than from the conglomeratic sediments and the sample sizes are not comparable. However, there does not appear to be any significant taxonomic difference between the samples from the different lithologies, though the relative proportions of taxa vary. With the possible exception of the casuariid species, all taxa known from the calcilutites are represented in the Blast Site. The two facies appear to differ in that the calcilutites are particularly rich in fish and aquatic animals, and proportionally poor in terrestrial animals. The distribution of crocodylian taxa is compatible with this observation. The crocodyline *Harpacochampsia* Megirian, Murray and Willis, 1991, (a specialist piscivore) was found in lacustrine sediments in which *Baru* Willis, Murray and Megirian, 1990, appears to be rare, whereas in the Blast Site, *Harpacochampsia* is repre-

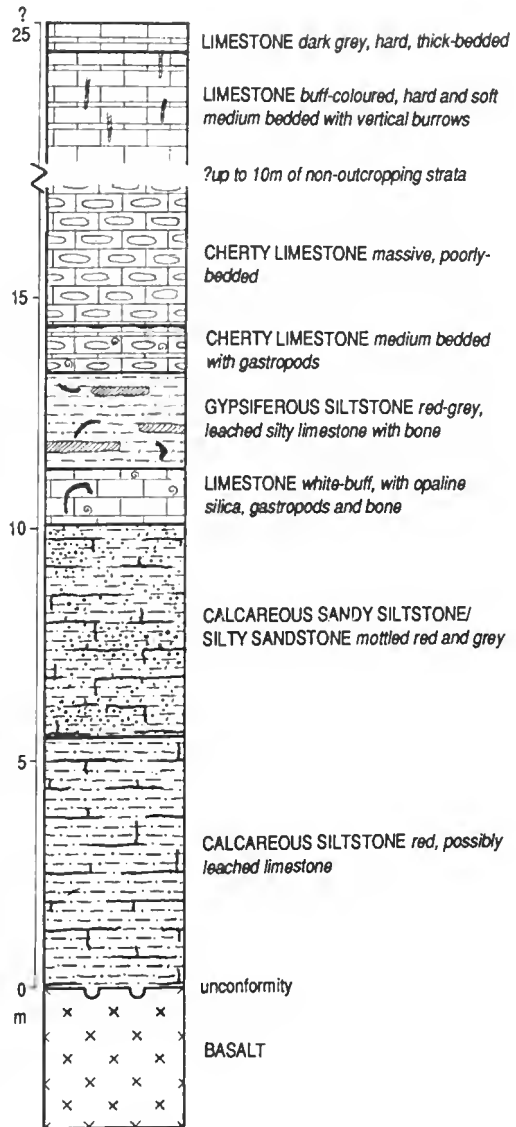


Fig. 2. Stratigraphic column of the Camfield Beds, based on a composite section measured along the Bullock Creek valley by Randal and Brown (1967:47).

sented by a single small individual found among numerous individuals of *Baru*. *Baru* was a stoutly-built, broad-snouted crocodyline with a massive dentition, and was interpreted by Willis *et al.* (1990) to be well adapted to quickly despatching large animals with its powerful bite. It may have inhabited shallow streams where dragging its prey into deep water was not an option. Excluding a few specimens of unrecorded provenance, all remains of a new species of *Quinkana* Molnar were collected at the Blast Site or from similar

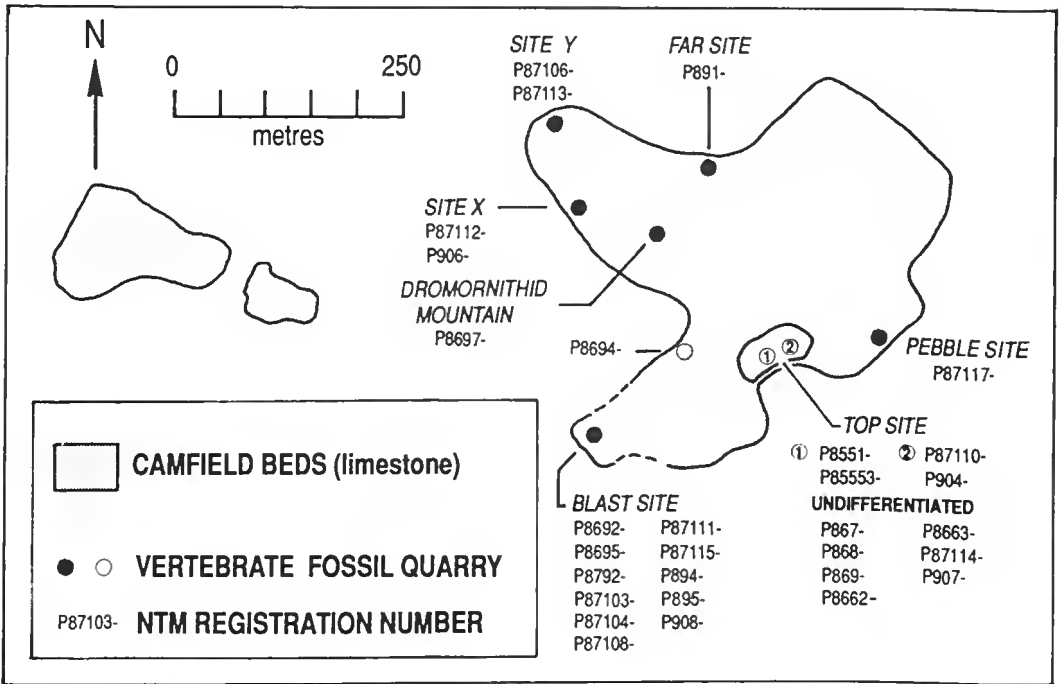


Fig. 3. Quarries worked by the Northern Territory Museum staff 1983-1989. Locality details are held on file at the Northern Territory Museum. Collections of fossiliferous limestone are initially given a registration number identifying their source. After extraction, individual fossils are uniquely identified by a numerical suffix, for example, P87103-25 is a specimen from the 'Blast Site'.

sites (Megirian in prep.). *Quinkana* was possibly a terrestrial erocodilian.

The fossilized bones are composed of apatite (calcium phosphate) (Fig. 4) as determined by powder X-ray diffraction. The presentation of the fossils ranges from poorly-sorted fragmentary lags to associations of partial skeletons among which complete erania, with delicate structures intact, are preserved. The Bullock Creek Local Fauna contains the taxa listed in Table 1, most of which are depicted in Figure 5.

The inferred age of the Camfield Beds is based upon the stage of evolution of the diprotodontid species *Neohelos* sp. which has been considered to be more advanced than the Kutjamarpu LF *N. tirarensis* but more primitive than the Alcoota LF diprotodontid *Kolopsis torus* (Woodburne *et al.* 1985).

Clemens and Plane (1974) considered the Kutjamarpu thylacoleonid species *Wakaleo oldfieldi* Clemens and Plane to be more primitive than the Bullock Creek LF *Wakaleo vanderleueri*. Additional Bullock Creek *Wakaleo* material described by Murray and Megirian (1990) shows fewer differences from *W. oldfieldi* than previously thought, indicating that the age of the

Bullock Creek Local Fauna is much closer to that of the Middle Miocene Kutjamarpu LF than to that of the Alcoota LF.

Propalorchestes novaculacephalus from Riversleigh 'System B' is indistinguishable from the Bullock Creek specimens (Murray 1990a). We agree with Woodburne *et al.*'s (1985) placement of Bullock Creek LF within the middle Miocene, but suggest that it might be situated a bit closer to the Kutjamarpu LF in age (transitional Bairnsdalian-Mitchellian Stage).

Alcoota locality. Two distinct Local Faunas have been identified in the Waite Formation: the Alcoota LF and the Ongeva LF (Murray *et al.* in prep.) (Fig. 6). The latter is significant in terms of biochronological estimation of the age of the Alcoota LF. Newsome and Rochow (1964) were the first to describe vertebrate fossils from Alcoota Station. A comprehensive study of the palaeontology of the Alcoota LF and geology of the Waite Formation was published by Woodburne (1967). Subsequent to Woodburne's investigation, sporadic excavations of the locality were undertaken by M. Areher, P.V. Rieh, T.H. Rieh and N. Pledge (Rieh *et al.* 1982, Areher and Rieh 1982). In 1984, the Northern Territory Museum

commenced an annual excavation program, establishing a permanent field station at the locality (Fig. 7).

The main fossiliferous units of the Waite Formation, Alcoota Station, are located about 350m apart. The lower lacustrine beds yielding the Alcoota LF are composed of unconsolidated, greenish-grey, silty sandstone with calcareous

partings and reddish-brown mottling. Evaporitic clasts, powdery carbonate residues and calcareous rinds are often associated with the fossil material. Patchy, tabular limestone bands occur sporadically above and below the fossil bed. Some limestone fragments have fine striations on their surfaces that resemble plant fossils (Woodburne 1967). These limestones differ from

Table 1. Bullock Creek Local Fauna. With the exception of Stirton, 1967, the unbracketed citations are both the authors of the taxon and the primary reference to the occurrence of that taxon at Bullock Creek. Bracketed citations are purely references to the occurrence of the taxon at Bullock Creek, and therefore should not be taken as an indication of a revision of the taxonomic concept.

MOLLUSCA	Gastropoda	(undetermined)
	Pelecypoda	(undetermined)
ARTHROPODA	Crustacea	ostracodes (undetermined)
PISCES (H.Larson pers. comm.)	Ceratodidae	(Lungfish) <i>Neoceratodus</i> (three species: Kemp 1991)
	Osteoglossidae	(Saratoga)
	Ariidae	(Fork-tailed catfish)
	Plotosidae	(Eel-tailed catfish)
	Centropomidae	(Barramundi)
	Tetrapontidae	(Grunters)
AMPHIBIA (M. Tyler, written comm.)	Anura	<i>Australobatrachus</i> sp. <i>Litoria</i> spp.
REPTILIA	Pythonidae	gen. et. sp. indet. (Smith and Plane 1985)
	Madtsoiidae	<i>Yurlunggur camfieldensis</i> Scanlon, 1992
	Elapidae (Scanlon, written comm.)	(undetermined)
	Varanidae	<i>Varanus</i> spp. ? <i>Megalania</i> sp. (giant varanid)
	Meiolaniidae	<i>Meiolania</i> sp. nov. Megirian, in press (Megirian 1989)
	Chelidae	(undetermined)
	Crocodylidae	<i>Baru darrowi</i> Willis, Murray and Megirian 1990 <i>Harpacochampsia camfieldensis</i> Megirian, Murray and Willis 1991 <i>Quinkana</i> sp. nov. (Megirian in prep.)
AVES	Dromornithidae	<i>Bullockornis planei</i> Rich 1979 <i>Bullockornis</i> sp.. (Rich 1979) <i>Dromornis</i> sp.
	Casuariidae	<i>Dromaius</i> sp. (Patterson and Rich 1987:87) (undetermined)
	Anatidae	(undetermined) Other undetermined non-ratites
MAMMALIA	Dasyuridae	(undetermined)
	Thylacinidae	<i>Nimbacinus dicksoni</i> Muirhead and Archer, 1990
	Peramelemorphia	"V.D." bandicoots (Muirhead pers.comm.)
	Thylacoleonidae	<i>Wakaleo vanderleueri</i> Clemens and Plane, 1974
	Diprotodontidae	<i>Neohelos</i> cf. <i>tirarensis</i> Stirton, 1967 Gen. et sp. nov ("Nimbador") <i>Propalorchestes novaculacephalus</i> Murray, 1986
	Palorchestidae	(undetermined)
	Phalangeridae	(undetermined)
	Pseudocheiridae	(undetermined)
	Potoroidae	(undetermined)
	Macropodidae	<i>Balbaroo camfieldensis</i> Flannery, Archer and Plane, 1982 <i>?Nambaroo</i> sp. (H. Godthelp and M. Archer written comm.) large kangaroo (?Sthenurinae) small kangaroo (high-crowned tooth) Other species of small, undetermined marsupials
	Chiroptera	(undetermined microchiropteran)

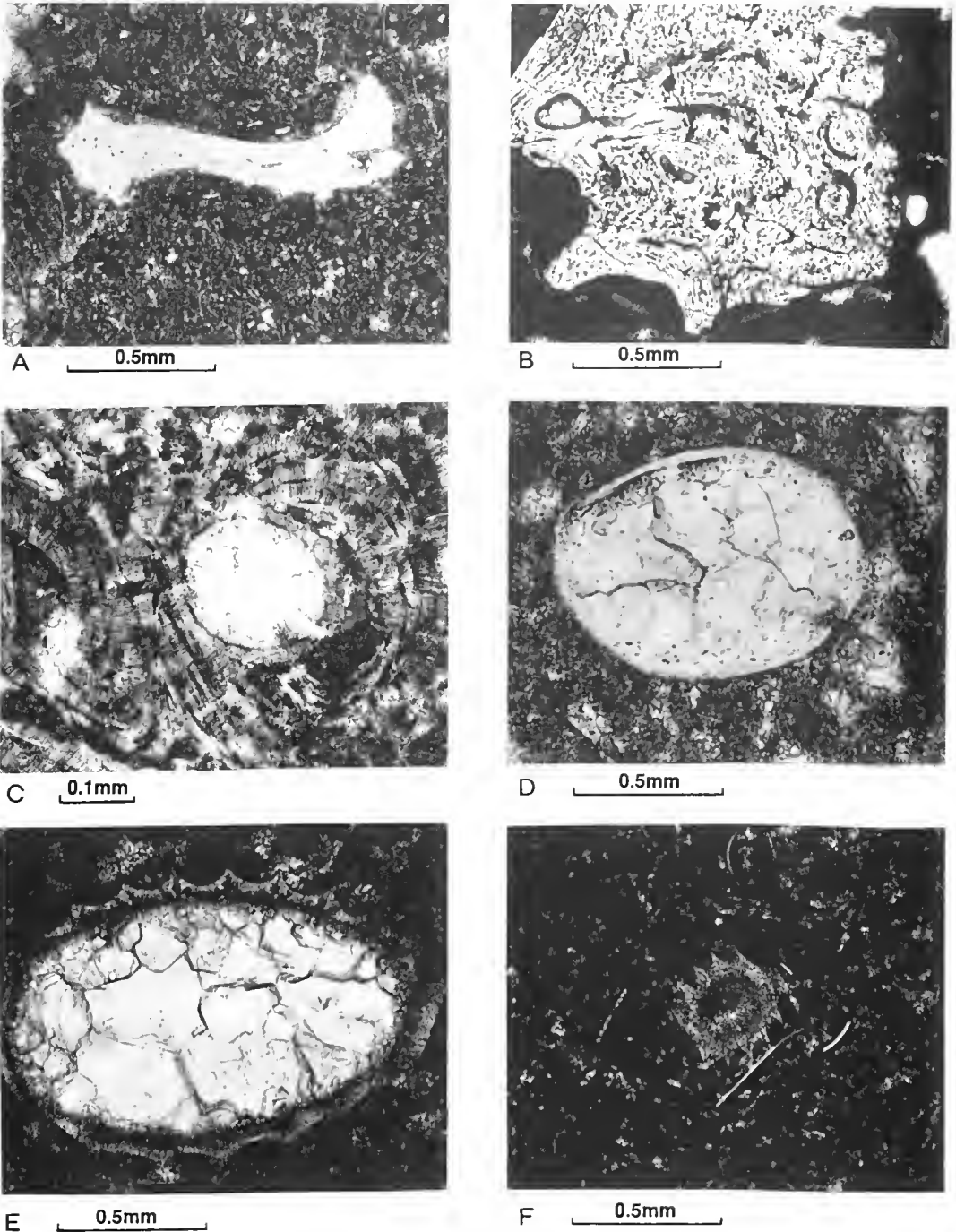


Fig. 4. Photomicrographs of thin sections of Camfield Beds limestone. **A**, probable fish bone in micritic matrix. Powder X-ray diffraction indicates the fossil bones are composed of calcium phosphate (apatite). The characteristic black colour of many Bullock Creek fossils is due to iron and magnesium oxides deposited within the bone, revealing internal structure clearly; (**B,C.**) detail of Haversian system; **D**, articulated ostracode valves in transverse section; **E, F**, oogonia of charophyte algae. All primary voids are filled with sparry calcite cement. All plane polarized light.

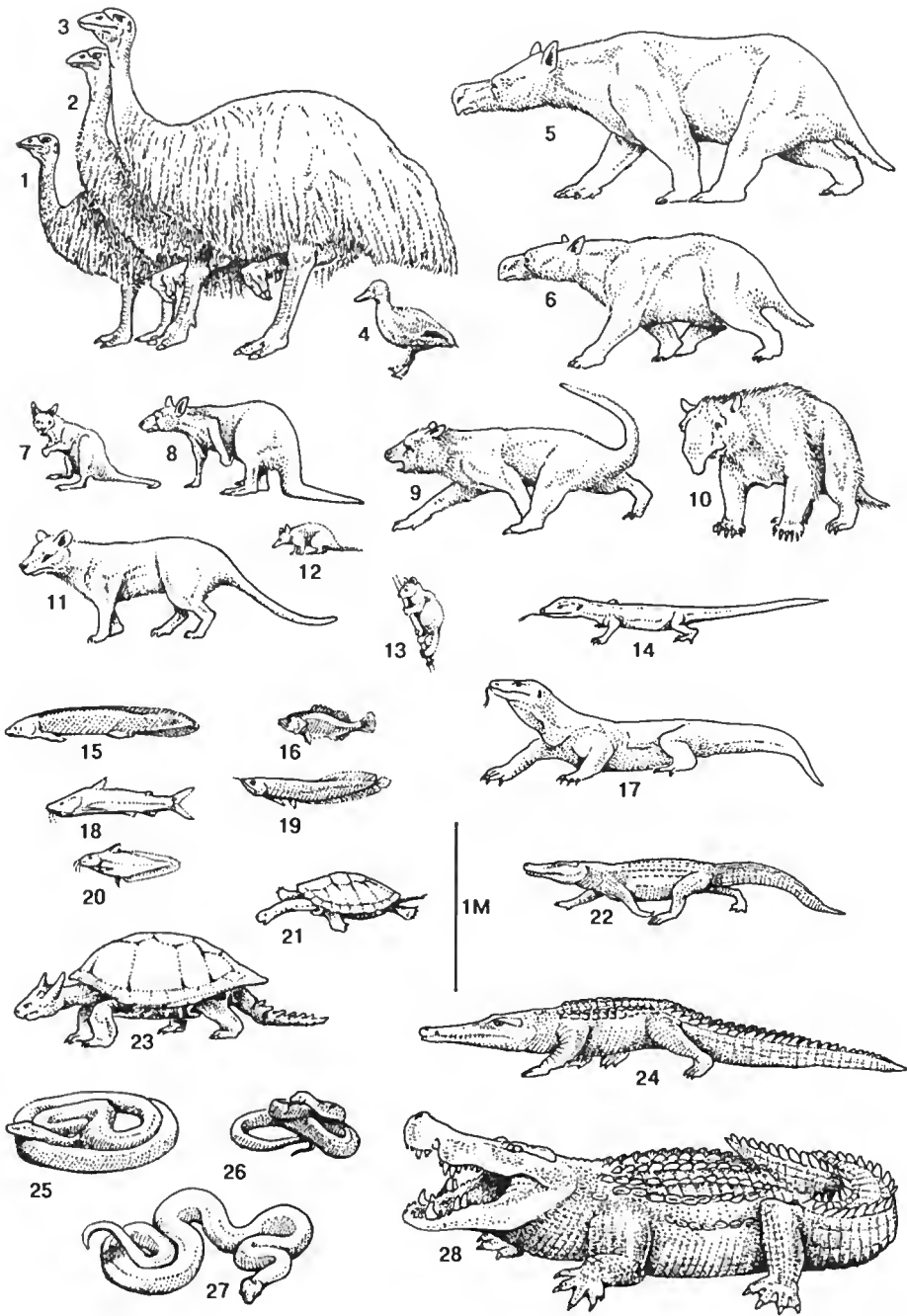


Fig. 5. Reconstructions of mid Miocene Bullock Creek Local Fauna, drawn approximately to scale; 1, casuariid; 2, dromornithid, *Bullockornis* spp. (one of two species); 3, *Dromornis* sp.; 4, Anatidae (undetermined duck); 5, *Neohelos* cf. *tirarensis*; 6, small zygomaturine diprotodontid "*Ninbadon*" (Hand *et al.*, unpublished); 7, Macropodidae (undetermined species with high-crowned molars); 8, Balbarinae (one of two species); 9, thylacoleonid *Wakaleo vanderleueri*; 10, palorchestid *Propalorchestes novaculacephalus*; 11, small thylacinid, *Ninbacinus dicksoni*; 12, Peramelamorphia ("VD" bandicoot); 13, one of three species of generically undetermined phalangeroids; 14, Varanidae, (undetermined, larger than *Varanus giganteus* (perentie), ?immature cf. *Megalania*); 15, Ceratodontidae (undetermined lungfish, cf. *Neoceratodus*); 16, Centropomidae (one of several undetermined perch-like fishes); 17, large varanid, *Megalania*-sized; 18, Ariidae (forktailed catfish); 19, Osteoglossidae (Saratoga); 20, Plotosidae (Eel-tailed catfish); 21, cmydid turtle (genus undetermined); 22, crocodylid, *Quinkana* sp nov.; 23, meiolaniid, *Meiolania* sp. nov.; 24, crocodylid, *Harpacochampsia camfieldensis*; 25, pythonid (genus undetermined); 26, elapid, (genus undetermined); 27, madtsoiid, *Yurlunggur camfieldensis*; 28, crocodylid, *Baru darrowi*.

the chalcidonic limestone caprock of pedogenic origin and may represent spring-related carbonate deposits or travertines.

The fossils sometimes occur as isolated, associated partial skeletons, but are more often concentrated in a bone bed or in poorly defined channel deposits encountered between 0.50m and 0.90m below the ground surface (Fig. 8). The condition of the material ranges from very complete crania with fragile structures intact to very fragmented, and totally dissociated, specimens concentrated together in an extensive, tangled mass of bones. Large, well-preserved specimens often occur in association with dissociated fragmentary concentrations of bone where the former have acted as snags.

The distribution and condition of the fossil material indicates very localized transport of the smaller bones and fragments, accompanied by rapid sedimentation. The partial association of the remains of large animals suggests a moderate degree of predepositional scattering, which appears to have taken place at the surface during and after decomposition. The bone bed has the

sedimentological attributes of short-interval, high-energy hydraulic transport similar to that which occurs in arid to semi-arid basins at present as a result of runoff from infrequent, but prodigious, downpours.

The fossilized bone of the Alcoota Local Fauna is distinctive in being extensively crazed by alternate expansion and contraction of the clay fraction of the matrix, due to fluctuations in the moisture content of the siltstone over millions of years. A curious product of this agency is the gradual expansion of structures by the incorporation of fines into the cracks as the matrix swells, gradually "exploding" some of the bones and teeth. Some burial compaction and distortion of the fossils seems to have occurred, but other causes of compaction and crushing are discussed below. Our analysis of the chemical composition of the fossil bone and its matrix is incomplete. Powder X-ray diffraction reveals that the primary component of the fossilized bone is calcium phosphate (apatite). The Alcoota Local Fauna contains the taxa listed Table 2, most of which are depicted in Figure 9.

Table 2. The Alcoota Local Fauna. Unbracketed citations are both the authors of the taxon and the primary reference of the occurrence of the taxon in the Alcoota LF. Bracketed citations are purely references to the occurrence of the taxon at Alcoota, and do not imply a revised taxonomic concept.

MOLLUSCA	Gastropoda	(undetermined)
REPTILIA	Testudines	Emydidae
	Crocodylidae	<i>Baru</i> cf. <i>darrowi</i>
	Varanidae	? <i>Megalania</i>
AVES	Casuariidae (undetermined)	<i>Dromaius</i> sp. (Patterson and Rich, 1987)
	Dromornithidae	<i>Dromornis stirtoni</i> Rich, 1979 <i>Ilbandornis lawsoni</i> Rich, 1979 <i>Ilbandornis woodburnei</i> Rich, 1979 (undetermined ducks)
	Anatidae	(undetermined hawks and eagles)
	Accipiteridae	(undetermined flamingo)
	Phoenicopteridae	(undetermined)
	MAMMALIA	?Peramelemorphia
?Dasyuridae		(undetermined)
Thylacinidae		<i>Thylacinus potens</i> Woodburne, 1967
Thylacoleonidae		<i>Wakaleo alcootaensis</i> Archer and Rich, 1982
(Vombatidae)*		(undetermined)
Diprotodontidae		<i>Pyramios alcootense</i> Woodburne, 1967 <i>Alkwertatherium webbi</i> Murray, 1990b <i>Plaisiodon centralis</i> Woodburne, 1967 <i>Kolopsis torus</i> Woodburne, 1967 <i>Palorchestes painei</i> Woodburne, 1967 <i>Pseudochirops</i> sp. <i>Hadronomas puckeridgei</i> Woodburne, 1967 <i>Dorcopsoides fossilis</i> Woodburne, 1967 cf. <i>Dorcopsoides</i> (<i>Protemnodon</i>)*
Palorchestidae		
Petauridae		
Macropodidae		

*The vombatid and the proteomodont kangaroo were reported by Woodburne (1967) as tentative identifications. We have not found any remains assignable to these groups during our investigations.

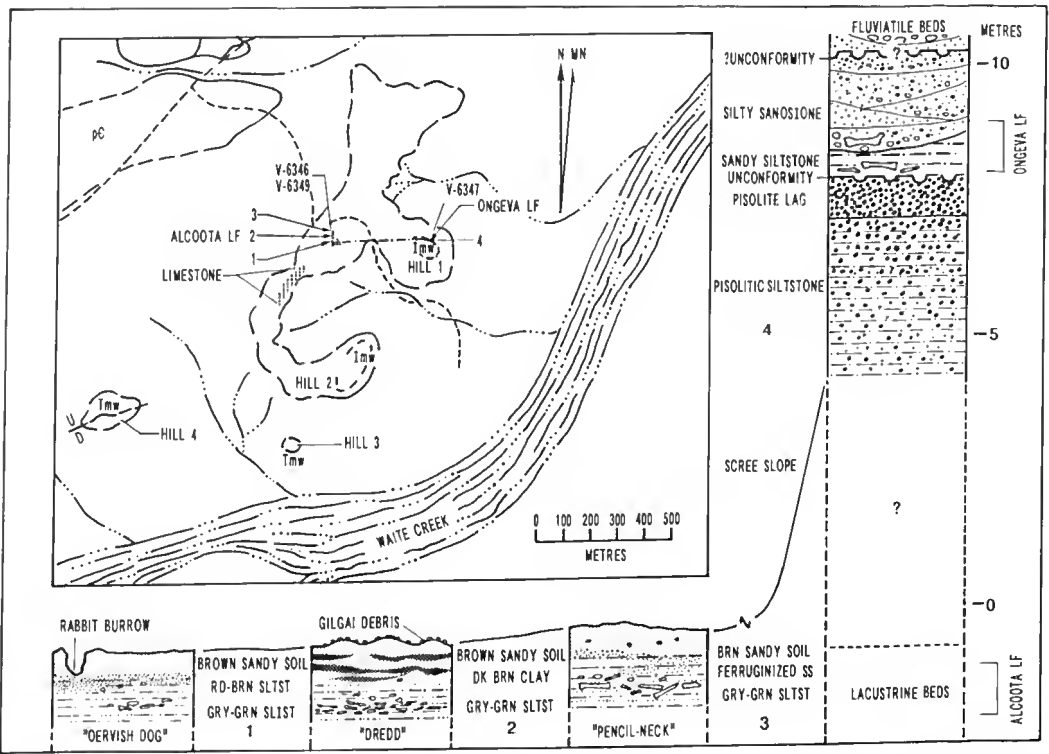


Fig. 6. Map and representative sections of Alcoota fossil localities; numbers correspond to sample sections from each of three main Alcoota Local Fauna quarries shown in Fig. 7. Geological map based on Woodburne (1967: Fig. 2); V-numbers correspond to Woodburne's University of California Museum of Paleontology locality designations. The stratigraphic section on the right shows the relationship of the Ongeva Local Fauna (not described in this paper) to the Alcoota Local Fauna. *Kolopsis* sp. nov. from the Ongeva Local Fauna constrains the age of the Alcoota LF more precisely than was previously possible (Murray *et al.* in prep.).

The age of the Alcoota Local Fauna was considered post-Kutajmarpu LF, pre-Beaumaris LF in age by Stirton *et al.* (1967) on the basis of the stage of evolution of the diprotodontid fauna. Woodburne *et al.* (1985:359) cast some doubt on the pre-Beaumaris age of Alcoota with the statement "The above discussion of problems concerning the material referred to *Zygomaturus gilli* (Beaumaris) raises the possibility that the Alcoota sample may have existed contemporaneously with or even later than, the Beaumaris Local Fauna". The recent discovery of a more derived *Kolopsis* species, similar to the Beaumaris form, in a fluvialite stratum of Hill 1, situated unconformably 6.8m above the Alcoota LF (Fig. 7), provides a strong indication that the lacustrine beds are significantly older than Beaumaris (Murray *et al.* in prep.). Consequently we suggest that the Alcoota Local Fauna is transitional Mitchellian-Cheltenhamian Stage equivalent (Late Miocene).

METHODS AND MATERIALS

Representative samples of fossil material from the Alcoota and Bullock Creek localities were analysed using the proximity method outlined by Shotwell (1955). Shotwell's descriptive statistical approach seems ideally suited to the faunal assemblages from Alcoota and Bullock Creek in which many postcranial elements are represented. The entire samples of Alcoota and Bullock Creek material, estimated to be of the order of three or four thousand specimens, have not yet been fully analysed. Furthermore, some sample collections of material sent to colleagues several years ago have not yet been identified or returned. Consequently, the assignments of smaller species are given at higher taxonomic levels, and accurate quantification of some forms, e.g. fishes, has not been possible.

We have assembled two samples of material that we can confidently identify at the level

indicated. Shotwell's method is not intended to test or assess the statistical significance of sample differences, but to elucidate patterns in faunal assemblages that would otherwise be extremely laborious or awkward to express verbally. Inevitably, because of the ongoing nature of our project, the quantitative details of the present analysis will be superseded as new material is acquired.

RESULTS

Systematic affinities. Although the Alcoota and Bullock Creek Local Faunas share no mammalian species and only a few mammalian and reptilian genera (Fig. 10), there is substantial evidence of systematic continuity in the majority of taxa. *Wakaleo alcootaensis* appears to be derived from *W. vanderleueri* (Murray and Megirian 1990). The postulated diprotodontid succession *Neohelos tirarensis* to *Kolopsis torus* is structurally of the order of a species-rank differentiation, but its principal distinction, the division of the paracone and metacone on P³, is a quintessential synapomorphy uniting *Kolopsis* with the more derived *Zygomaturus* clade (Stirton *et al.* 1967).

The genus *Plaisiodon* may share an ancestor with *Neohelos* (Stirton *et al.* 1967). There are no features of *Propalorchestes novaculacephalus* that would preclude its ancestry to *Palorchestes painei* (Murray 1990a). Specific antecedents to the Alcoota zygomaturine *Alkwertatherium webbi* or the diprotodontine *Pyramios alcootense* have not been found in the Bullock Creek assemblage. Primitive nototherines, structurally suitable as ancestors to *Pyramios*, are known in early to mid Miocene sediments at Riversleigh, Queensland (Archer *et al.* 1989).

Macropodid phylogeny in mid to late Miocene Local Faunas is also poorly documented. *Balbaroo* and *Nambaroo* both share a few dental and anatomical features with *Hadronomas* (Murray 1991). A sthenurine-like femur from Bullock Creek could represent a *Hadronomas* annectant. The small undetermined wallabies from Bullock Creek could represent early members of the *Dorcopsoides* clade. *Nimbacinus*, a thylacinid genus from Bullock Creek, possesses no features that would preclude its ancestry to *Thylacinus* (Muirhead and Archer 1990).

The three Alcoota dromornithid species may be descendants of a large undetermined Bullock Creek species. Rich (1979) considered *Bullockornis* a sister genus to *Dromornis*. Of these, only *Dromornis* is a structurally suitable ancestor for *Ilbandornis*. The Alcoota casuariid, an unnamed species with features structurally intermediate to the emu and cassowary, differs from the Camfield form primarily on the basis of its slightly larger size.

Preliminary work on the Alcoota crocodylids indicates the presence of the genus *Baru*. The Alcoota *Baru* species closely resembles *Baru darrowi* from the Bullock Creek LF but may represent a chronospecies. Systematic evidence suggests that the majority (about 85 per cent) of mammalian and avian genera and species in the Alcoota Local Fauna could have been derived from Bullock Creek species during the intervening three million years.

Sampling Variation. Comparison of the NTM Alcoota collection with Woodburne's (1967) published inventory provides an example of the statistical variation in the sampling (Fig. 11). The proportions of species in the NTM samples vary from year to year, but the combined 1984-1990 samples have resulted in proportions similar to those calculated from data in Woodburne (1967). The primary differences are registered in our lower frequencies of *Pyramios alcootense* and

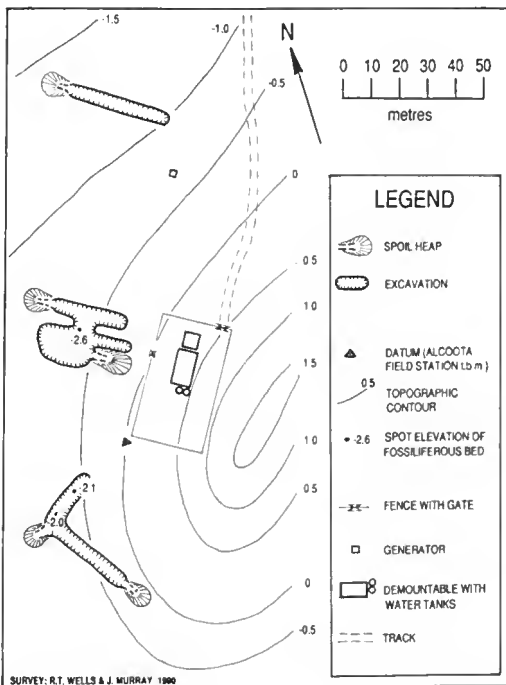


Fig. 7. Plan of Alcoota Local Fauna fossil quarries and NTM field station.

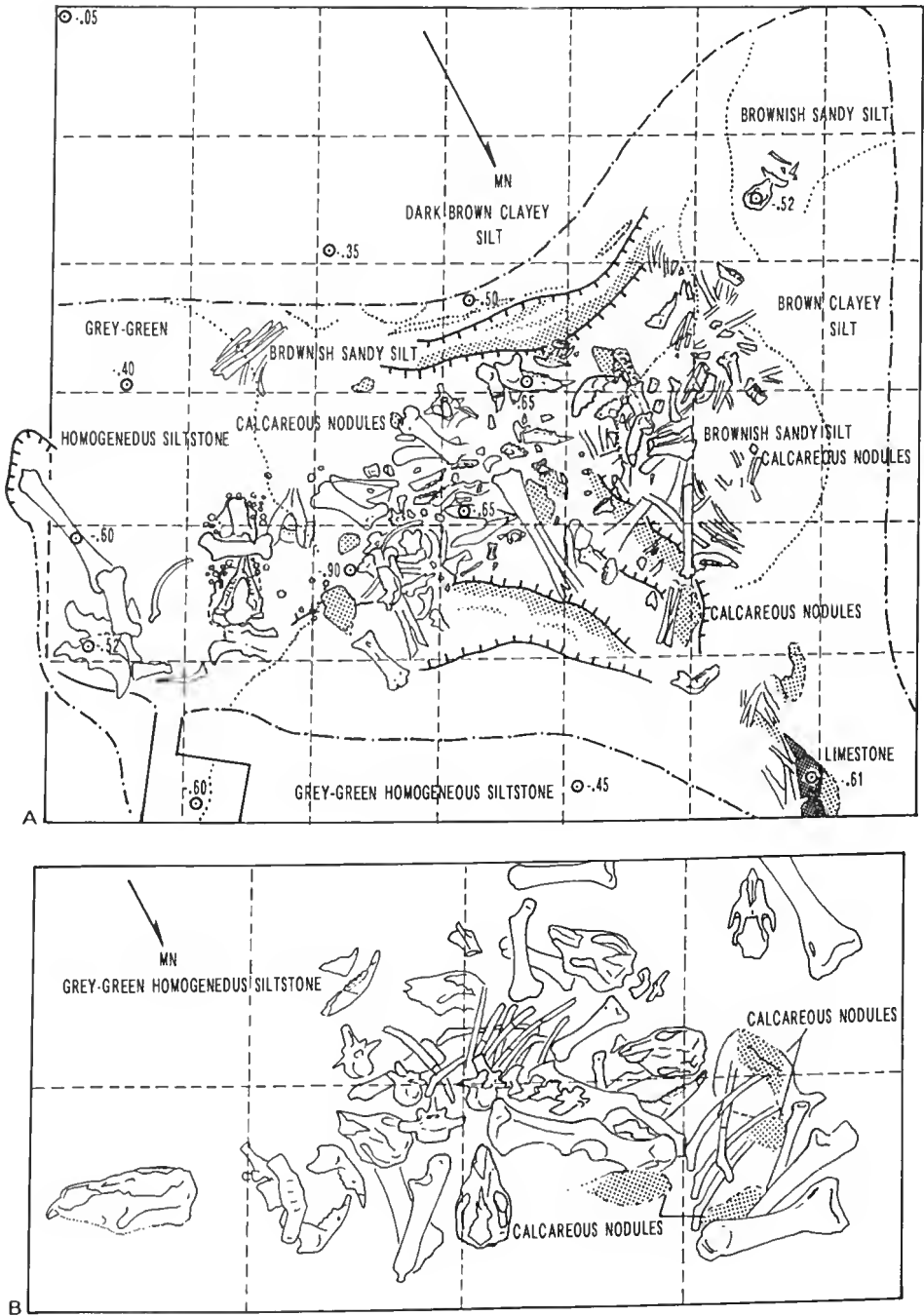


Fig. 8. Two types of assemblages at Alcoota: A, channel deposit containing dense mixture of fragmented specimens: about one-third of them have been depicted here (field sketch 3-7-88 to 5-7-88); B, associated remains of a single large diprotodontid (*Plaisiodon centralis*) acting as a trap for smaller remains, in this case six crania, partial postcranial remains and several dentaries of *Kolopsis torus* (field sketch, 23-8-87). Spot elevations were determined with line-level from the south corner of the excavation; stipple represents a localised concentration of soft, powdery and chalky, or crystalline minerals thought to represent evaporites, together with diagenetic calcareous nodules. The left lower quadrant of A shows a concentration of gastroliths in association with dromornithid sternum and synsacrum fragments. In B, the large cranium to the left is *Plaisiodon*, which is considered to represent the species of the larger associated diprotodontid remains. The *Plaisiodon* specimen and one of the more complete *Kolopsis torus* skeletons from this assemblage are on display as armatured partial restorations in the Spencer and Gillen Museum, Alice Springs.

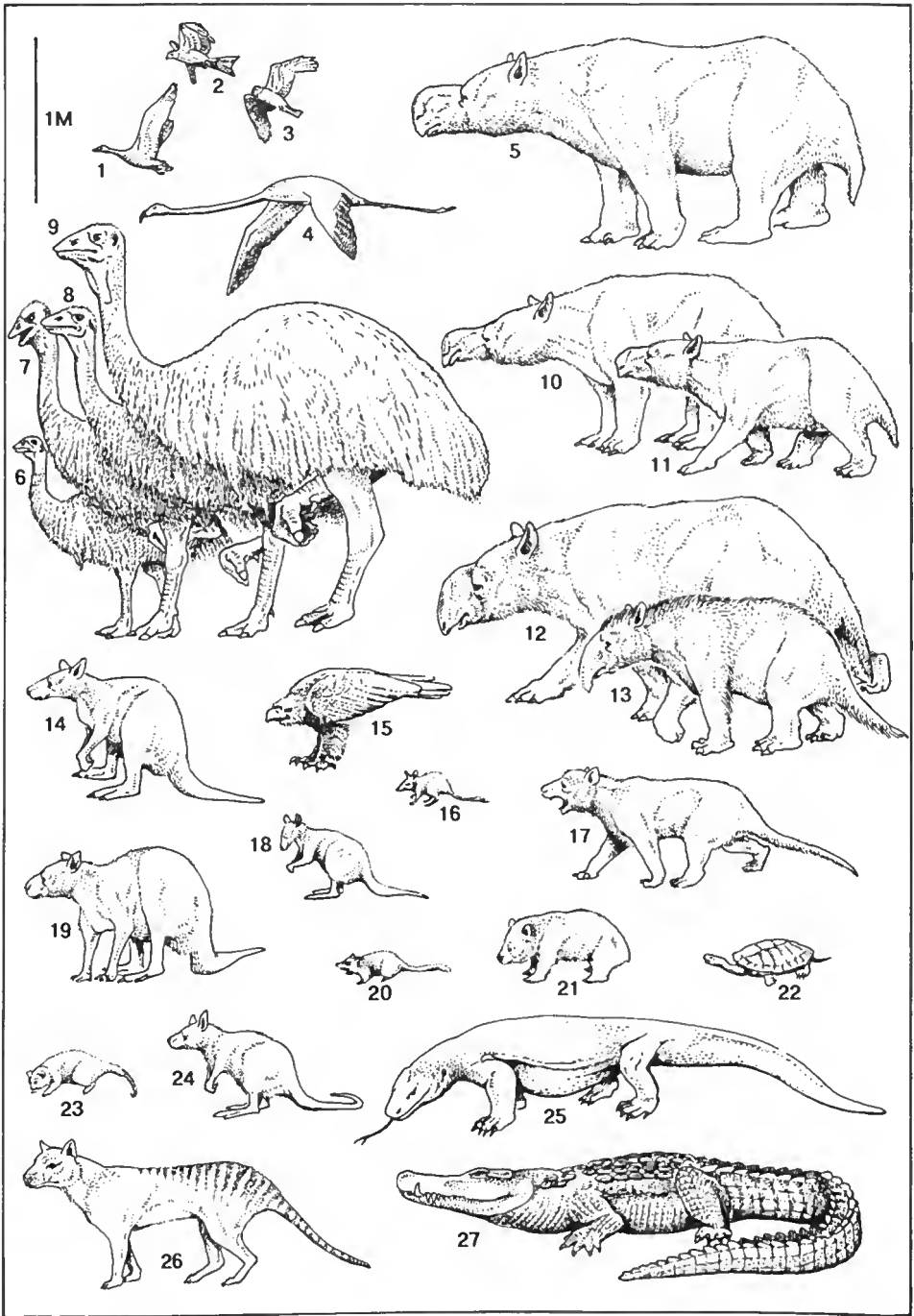


Fig. 9. Reconstructions of the late Miocene Alcoota Local Fauna, drawn approximately to scale; 1, anatid (undetermined duck); 2-3, smaller accipiterids, at least two species; 4, phoenicopterid, undetermined flamingo; 5, zygomaturine diprotodontid, *Plaisiodon centralis*; 6, casuariid, 7, dromornithid, *Ilbandornis woodburnei*; 8, *Ilbandornis lawsoni*; 9, *Dromornis stirtoni*; 10, zygomaturine diprotodontid, *Alkwerratherium webbi*; 11, zygomaturine diprotodontid, *Kolopsis torus*; 12, diprotodontine diprotodontid *Pyramio alcootense*; 13, palorchestid, *Palorchestes painei*; 14, macropodid, ?*Protennodon* (Woodburne 1967); 15, large accipiterid, possibly an eagle; 16, perameloid (undetermined genus); 17, thylacoleonid, *Wakaleo alcootaensis*; 18, macropodoid, *Dorcopsoides fossilis*; 19, macropodid, *Hadronomas puckeridgei*; 20, dasyurid (undetermined); 21, ?vombatid (Woodburne, 1967); 22, emydid (undetermined genus); 23, petaurid, *Pseudocheirops* sp.; 24, macropodid (undetermined genus); 25, varanid, cf. *Megalania*; 26, thylacinid, *Thylacinus potens*; 27, crocodylid *Baru* cf. *darrowi*.

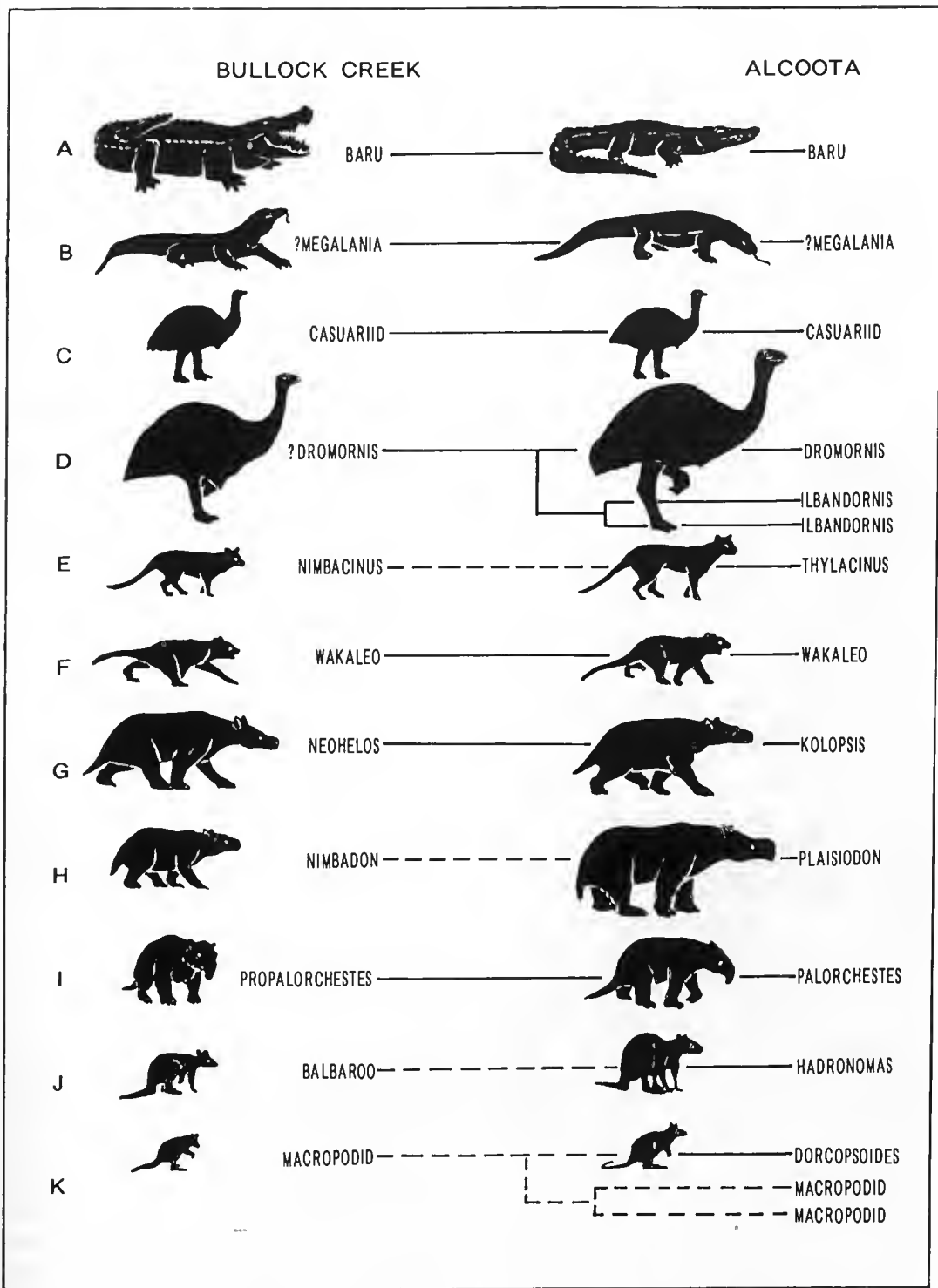


Fig. 10. Hypothesis of ecological succession of closely related, ecomorphically similar species; A, *Baru darrowi*-*Baru* cf. *darrowi*; B, *?Megalania* sp.-*Megalania* sp.; C, casuariid - casuariid; D, *?Dromornis* sp.-*Dromornis stirtoni*; E, *Nimbacinus dicksoni*-*Thylacinus potens*; F, *Wakaleo vanderleueri*-*Wakaleo alcootaeusis*; G, *Neohelos* cf. *tirareusis*-*Kolopsis torus*; H, "*Nimbadon*"-*Plaisiodon centralis*; I, *Propalorchestes novaculacephalus*-*Palorchestes painei*; J, *Balbaroo caufieldensis*-*Hadronomus puckeridgei*; K, macropodid-*Dorcopsoides fossilis*.

Palorchestes painei, complemented by a higher frequency of *Dorcopsoides fossilis* (plus a similar but larger unidentified macropodid species) and *Kolopsis torus*. At present there is no comparable control for the NTM Bullock Creek Local Fauna sample, but the potential exists for eventual comparison of the NMV collection made by T. Rieh and associates.

Community structure. According to the model of Shotwell (1955), taxa showing a large number of specimens per individual and a high relative abundance may, *in general*, be considered members of the community in closest proximity to the depositional environment ('proximal community'). The obvious corollary is that taxa represented by few specimens per individual at a low relative abundance probably belong to a distant community. Clearly there are a large number of uncontrolled variables that can influence the relative abundance of a species and the estimated number of specimens per individual. In the following interpretation we first draw attention to the similarity between the Bullock Creek and Alcoota Local Faunas, before accounting for the differences.

Comparison of the frequency distributions of Bullock Creek LF and Alcoota LF species-equivalents (i.e. shared eomorphs) shows that in this category the two faunas are quite similar in relative abundance of species and in species diversity (Fig. 12). The most conspicuous contrast between the two assemblages is the large number of aquatic and stream-bank species in the Bullock Creek Local Fauna. Over half the identified species at Bullock Creek are fish, crocodiles, snakes, varanids and turtles. These groups account for less than one quarter of Alcoota species (Fig. 13), indicating that permanent aquatic-riparian habitats at Alcoota were remote from the depositional setting. Pythonids, pythonid-like madtsoiid snakes, and meiolaniid tortoises (all absent from Alcoota) are represented at Bullock Creek at a low relative abundance but by a high number of specimens per individual, and are thus considered to represent the proximal habitat at Bullock Creek.

Other differences in the faunas are the occurrence of two additional, though rare, diprotodontid species and a higher relative abundance of macropodids at Alcoota. Our interpretation of the Alcoota sample suggests that the diprotodontid genera *Pyramios* and *Alkwertallierium* belong to a distant community. The Alcoota macropodid sample contains ap-

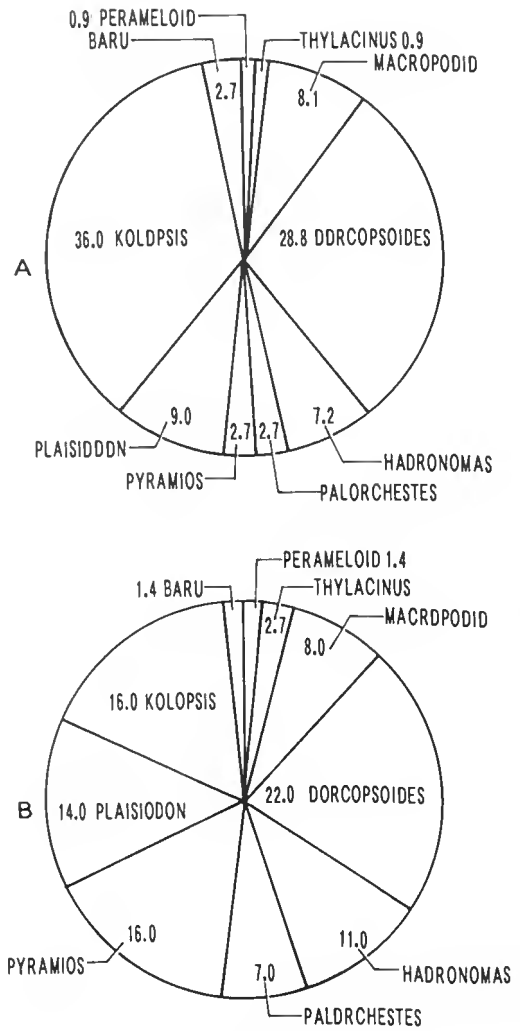


Fig. 11. Relative abundance of equivalent taxa collected from Alcoota by the NTM to 1980 (A) for comparison with Woodburne (1967) (B).

proximately four times as many individual kangaroos as the Bullock Creek LF, and on the average, they are represented by much larger species (Fig. 14). Because the number of specimens per individual for kangaroos does not differ greatly between the two assemblages, an ecofacies bias seems unlikely, hence kangaroos can be considered elements of the proximal community at both localities. The frequency difference is attributable to an increase in favourable kangaroo habitat in combination with a concomitant increase in kangaroo numbers at Alcoota. Although body size enlargement and morphological specialization is apparent in the Alcoota macropodid species, the diversity of genera re-

mains low in comparison to Plio-Pleistocene Local Faunas.

Secondary consumers such as mammalian carnivores are normally present in small numbers relative to the number of primary consumers. Thus, the carnivorous marsupials *Wakaleo* and *Thylacinus* are considered members of the proximal community at both localities. Browsing palorchestines are known from numerous Neogene assemblages, but are uncommon in all of them, including in the Aleoota and Bullock

Creek Local Faunas. Their low frequency in a wide variety of depositional settings might reflect solitary habits, and therefore we tentatively include palorchestines with the proximal community of both Aleoota and Bullock Creek.

Casuariids are rare and poorly represented in terms of specimens per individual, indicating that they are distant community species in both assemblages. Phalangeroids are uncommon at both localities, although the species diversity is higher at Bullock Creek (the sample includes

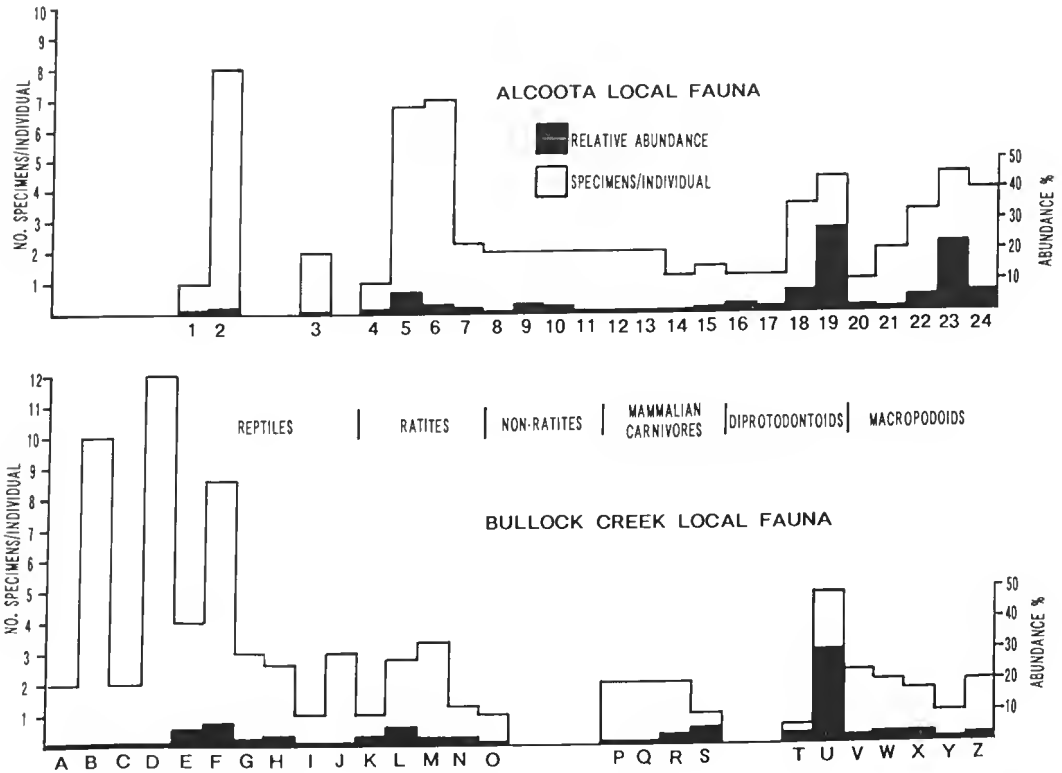


Fig. 12. Histogram comparing relative abundance of species (black columns) and estimated number of specimens per individual (white columns) from Alcoota and Bullock Creek faunal assemblages using the procedure originated by Shotwell (1955) and employing a standard number of elements of 50. Annectant and/or closely related ecomorphic species and genera are aligned. Numerical abbreviations (Alcoota): 1, emydid (undetermined); 2, *Baru* cf. *darrowi*; 3, large varanid (probably *Megalania*); 4, casuariid; 5, dromornithid *Dromornis stirtoni*; 6, *Ilbandornis woodburnei*; 7, *Ilbandornis lawsoni*; 8, Anatidae (undetermined duck); 9, Accipiteridae (?two species); 10, Accipiteridae (?eagle); 11, Phoenicopteridae (undetermined Flamingo); 12, perameloid (undetermined genus); 13, dasyurid (undetermined); 14, thylacinid, *Thylacinus potens*; 15, thylacoleonid, *Wakaleo alcootaensis*; 16, diprotodontid, *Pyramios alcootense*; 17, diprotodontid, *Alkwertatherium webbi*; 18, diprotodontid, *Plaisiodon centralis*; 19, diprotodontid, *Kolopsis tornus*; 20, palorchestid, *Palorchestes painei*; 21, petaurid, *Pseudocheirops*; 22, macropodid, *Hadronomus puckeridgei*; 23, macropodid, *Dorcopsoides fossilis*; 24, macropodoids (undetermined). Alphabetical abbreviations (Bullock Creek): A, pythonid (undetermined); B, madtsoiid, *Yurlanguur canfieldensis*; C, elapid (undetermined); D, meiolaniid, *Meiolania* sp. nov.; E, emydid (undetermined); F, crocodylid, *Baru darrowi*; G, crocodylid, *Harpacochampsia canfieldensis*; H, crocodylid, *Quinkana* sp. nov.; I, large varanid (cf. *Megalania*); J, small varanid (undetermined); K, casuariid.; L, dromornithid, *Bullockornis* sp.; M, dromornithid, *Bullockornis plaueri*; N, dromornithid, ? *Dromornis* sp. O, Anatidae (undetermined duck); P, perameloid, ("VD" bandicoot); Q, dasyurid (undetermined); R, thylacinid, *Nimbacinus dicksoni*; S, thylacoleonid, *Wakaleo vanderleueri*; T, diprotodontid, "*Nimbadon*" gen. nov.; U, diprotodontid, *Neohelos* cf. *tirarensis*; V, palorchestid, *Propalorchestes novaeaculacephalus*; W, phalangeroids (undetermined); X, Macropodidae, *Balbaroo canfieldensis*; Y, ?Balbarinae (undetermined); Z, macropodoids (undetermined).

three species represented by isolated teeth). Phalangeroids appear to be distant community representatives in both assemblages, from which relatively few other species of small mammals have been recovered.

The higher frequency of specimens per individual of large ratite birds (dromornithids) at Alcoota may be attributable to the greater massiveness of the elements which were less likely to be destroyed or dispersed by surface weathering and depositional agencies. The more active fluvial depositional environment at Bullock Creek may have resulted in greater dispersal of ratite elements.

Taking all species in each assemblage into account, the secondary consumer to primary consumer ratios based on categorical numbers are basically the same (Fig. 15 A,D). However, there are marked contrasts between Alcoota and Bullock Creek taxa when expressed in terms of relative abundance. (Fig. 15 B,E). At Alcoota, the carnivore guild is poorly represented in taxonomic diversity and in relative abundance. The mammalian predators in the Alcoota carnivore guild are somewhat larger than the Bullock Creek forms, which, when expressed in terms of estimated biomass, results in a slightly higher ratio of primary to secondary consumers (Fig. 15 C,F).

The poor representation of the carnivore guild at Alcoota and the apparently contrasting abundance of carnivores at Bullock Creek is probably not indicative of the typical predator-prey ratios in either of these communities. Explanation of the differences requires additional information from taphonomy and inferred habitat structures, as detailed below.

Palaeoenvironments. *Bullock Creek Locality.* The geology and biology of the Bullock Creek assemblage indicates a fluvio-lacustrine environment with permanent and at least seasonally-abundant water. The existence of seasonally shallow, ephemeral lacustrine, pond or oxbow slough habitats are denoted by the presence of numerous, uniformly small teleosts that had become trapped in the basins and died due to deoxygenation of the water or possibly as a result of total dessication. A slow-moving, relatively warm riverine environment is indicated by the presence of freshwater stromatolites.

A moderately large meandering river, subject to significant seasonal fluctuations in flow sufficient to produce oxbow sloughs, and a large flood plain accounts for the Bullock Creek biocoenosis. The low frequency of phalangerids supports the inference that the local vegetation

was not arboreous. A typical active floodplain might be dominated by subclimax associations of sedges, possibly grasses and scrub. If a woodland or forest habitat was present at all, it was situated a considerable distance from the depositional environments. The fauna reflects a waterhole assemblage around which larger

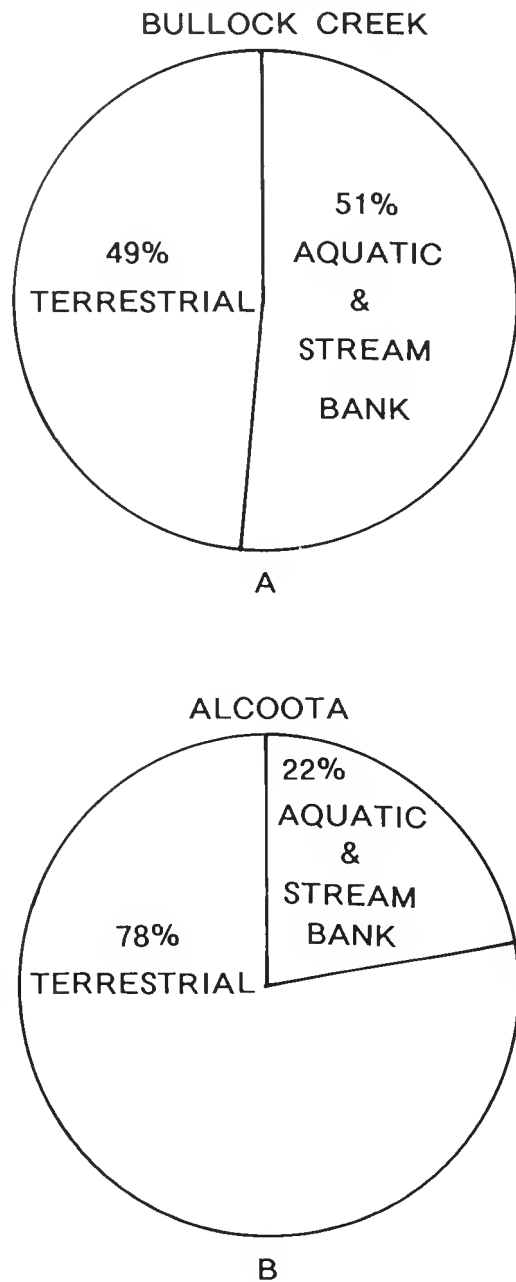


Fig. 13. Comparison of relative proportions (by number of individuals) of aquatic to non-aquatic fauna between A, Bullock Creek Local Fauna and B, Alcoota Local Fauna.

predators would be expected to congregate (Fig. 16A).

Two or more specific ecotopes are discernable among the several quarry samples from the

Camfield Beds limestone. The massive calcilutites at Sites X and Y, containing numerous fish remains and a piscivorous crocodylian, signify a relatively deep basin which may represent a reach of a sluggish river or a seasonally flooded oxbow slough, associated with nearby swamp and shallow ponds. The fossil material is dispersed throughout the sediment as though flushed out and held in suspension for a short distance away from its original source. The Blast Site, Top Site and Dromornithid Mountain Site may represent point bar accumulations or low energy fluvio-lacustrine deposits in which minimal transport and dissociation has occurred. Unfortunately, the samples from Sites X and Y are too small for quantitative comparison using the method proposed by Shotwell (1955).

During intermittent or seasonal droughts, large species such as *Neohelos* congregated near the water. Crocodile predation, for which there is evidence in the form of tooth punctures in bones, accounts for an as yet undetermined, but perhaps significant, proportion of the mortality of *Neohelos* and *Palorchestes*. We have not statistically analysed the mortality of *Neohelos* on the basis of tooth-wear estimates of age, but all age-categories are present, with very old specimens and very young specimens being rare. We consider our *Neohelos* sample to represent a normal (i.e. having typical mortality patterns) population structure.

The sedimentologically complex deposits at Bullock Creek indicate that the fossil accumulations are not confined to a single event or to a temporally-restricted series of events. The assemblage represents sequential accumulations, possibly punctuated by seasonality and local sedimentological conditions over some unknown, but perhaps geomorphologically significant, period of time (i.e. a period of time not resolvable by stage-of-evolution methods). The biological evidence supports the sedimentological evidence of the existence of relatively dry conditions over northern Australia during the Miocene (McGirian 1992).

Alcoota Locality. The Alcoota Locality represents an ephemeral fluvio-lacustrine environment with a very localized, possibly spring-fed, permanent water source. The sedimentology indicates that the deposit represents a shallow lacustrine basin subject to large fluctuations in water level. When full, the basin would have held a very shallow lake several kilometres in diameter (Fig. 16B). The low water level condition of the basin is indicated by partially articu-

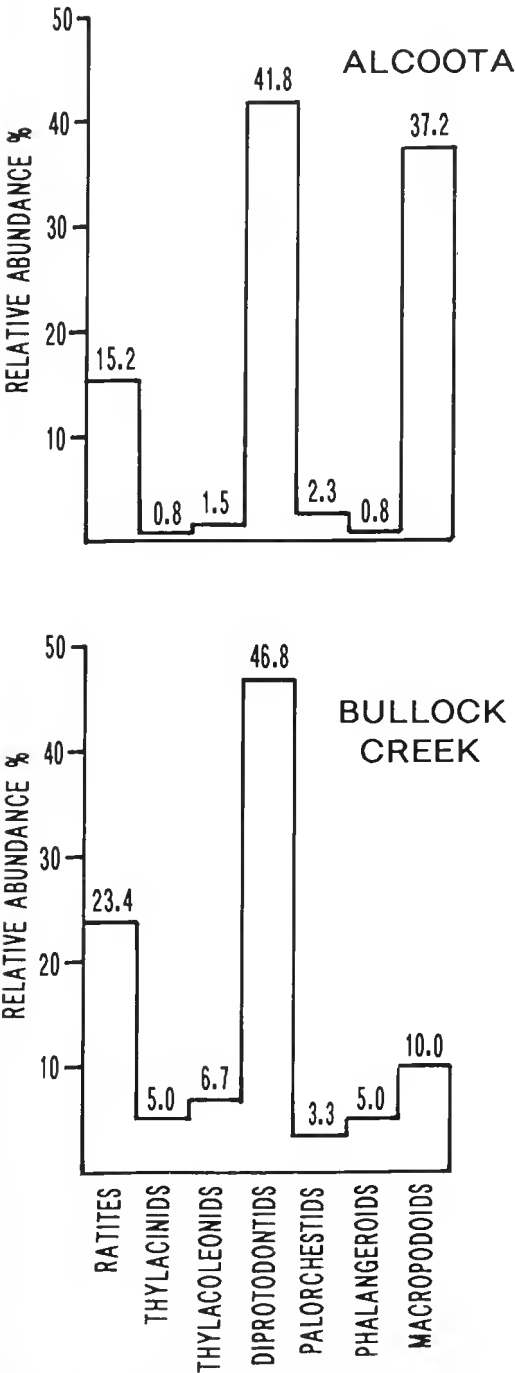


Fig. 14. Histograms comparing relative abundance of the predominant terrestrial taxa in the Alcoota and Bullock Creek Local Faunas.

lated skeletons being concentrated near what appears to be the centre of the basin. If these animals died locally, as opposed to having been transported, their presence is indicative of a dry basin. Even in the unlikely event that these associations represent bloated floating carcasses, a drastically reduced water level or relatively small lake or pond must still be postulated in order to account for the concentration.

An ephemeral lacustrine environment is also indicated by the extreme rarity of turtles and the absence of fish. Crocodiles, though well represented in terms of numbers of specimens, are not abundant in terms of numbers of individuals. The low relative abundance of crocodiles can be explained by their propensity to move overland or follow water courses to avoid being trapped and overcrowded in shrunken waterholes (Weigelt 1989). The large, localized accumulation of uniformly weathered fossils, in combination with the sedimentological evidence for rapid, short distance, and high sediment-yielding hydraulic transport, suggests that the Alcoota LF represents an event-controlled assemblage.

The taphonomic features of the Alcoota assemblage are very specific. There are more species of Diprotodontidae found together than

in any other described Local Fauna. The fossil material is highly localized and concentrated, uniform in pre-burial weathering, but varies widely in extent of fragmentation. The deposit is evidently synchronous and sedimentologically uniform. Partially articulated or associated large species are often devoid of their small elements such as phalanges. The large elements (diprotodontid skulls, innominates, femora) trap smaller elements and fragments transported from some short distance upstream. Members of the same species of larger animals are found in association with one another more often than expected if the distribution were random. Large dromornithid birds have been found in association with concentrations of gastroliths (Fig. 8A).

Uniform weathering of the material indicates that the assemblage was exposed at the surface long enough for complete soft-tissue decomposition and secondary scattering, but not sufficient to allow disintegration of the outer surface of the bone. Differential fragmentation of skeletons is partially explained by hydraulic transport, but some material was unevenly fragmented *in situ* due to crushing. If this crushing was entirely attributed to burial compaction, the damage should be locally uniform and all broken

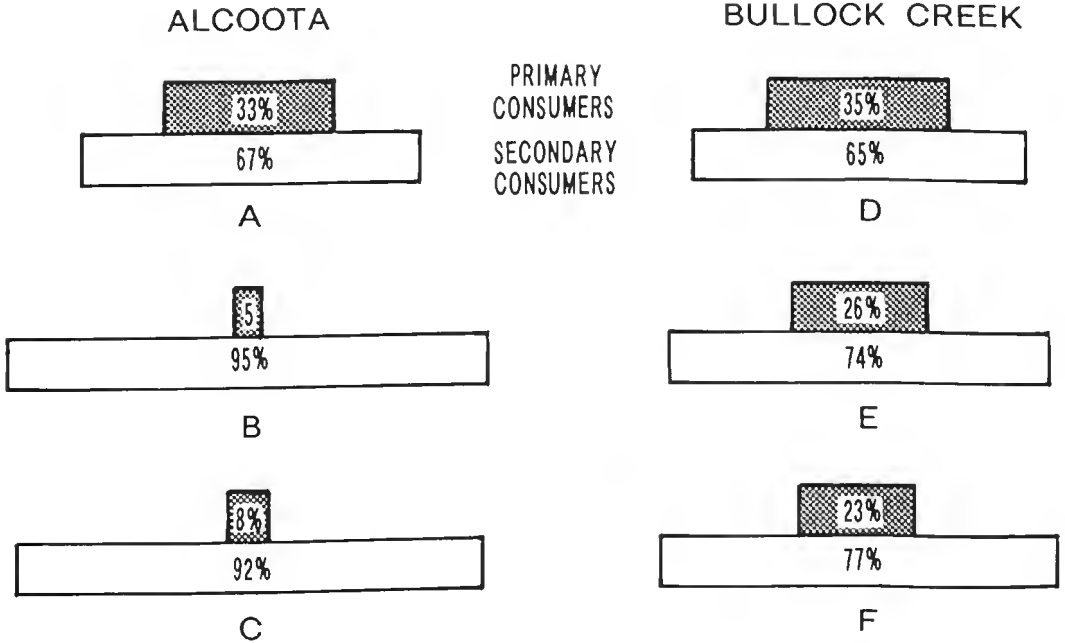


Fig. 15. Ratios of primary to secondary consumers in the Alcoota LF, A-C, with the Bullock Creek LF, D-E. Three types of comparison are made: A, D, (top) number of species, all taxa; B, E, (middle) relative abundance, each species; C, D, (bottom) relative abundance X estimated weight of each individual (biomass). Fish species have not been quantified and are therefore not included in the middle and lower graphs. Small mammalian carnivores (perameloids and dasyurids) are included with secondary consumers in the middle and lower graphs.

pieces would be present. However, there are specimens in the Alcoota assemblage that appear to have been crushed before burial, because some fragments produced by crushing are missing, presumably due to transport.

A possible cause of this type of damage could be trampling by large animals. There are also localized areas of dense compaction and flattening of elements in the bone bed. Animals of the same species are often found together, independent of their size, within very circumscribed areas. For example, the two *Hadronomas* crania occurred close together, while six *Kolopsis* crania, associated dentaries and postcranial elements were found in one small area (Fig. 8B). These observations suggest that the assemblage represents a mass mortality caused by 'waterhole tethering', a relatively common phenomenon that takes place during periods of prolonged drought (Weigelt 1989, Behrensmeyer and Boaz 1980). As ephemeral waterholes dry out, animals become concentrated around remaining permanent water sources, greatly increasing the biomass of the local community. As a result, the available forage is overconsumed, leaving the animals to die of starvation in the proximity of the waterhole.

Herding animals mill around the waterhole until they die, often in close proximity to one another. Survivors trample and pad over deceased animals, compacting and scattering their remains. Under extreme conditions, such animals normally associated with distinct and sometimes distant communities are congregated together, hence the exceptionally large number of diprotodontid species at the site. Eventually the majority of them die of starvation around the water hole; others wander off in search of food to eventually die of thirst.

The comparatively low number of carnivores at Alcoota is probably due to the local guild being overwhelmed by a rapid influx of large herbivores from other communities. There is no evidence of carnivore damage to the Alcoota material. Moreover, it is unlikely that carnivores would respond reproductively to a tethering event, or abandon their territories in the short term, in order to scavenge a distant concentration of carcasses (Behrensmeyer and Boaz 1980).

The remains of these tethered animals lay on the dry surface of the lake until they were incorporated into the sediments when the drought was broken by significant rainfall. Runoff from a single rainfall event would have been sufficient

to orient, scatter and bury the Alcoota assemblage exactly as palaeontologists have found it.

The Alcoota palaeoenvironment is considered to represent a subtropical savanna with local forest in the protected gullies of the Proterozoic hills surrounding the basin. The rarity of small, arboreal animals in the assemblage supports the inference that the proximal landscape was sparsely vegetated with possibly sedge, tussock grasses and subclimax scrub formations immediately around the lake shore, and savanna beyond, extending to the ranges. The thick, poorly-sorted sediment layer, resulting from fluvial activity associated with sporadic flooding suggests the presence of a considerable area of unvegetated or sparsely vegetated ground surface in the catchment (Schumm 1968). The biological and sedimentological evidence of periodically severe aridity indicates that the nearby presence of a closed canopy forest formation on the surrounding plain was unlikely.

CONCLUSIONS

The major conclusions are that the Bullock Creek and Alcoota Local Faunas demonstrate systematic and community structural continuity from the mid to the late Miocene in northern Australia. The Camfield Beds (yielding the Bullock Creek LF) assemblage contains biological evidence of seasonality (trapping of small fish in drying backwaters), while lithostratigraphic evidence (interbedded evaporites) suggests longer periods of low precipitation and probably high ambient temperatures.

The Waite Formation at Alcoota contains biological and taphonomic evidence of stress (temporarily unbalanced predator-prey ratio; indications of event-based mortality; massive, uniformly weathered fossil accumulations) and geological evidence of periodic aridity (presence of evaporites; evidence of fluctuating water table; evidence of rapid erosion and deposition of texturally-immature sediments, suggesting locally-poor vegetation cover). Both palaeocommunities have small mammal species as a background element, and the dearth of arboreal forms indicates an absence (locally) of closed canopy or evergreen rainforest.

Our palaeoenvironmental reconstruction of the Bullock Creek mid Miocene (Bullock Creek LF time) habitat is that of a meandering river on a wide floodplain, with oxbow lake and

streambank communities predominating. Local fringing forest may have been present on stable outer oxbow margins and on the erosive bank of meanders. Successional plant formations such as sedges and subclimax scrub, grading to woodland, may have been present on the accumulative margins (Fig. 16A). The precipitation regime oscillated from subhumid to semi-arid on an annual basis. Interbedded evaporites in the Camfield Beds indicate periods of aridity during the mid Miocene, reflecting longer term climatic variability.

The Alcoota Locality appears to have represented a small but permanent, possibly spring-fed pond or lake, sometimes expanding to a temporary, large, shallow lake. A wide margin of sedge or grassland, grading to woodland and gully forest, surrounded the outer margin of the basin (Fig. 16B). The region was subject to periodically severe drought, resulting in tethered congregations of large mammals and event-controlled mortality. The precipitation regime oscillated between subhumid and semi-arid, but was apparently less reliable than at Bullock

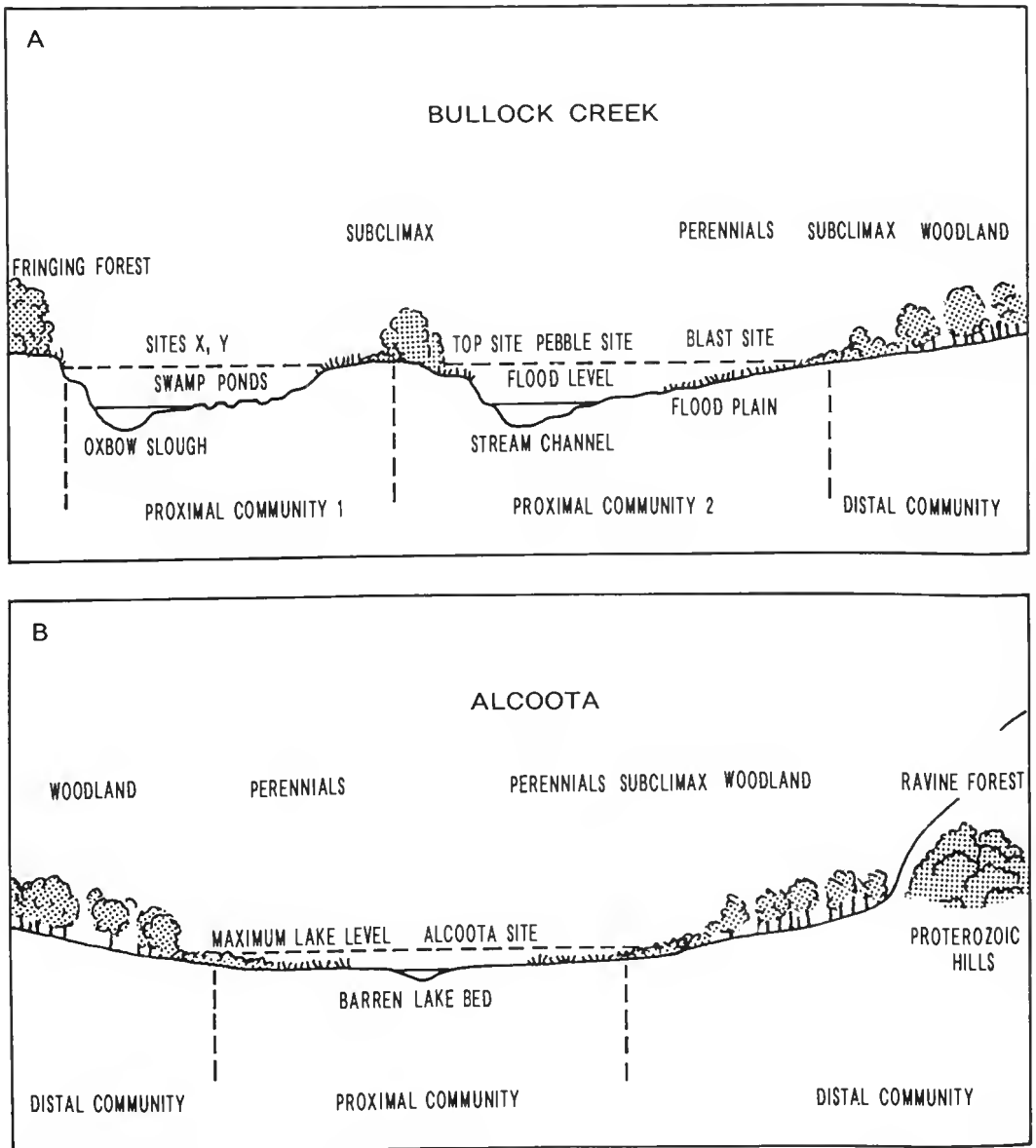


Fig. 16. Schematic reconstruction of palaeohabitats at A, Bullock Creek and B, Alcoota, (vertically exaggerated).

Creek during the times represented by limestone deposition (i.e. Bullock Creek LF time).

These hypotheses convey several implications for Australian Neogene community evolution and biogeography. Principal among them is evidence from mid and late Miocene fossil assemblages that aridification and concomitant habitat diversification was in progress in northern Australia during the mid Miocene and had probably commenced much earlier. Supporting evidence comes from the palaeobotanical record (Kemp 1978, Lange 1983, Truswell and Harris 1982, Nix 1982, Hill 1992) which suggests that aridity was already a feature of central Australia in Eocene times. The concept of a pan-Australian closed canopy rainforest persisting into the mid to late Tertiary from the Paleocene is not supported in any of these investigations.

The extant plant formations of northern Australia are neither venerable remnants of ancient widespread rainforests, nor geologically young communities established since the continent reached its present position in relation to Sundaland. They are unique communities that have gradually evolved in response to the tectonic movement of the continent northward, and to a lesser extent in relation to increased biogeographic influences from Southeastern Asia (Webb *et al.* 1986, Truswell *et al.* 1987). Similarly, Australia's arid-adapted flora, now covering much of the interior of the continent, has an equally long evolutionary history (Truswell and Harris 1982, Nix 1982). Consequently, there are no model plant communities or existing analogous plant communities to which we can refer that would specifically characterize the formations inferred for the Miocene of northern and central Australia.

However, it is possible to characterize the structural aspect of these communities. The geological evidence for significant fluctuations in precipitation combined with tropical or subtropical temperature regimes is very substantial. The local vegetational patterns of both the Alcoota and Bullock Creek localities must have been heavily dominated by flood plain successions, resulting in a significant corridor of un-forested habitat around the depocentres. Fluctuations in the precipitation regime of the magnitude suggested by our observations would not support a predominantly closed canopy forest, but might support local rain green formations and woodland or tree savanna. The possibility of the existence of extensive savanna-like communities in northern Australia during the mid to late

Miocene should not be ruled out, as the conditions appear to have already been suitable for such structures.

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INTERPRETATION OF THE MIOCENE CARL CREEK LIMESTONE, NORTHWESTERN QUEENSLAND.

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ABSTRACT

The Miocene Carl Creek Limestone of Riversleigh, northwestern Queensland, is a clastic deposit composed of sediments characteristic of humid alluvial fans and tufas (*sensu* Pedley 1990). Factors influencing elastic-carbonate yield and processes of carbonate deposition indicate that the calciclastic alluvial outwash comprising the Carl Creek Limestone could only have accumulated under relatively dry, perhaps semi-arid, conditions. This palaeoclimatic interpretation for northern Australia during the Miocene is consistent with interpretations from other data-sets. Other limestone formations of similar age, widely distributed across northern Australia in various sedimentary basins represent different depositional environments, but are here related to the Carl Creek Limestone through a hypothetical hydraulic flow system. Archer *et al.* (1989) postulated the former presence of rainforest at Riversleigh on the basis of an exceptionally diverse mammal fauna, interpreted by them as being a sympatric assemblage. Under climatic conditions postulated here for the region during the Miocene, any rainforest was probably restricted to the proximity of perennial, spring-fed streams within the Carl Creek Limestone depositional basin. The high mammal species diversity in the Carl Creek Limestone might result from a combination of a rainforest-adapted proximal community, and mesically-adapted distant communities whose members travelled to permanent water sources during dry periods. Thus, radiation of Australia's marsupial faunas into drier habitats was already well advanced by earliest Carl Creek Limestone times, and Miocene rainforest at Riversleigh represented a refugium for rainforest-adapted taxa.

Keywords: Carl Creek Limestone, Miocene, Queensland, calciclastic alluvium, tufa, karst, palaeoclimate, palaeoenvironment.

INTRODUCTION

This paper constitutes an initial report on a detailed study in progress of the geology of the Carl Creek Limestone at Riversleigh, northwestern Queensland. As outlined below, the Carl Creek Limestone is one of many limestone formations distributed across the northern half of Australia, west of the Great Dividing Range (Fig. 1). These formations appear to have been deposited during the Miocene, and their geographic and temporal distribution reflects common factors in their genesis.

A general model for continental carbonate deposition in Australia is proposed, based on preliminary interpretations of the Carl Creek Limestone, observations made of other forma-

tions, and previous studies reported in the literature. Sedimentological data are used to reconstruct palaeoenvironmental conditions prevailing across northern Australia during the Miocene in general, and at Riversleigh in particular, and provide a means of testing environmental reconstructions based on vertebrate palaeontology.

AGE AND DISTRIBUTION OF LIMESTONE FORMATIONS IN NORTHERN AUSTRALIA

An understanding of the Cainozoic stratigraphy of Australia in the region west of the Great Dividing Range has evolved slowly. Cainozoic sediments are typically thin, unlithified, poorly

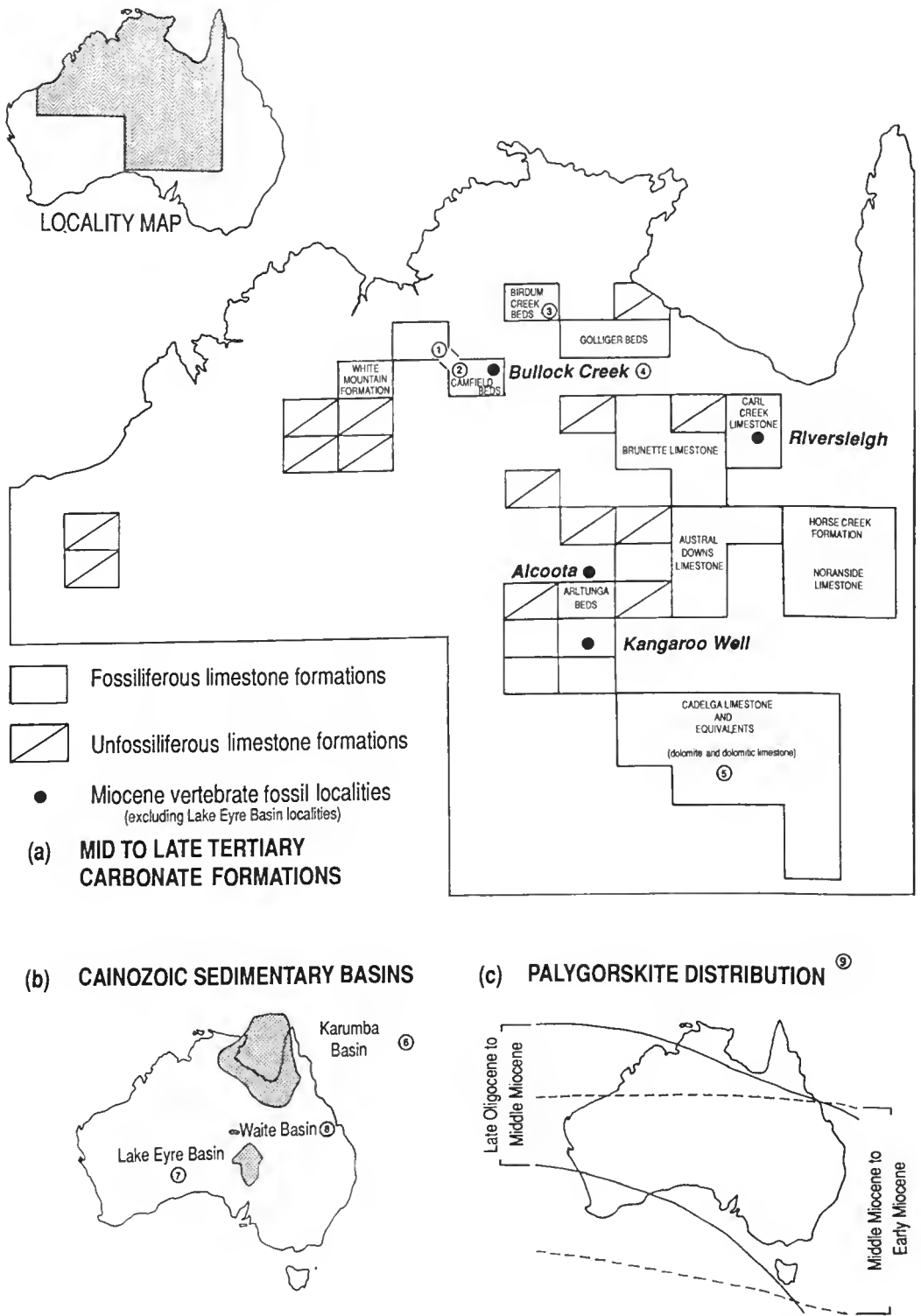


Fig. 1. a, plot of 1:250 000 map sheet areas containing Miocene carbonates; b, Cainozoic sedimentary basins referred to in the text, and (c) distribution of palygorskite clays in the mid to late Tertiary. Compiled from Lloyd 1965a and (1) Sweet (1973), (2) Bultitude (1973), (3) Randal (1969), (4) Plane and Gatehouse (1968), (5) Wopfner (1974), (6) Senior *et al.* (1980), (7) Wells and Callen (1986), (8) Woodburne (1967) and (9) Callen (1984).

exposed in outcrop and often deeply weathered. Apart from duricrusts (indurated weathered surfaces), only the carbonates are lithified and as a consequence of their relative durability, stand out in relief in the landscape and are amenable to study in outcrop. Historically, the major handicap to the development of a stratigraphic framework has been the lack of effective means of correlation. Over the past 50 years, lithostratigraphic techniques and biostratigraphy have advanced to the stage where tentative regional correlation charts have been proposed, such as that of Smart *et al.* (1980:Table 7) which extends from the Gulf of Carpentaria, west into the Northern Territory, and south into the desert regions of South Australia.

The Cainozoic geological history of the region is characterised by long periods of sub-aerial weathering interspersed with shorter term depositional events (e.g. Wopfner 1974). The weathered surfaces are morphological features of great lithostratigraphic value, equal to that of deposited units themselves (Wopfner 1974, Grimes 1979, Smart *et al.* 1980). Smart *et al.* (1980:70) describe the relationship of weathered surfaces to deposited formations through a cycle of events. Each cycle commences with uplift or some other event that initiates the active phase of the cycle. Erosion occurs in the higher, uplifted areas, and sediment is transported to, and deposited in, the lower downwarped areas. A diachronous unconformity surface forms as the depositional area expands or shifts. The process continues until the uplands are worn down and the potential energy of the system is reduced. The passive phase of the cycle is characterised by a long period of deep weathering of a more or less planar land - surface, and results in a terminal weathered surface. A new cycle begins with renewed tectonism or other event. In Australian continental stratigraphy, terminal weathered surfaces represent mappable units that serve as marker horizons over large areas (e.g. Hays 1967). Some have been successfully dated using palaeomagnetic methods (e.g. Idnurm and Senior 1978).

Relative ages of geographically-isolated formations containing vertebrate fossils have been established from the stage-of-evolution of marsupials (Woodburne *et al.* 1985). Primary support for the scheme of Woodburne *et al.* (1985), as it covers the Miocene, is derived from the geology and palaeontology of the Lake Eyre Basin of South Australia. In the Lake Eyre Basin, vertebrate faunas (Local Faunas) are in

superposed formations, providing chronostratigraphic support to the interpretations of marsupial stage-of-evolution. From within the Etadunna Formation, geochronological constraints are provided by palaeobotanical and foraminiferal correlation to sequences outside the region, and to a single radiometric date on illite (Norrish and Pickering 1983), while magnetostratigraphic studies suggest an early Pliocene age for the Tirari Formation (Tedford *et al.* 1992). The age interpretations for the Etadunna Formation are not all consistent, ranging from late Oligocene to mid Miocene. An early Miocene age is shown for the Etadunna Formation in Figure 2 (*contra* Woodburne *et al.* 1985), but the relative ages of other formations containing Local Faunas are not in dispute.

Because of difficulties in lithostratigraphic correlation within the formation, each concentration of vertebrate fossils sampled from the Carl Creek Limestone is initially designated a unique Local Fauna (Archer *et al.* 1989). For the purposes of discussion, Archer *et al.* (1989) group Local Faunas of apparently similar age, geographic position and lithofacies into discrete "systems". In this paper, these "systems" are redefined to have only biostratigraphic meaning (Fig. 2), in order to clearly separate interpretations of age from any other attributes.

Lloyd (1965a) compiled the then available data on the distribution of Tertiary sediments in northern Australia, and reported on the occurrence of the foraminiferan *Ammonia beccarii* in the White Mountain Formation, Brunette Limestone and Austral Downs Limestone (Lloyd 1965b). *Ammonia beccarii* is not a good index fossil, ranging from the Lower Miocene to Recent, but does provide a maximum age for these formations. However, the three formations also contain terrestrial and freshwater gastropods found in the Carl Creek Limestone (Riversleigh Local Fauna of Tedford 1967; part of "system A" of Archer *et al.* 1989), and the un-named formation containing the Kangaroo Well Local Fauna (McMichael 1965). There are insufficient data to establish a biostratigraphic utility for the gastropods, but Lloyd (1965a:126) considered their distribution, other faunal consistencies such as the presence of ostracodes, together with the geomorphological interpretations of geologists mapping the region, as sufficient basis for assigning fossiliferous limestones to the Miocene. The subsequent recognition of the Camfield Beds and the discovery of the Bullock Creek Local Fauna (Randal and Brown 1967, Plane and

Gatehouse 1968, Bultitude 1973) and Birdum Creek Beds (Randal 1969) are consistent with this interpretation, but do not provide further constraints on age. Gastropods in the Camfield and Birdum Creek Beds, and Riversleigh "systems B and C" have not been described.

Lloyd (1965b) attributed the distribution of *A. beccarii* to a marine influence, postulating a widespread northern Australian marine transgression possibly co-occurring with early Miocene transgressions in southern Australia. Implicitly at least, Lloyd (1965) favours an earlier Miocene age for the White Mountain Formation, Brunette Limestone and Austral Downs Limestone.

Figure 2 portrays the probable maximum time-span of limestone deposition across northern

Australia. It represents a relatively brief episode of mid to late-Tertiary sedimentation, probably ceasing before Waite Formation (Alcoota Local Fauna) time. The Carl Creek Limestone is of particular interest because it provides some good exposures in outcrop, contains a strikingly rich assemblage of vertebrate fossils, and is diachronous, apparently spanning the complete time-range of limestone deposition.

GEOLOGY OF THE CARL CREEK LIMESTONE

Previous investigations. The Carl Creek Limestone was named by Jack (1896), who quotes a more detailed report (Jack 1885) of his

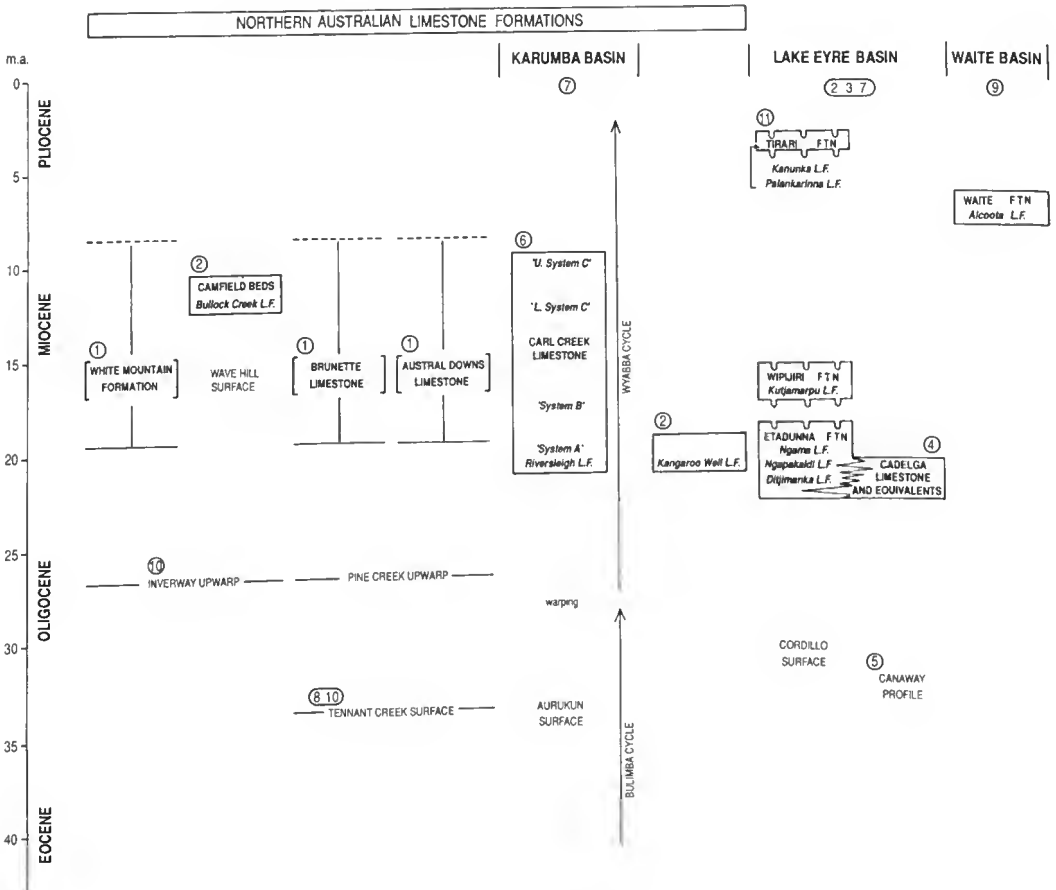


Fig. 2. Correlation chart of northern Australian limestone formations, and other selected formations and weathered surfaces providing geochronological control. Compiled from (1) Lloyd (1965a, 1965b), (2) Woodburne *et al.* (1985), (3) Wells and Callen (1986), (4) Wopfner (1974), (5) Idnurm and Senior (1978), (6) Archer *et al.* (1989), (7) Senior *et al.* (1980), (8) Grimes (1980), (9) Woodburne (1967), (10) Hays (1967) and Tedford (11) *et al.* (1991). The ages of the Wave Hill Surface and Inverway Upwarp are uncertain. The geochronology shown for them is an interpretation of details presented in Hays (1967), specifically (i) the Inverway Upwarp pre-dates the Wave Hill Surface, (ii) the Wave Hill Surface post-dates the Tennant Creek Surface, (iii) the Inverway Upwarp may be genetically related to the Pine Creek Upwarp, and (iv) the White Mountain Formation was deposited during the formation of the Wave Hill Surface.

discovery in 1881, behind the Police Barracks at Carl Creek, of a "hard yellowish limestone, horizontally bedded, unconformably overlying the nearly vertical sandstones etc, which rises on the right bank of the O'Shanassy to a greater elevation than the limestone" (Jack 1896:73). This description of the unit and the location of the outcrop is accurate, though minimal.

Jack (1896) believed, on geomorphological grounds, that the Carl Creek Limestone was the same as that mentioned by Daintree (1872), who referred to a shell of *Tellina* (a marine pelecypod) "from a bed of horizontal limestone at the head of the Gregory on the Barkly Tableland and forwarded to me by Rev. W.B. Clark of Sydney". Jack (1885, 1896) makes no mention of fossils in the Carl Creek Limestone, but on the basis of his correlation with Daintree's (1872) stratum, thought the deposit to be Cretaceous, or possibly Lower Silurian, according to the two hypotheses then current on the age of Barkly Tableland strata. Jack (1896) was aware that limestones of varying ages might be present, a conclusion also reached by Danes (1911) who studied karst development in the region (Danes 1911, 1916).

The earliest report of fossils in the Carl Creek Limestone comes from Cameron (1901). Two species of gastropod, one freshwater and one terrestrial, identified by R. Etheridge Jr in Cameron (1901:14) as *Helix* and *Isodora* (*Therrites forsteriana* and *Isodora* near *I. pectorosa*), were found at the Carl Creek outcrop. Fragments of marsupial bones were found "in the same limestone at a point near the Verdon Rock, a few miles south of Verdon Creek" (Cameron 1901:14). The marsupials were assigned to the family Nototheriidae by de Vis (in Cameron 1901:14). On the basis of the palaeontology, lithology and structure, Cameron (1901) clarified the distinction of the Carl Creek Limestone, which he considered to be Post-Tertiary, from the much older limestones of the Barkly Tableland. Cameron (1901) also provides the earliest interpretation of the geology of the Carl Creek Limestone. Unfortunately, the accompanying map to Cameron's (1901) report greatly exaggerated the extent of the Carl Creek Limestone. Ball (1911), reporting on mining activities and the geology of the Burketown Mineral Field, centred to the north of the study area, realised that a mistake had been made in mapping, but assigned even more of what is now recognised as Cambrian outcrop to the Post-Tertiary (i.e. Carl Creek Limestone). In addition to an account of prevailing stratigraphic confusion, Ball (1911)

provides some interesting details of geomorphic evolution of the area, including evidence for relatively recent tectonism.

Subsequent authors refer to the Carl Creek Limestone by a variety of synonyms. David (1914:255), in referring to the formation as a "*Helicidae* limestone" was not proposing a formal name, but was using *Helicidae* as an adjective to describe a lithology; he also refers to a *Helicidae* sandstone from the Bass Strait islands, *Cellepora gambierensis* limestone from the Australian Bight, and so on. Nevertheless, "Helicidae Limestone" gained acceptance (e.g. Bryan 1928, Whitehouse 1940, Bryan and Jones 1944). Chapman (1937, cited in Bryan and Jones 1944:38) refers to it as "*Helix* Sandstone", while Noakes and Traves (1954:40) proposed the name "Verdon Limestone" for:

"... isolated outcrops (occurring) as poorly-bedded deposits which form the cap of mesas in the vicinity of Riversleigh Station, in the Gulf Fall. The limestone is tough, crystalline to amorphous, and massive, and is about 40ft thick. It contains abundant pebbles of chert some of which has been derived from Cambrian Limestone, and a bed in which shells and fossil bones have been found. Palaeontological evidence is not yet conclusive and the limestone could be either Cretaceous or Tertiary in age."

Noakes and Traves (1954) do not provide references for the literature to which they allude, but there can be no doubt that they refer to the Carl Creek Limestone. The name Carl Creek Limestone was resurrected by Paten (1960) and followed by later workers. The earliest reasonably detailed study of the geology of the Carl Creek Limestone was included by Whitehouse (1940) in an account of Cainozoic limestone formations across Queensland and the eastern Northern Territory. Whitehouse (1940) provides few lithological descriptions of the Carl Creek Limestone, but gives a useful account of stratigraphy, depositional setting, and some comparisons with recent carbonate sedimentation in the Gregory River. He assigned the formation to the Pliocene and, like Cameron (1901), postulated a relatively dry climate during Carl Creek Limestone time. Whitehouse (1940) also found evidence that the limestones he examined in western Queensland occurred stratigraphically between two regionally-extensive weathered surfaces.

During a brief visit to Riversleigh in 1963, Richard Tedford and co-workers collected enough marsupial fossils to firmly establish a mid-Ter-

tiary age for the Carl Creek Limestone (late Oligocene: Tedford 1967; Archer *et al.* 1989; mid-Miocene: Woodburne *et al.* 1985). Tedford (1967) provides good lithological descriptions, a number of stratigraphic sections and an interpretation of the depositional environment.

The geology of northwestern Queensland was investigated by geologists of the Bureau of Mineral Resources, Geology and Geophysics (BMR) and Geological Survey of Queensland (GSQ) as part of a major study started in 1969. A review of the Tertiary geology, and references to earlier literature is provided by Smart *et al.* (1980). As part of the project, BMR and GSQ issued a 1:100,000 scale geological map of the Lawn Hill Region (Sweet and Hutton 1982), which includes the area of the Carl Creek Limestone. Grimes (1974) names and describes the Gregory Limestone, cropping out on the Carpentaria Plain north of the study area, as a possible facies equivalent of the Carl Creek Limestone.

Further palaeontological investigations by Michael Archer and associates during the 1980s led to the recognition of additional outcrop in the western part of the study area, and discovery of new and very diverse faunas of apparently younger age than the Riversleigh Local Fauna described by Tedford (1967) (Archer *et al.* 1986). The study of these faunas is still in progress. The most recent summary of palaeontological activities in progress at Riversleigh and preliminary interpretations are presented in Archer *et al.* (1989).

Depositional setting. The Carl Creek Limestone crops out as a series of small mesas and poorly-exposed rubbly outcrops along a 35 kilometre stretch of the Gregory River drainage system on Riversleigh Station (Fig. 3a). Erosion has reduced the area of outcrop to about 25 km². In the southwest, basement to the Carl Creek Limestone consists of essentially flat-lying Cambrian sediments. These are composed of limestone and dolomite with bands of chert nodules, (Thorntonia Limestone) and minor phosphorite, chert and chert breccia (Border Waterhole Formation) of the Late Proterozoic to Devonian Georgina Basin (Fig. 3b). Within the study area, the Cambrian carbonates have been largely stripped away, leaving a coarse lag of chert nodules and other siliceous remnants over the landscape. Technically, this lag-deposit represents a post-Cambrian weathered surface, but is mapped as Cambrian in Sweet and Hutton (1982), which is a satisfactory arrangement (Fig. 3b) for discussions presented in this paper. The Cambrian

carbonate residuals show advanced karst development. Flat-lying Late Jurassic or Early Cretaceous fluvial sandstones and conglomerates rest unconformably on the Proterozoic basement along the northern part of the study area. No Carl Creek Limestone is deposited directly upon the Mesozoic sediments.

To the northwest, the Carl Creek Limestone is deposited on folded and faulted sandstones, siltstones and conglomerates of the Proterozoic Lawn Hill Platform. The Proterozoic crops out as strike ridges trending northwest-southeast. The linear contact between the Georgina Basin and Lawn Hill Platform parallels the Termite Range Fault, a major structural feature in the Lawn Hill Platform, suggesting that the contact is a remaining manifestation of a fault scarp of Cambrian limestone. Faults have been recorded in the study area in the Cambrian sediments, and have apparently resulted from further movement along pre-existing faults in the Proterozoic basement.

The Gregory River, and its tributary, the O'Shanassy River, are perennial streams maintained by spring-flow discharging from a major aquifer centred to the southwest beneath the Barkly Tableland. Carl Creek, from which the Tertiary limestone takes its name, is a minor tributary of the Gregory River, flowing into the O'Shanassy upstream of the confluence of the two larger rivers. Formerly, it may have been the major channel of the Gregory River. River water is rich in dissolved calcium carbonate, and localised barrage tufa formation presently occurs at rapids on the river.

In the study area, the landscape has a relief of about 160m, with the Proterozoic strike-ridges peaking at about 260m A.H.D. (Australian Height Datum: approximately sea-level). Outside the study area to the southwest, the Cambrian carbonates reach an elevation of 200m to 300m A.H.D. on the Barkly Tableland. The Carl Creek Limestone is restricted to between the 120m and 200m A.H.D. topographic contours.

The Gregory and O'Shanassy Rivers are superposed drainages, cutting across structure in the Proterozoic basement. The confinement of the Carl Creek Limestone to the present Gregory drainage system, and topographic relationships, indicate that the Gregory River valley is an ancient feature, formed in pre-Carl Creek Limestone times.

Stratigraphy. The thickest exposures (about 30m maximum) of Carl Creek Limestone are

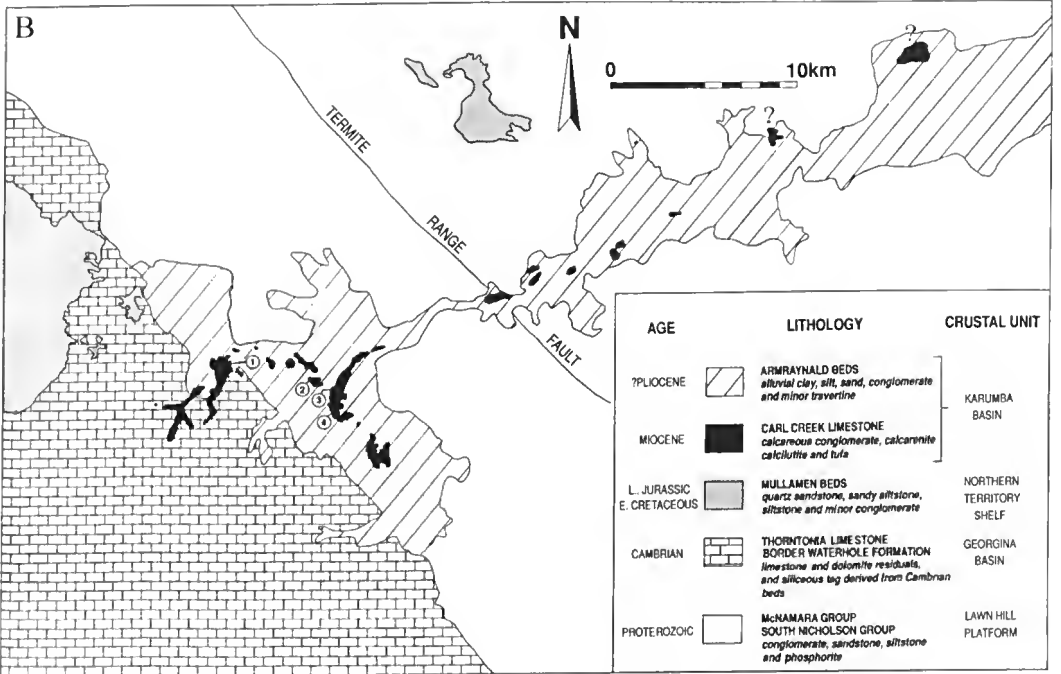
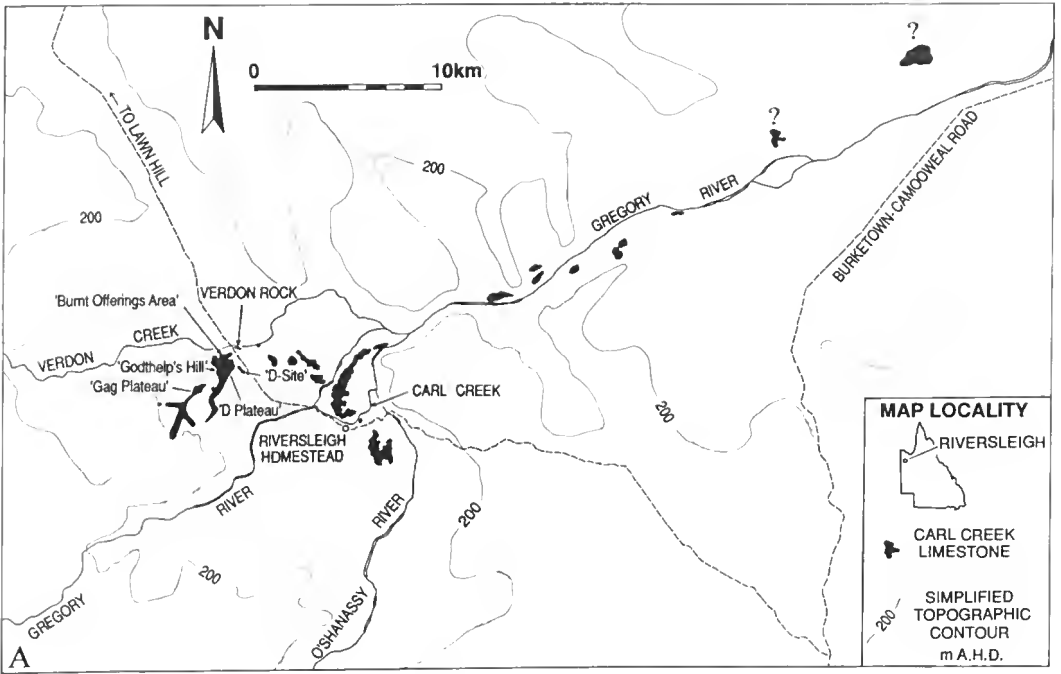


Fig. 3. a. Distribution of the Carl Creek Limestone in relation to geographical features; b, geology of the study area. Informal geographical place-names used by palaeontologists are shown in inverted commas. The position of the Verdon Rock is taken from Ball (1911); the current topographic map of the area identifies a Cambrian limestone mesa five kilometres to the northwest as the Verdon Rock.

found on mesas (Fig. 4a) in the southwestern part of the study area: to the northeast, Pliocene and younger alluvium partially buries the formation, which may be expressed at the surface by little more than a mound of limestone rubble. On the mesas, the limestone has been etched into a karst topography. Clints, grikes, rillenkarren, kamenitza and lapies are common surface features at the edges of the escarpments (Fig. 4b,e), while large blocks have slumped onto the scree slopes.

Irregular and discontinuous bedding planes, delimiting sedimentary units up to three metres thick are discernible on the escarpments. The beds are horizontal or dip at low angles. At the tops of the mesas, a thin mantle of soil and regolith (Fig. 4d) often obscures these contacts, while scree around the base masks the lowest units and their contact with basement. On the ground, bedding is difficult to trace laterally. The generally massive appearance of these large-scale beds, and the formation in general, results

from the effect of the surface-weathering of a limestone of fairly uniform bulk composition, and the appearance in outcrop belies the textural heterogeneity and finer-scale bedding geometries described below. Often the best clues to primary depositional texture are the siliceous clasts that stand out in relief.

The vertical and areal distribution of lithologies and relationship of the Tertiary limestone to the undulating basement are summarised in a series of stratigraphic logs in Figure 5, with additional stratigraphic information shown in Figures 6 and 7. Assuming an average thickness of 20m for the formation, over an outcrop area of 25km², the Carl Creek Limestone has an estimated volume of 0.5km³. The extent of the original depositional basin is more difficult to determine, but Fig. 3a indicates deposition was confined to a relatively narrow valley, probably no wider than the area encompassed by the present 200m topographic contour.

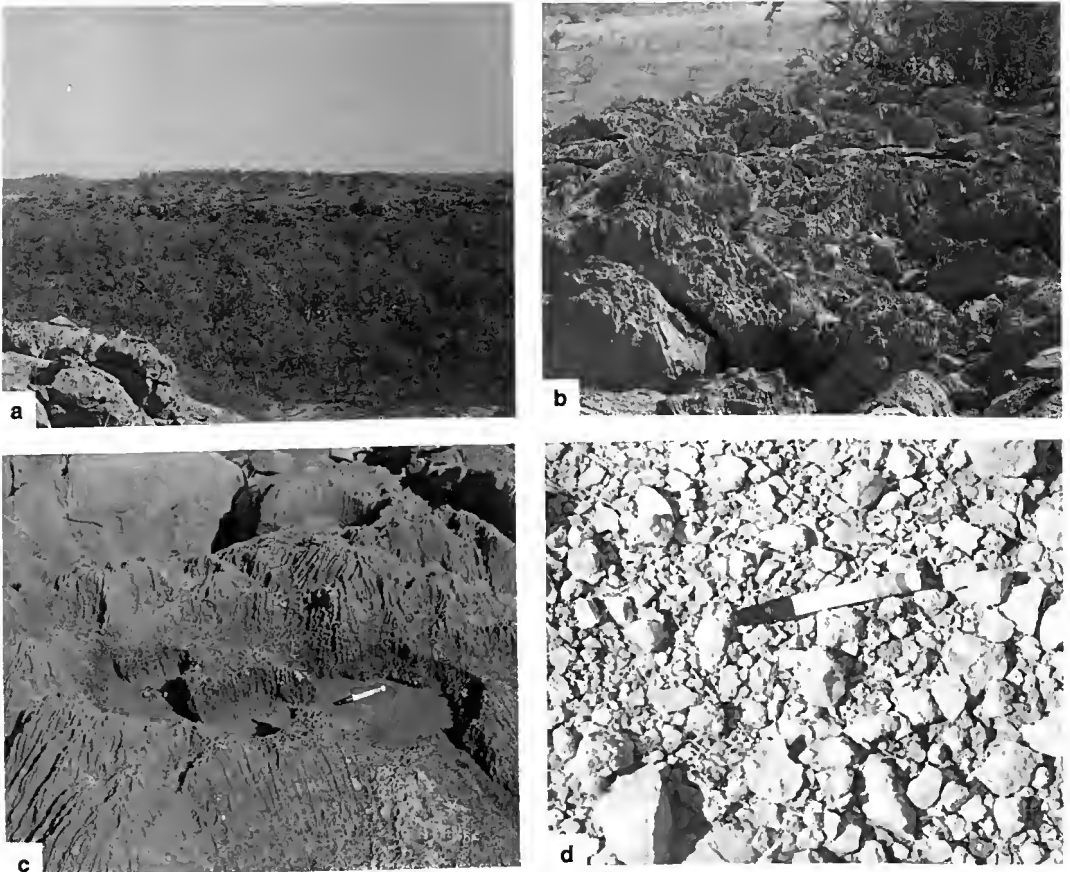
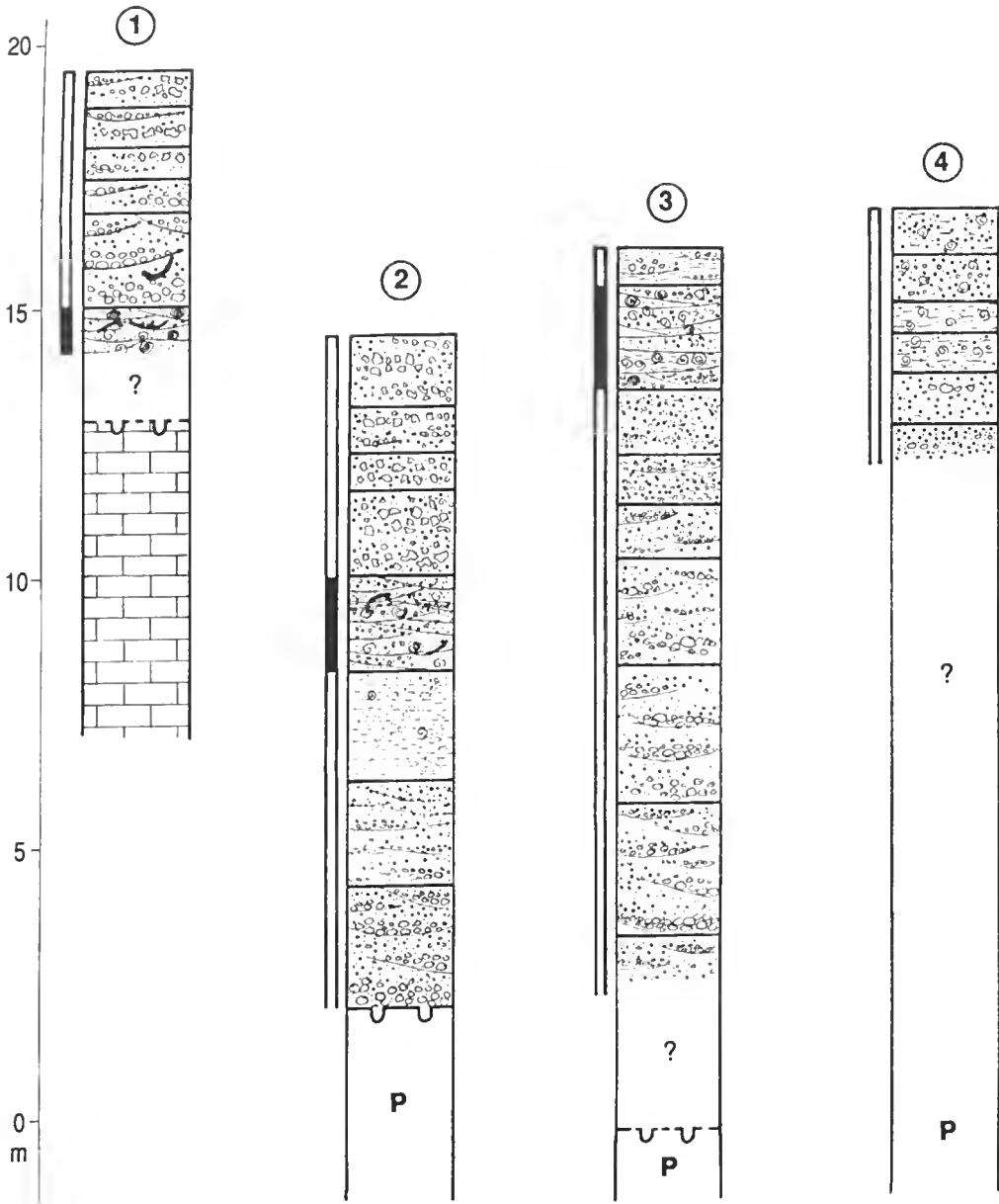


Fig. 4. a, A mesa of Carl Creek Limestone: the thickly-vegetated zone in the foreground bounds the Gregory River; b and c, etched limestone on the mesa escarpment; d, recent colluvium developed on the Carl Creek Limestone. The pen used for scale is 15cm long.



CLAST SIZE-LIMITS	PALAEONTOLOGY	STRATIGRAPHY
silt and micrite	oncolites or other phytoherm	Alluvial facies } Tufa facies } CARL CREEK LIMESTONE
fine to medium sand	gastropods	
coarse sand to gravel	vertebrate fossils	CAMBRIAN LIMESTONE PROTEROZOIC SILICLASTICS P
pebbles and cobbles		

Fig. 5. Selected stratigraphic logs of the Carl Creek Limestone, from locations shown in Figure 3b. Complementary stratigraphic information is given in Figures 6 and 7. No tufa facies have been recognised in the northeastern (downstream) outcrops of Carl Creek Limestone, where exposure is poor. Lithologies present in the northeastern outcrops correspond most closely with those shown in logs 3 and 4.

Lithologies present in the Carl Creek Limestone are classified where possible by depositional textural criteria according to the scheme of Dunham (1962: sec c.g. Pettijohn 1975). The deposit is composed largely of white, pale yellow and orange clastic limestone, including interbedded conglomeratic limestone, limestone breccia, calcirudite, calcarenite, calcwacke and calcilitite. The calcilitites (micritic limestone) are thought to be primarily of clastic origin because of their association with coarser sediments. With the exception of the calcilitites,

the sediments are poorly-sorted and texturally immature. They comprise a distinctive lithological suite accounting for perhaps 95% of the deposit. The remainder consists of mostly of tufa (*sensu* Pedley, 1990), while fissure-fills and cave sediments are the least significant volumetrically. However, the tufas and fissure-fills are of particular interest because they host the bulk of Riversleigh's vertebrate fauna. The stratigraphic sections depicted in Figures 5, 6 and 7 were specifically chosen to indicate the relationship of the tufa facies to the remainder of

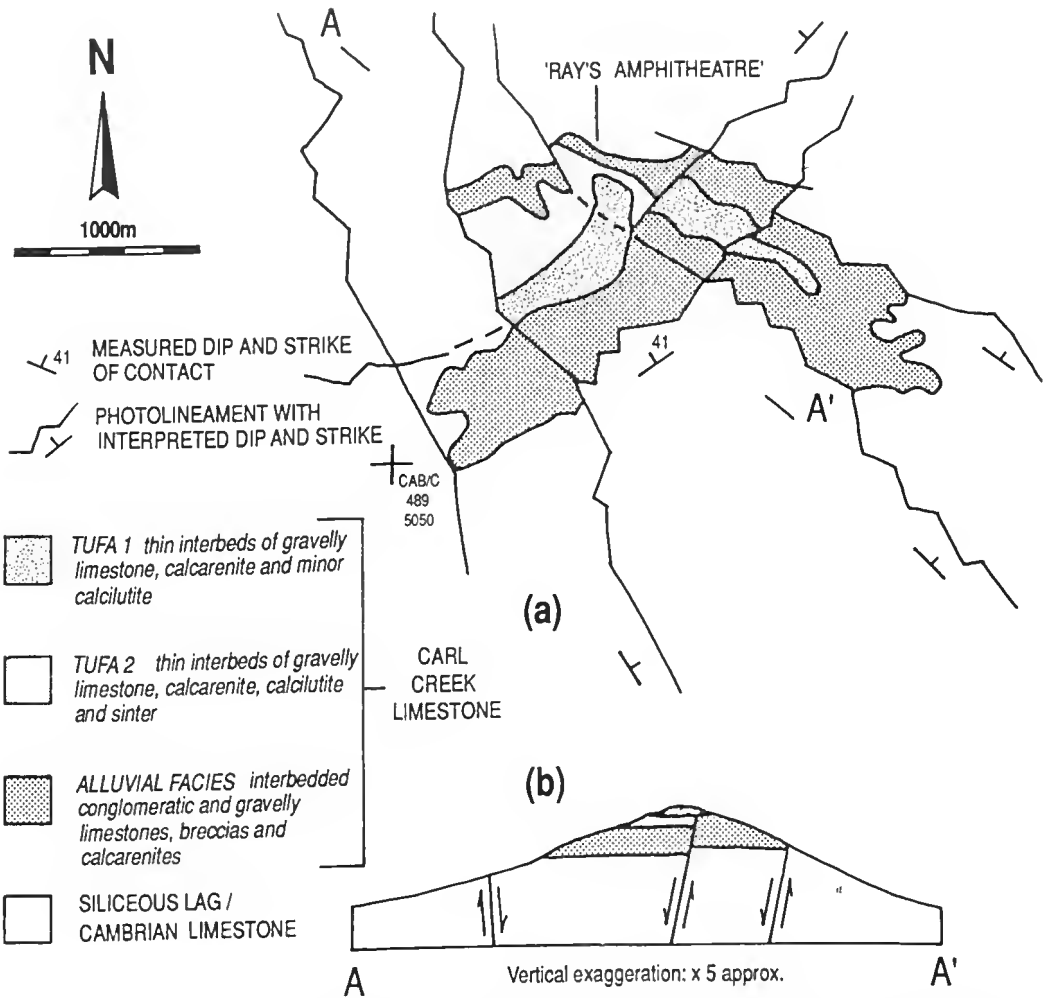


Fig. 6. a. A provisional photogeological interpretation of the eastern part of the "Gag Plateau", with some ground data, showing the relationship of the Carl Creek Limestone to photo-lineaments; **b.** schematic cross-section showing a possible relationship of rock units. These lineaments may represent faults. The area shown is the type locality of the "system C" Local Faunas of Archer *et al.* (1989), who subdivided "Gag Plateau" Local Faunas into three assemblages according to topographic elevation (lowest, middle, highest: Archer *et al.* 1989:65), but on the basis of marsupial stage-of-evolution correlations to South Australian and Northern Territory Local Faunas, recognise "upper" and "lower system C" (Archer *et al.* 1989:55; see Fig. 2, this work). There is a suggestion of a depositional hiatus in "Ray's Amphitheatre" between the two tufa units recognised here. However, the extent of the two units outside "Ray's Amphitheatre" is largely interpreted from photogeology. This figure is intended as a lithostratigraphic hypothesis that may be testable by mammal stage-of-evolution.

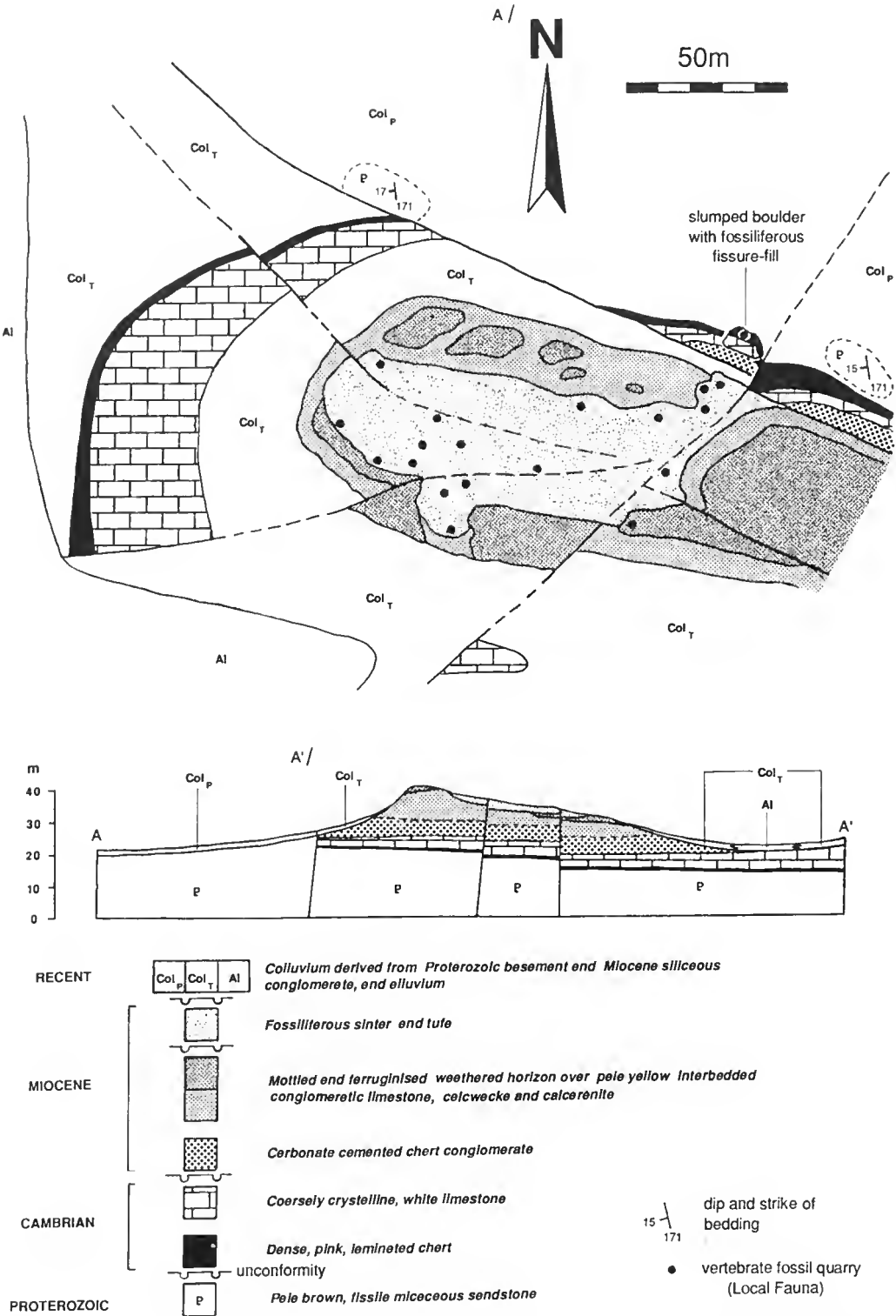


Fig. 7. Plane-table geological map of the "Godthelp's Hill" area, which is the type locality of "system B"-aged Local Faunas of Archer *et al.* (1989). The vertebrate faunas are concentrated in tufas, or in fissure-fills in older limestones. The Miocenc mottled-unit is interpreted as an ancient weathered surface.

the deposit, but are not intended to give an indication of the relative volume of tufa present in the Carl Creek Limestone.

The conglomerates and breccias are variously matrix-supported or clast-supported, and are

massive to poorly-bedded with normal grading. Clast alignment is random. Where they can be traced in section, these beds are lenticular and do not appear to be scoured into underlying strata. They reach a maximum thickness of one metre,

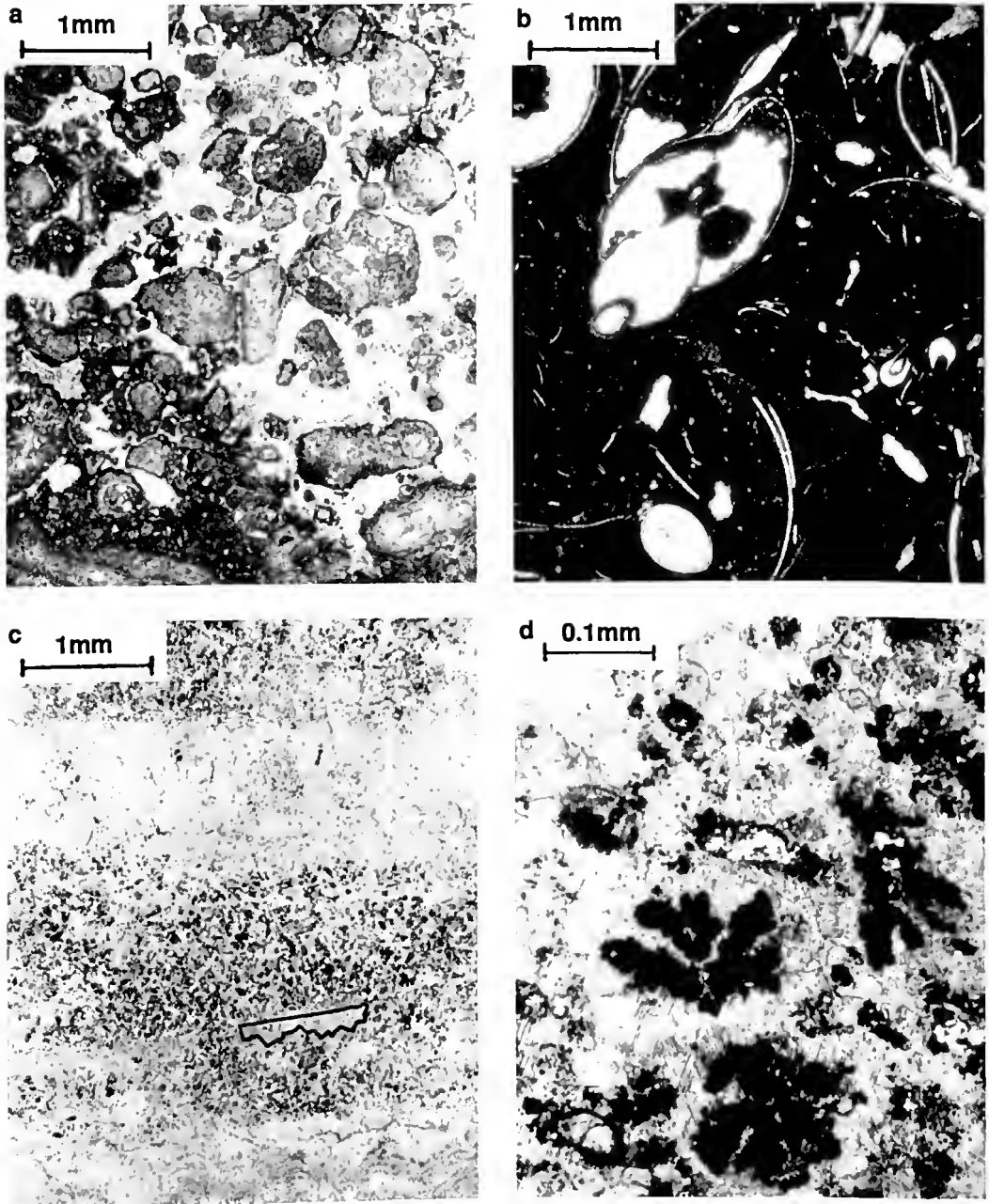


Fig. 8. Thin-sections of: **a.** peloidal calcarenite; **b.** bioclastic calcilutite containing gastropods and ostracodes; **c.** bacterial travertine, Upper Site, "Godthelp's Hill" with **d.** detail of structures resembling the bacterial "shrubs" of Chafetz and Folk (1984). The speckled, bacterial zones in **c.** are interbedded with sinters showing typical algal lamination (bottom). These features suggest that bacteria flourished during periods when physical and chemical conditions were too harsh for algae. The bacterial zones sometimes contain evaporitic calcite plates (one example outlined in ink), morphologically similar to those shown in Figure 12. All plane polarised light.

with horizontal extents of a few tens of metres. Siliceous clasts and fragments of Cambrian limestone are rarely found in these lithologies. Larger limestone clasts are often fossiliferous, containing gastropods, and represent reworked Tertiary limestone.

The clast-supported conglomerates and associated coarser lithologies also show lenticular bed-forms in section, and comprise the bulk of the formation. The coarsest sediments, with cobbles and pebbles sometimes weakly imbricated, occupy the base of scours and grade upwards and laterally into gravelly calcarenites and calcwackes. Such graded sequences are typically one half to one metre thick. Although composed primarily of reworked Tertiary limestone, other rock-types are also present, including chert, sandstone and quartz pebbles and cobbles derived from the basement complex. Siliceous clasts are more common near the base of the Tertiary sequence. Amorphous peloids and reworked Tertiary calcarenite and calcilutite comprise the bulk of the conglomerate matrix

and are the dominant fabric-elements of the calcarenites and calcwackes. These grains are typically coated with a thin layer of micrite (e.g. Fig.8a). Gastropod fragments, laminated limestone particles and quartz sand grains are also commonly present. Aquatic gastropods are common, while isolated vertebrate bone-fragments are occasionally encountered. At a few localities the conglomeratic limestone contains a sufficient concentration of bone to warrant quarrying by vertebrate palaeontologists, as described in more detail later.

Some calcarenites are relatively better sorted, with high initial porosities. Primary voids were later wholly or partially filled by carbonate silts during subsequent episodes of sedimentation, producing geopetal fabrics (e.g. Fig. 9). The massive calcilutites contain an abundance of land snails, or freshwater snails and ostracodes (e.g. Fig. 8b), or a mixture of these invertebrates, but no fish or other vertebrate remains were observed. They were deposited in relatively extensive planar beds, traceable on some outcrops for several hundred metres.

Interbedded with, or cross-cutting, the predominantly coarse calciclastics described above is a distinctive lithological suite characterised by the presence of sinters (travertine), stromatolites, various calciclastic sediments and frequently rich concentrations of vertebrate fossils (Figs 6 and 7). The sinters variously line erosional features in the host sediment, or occur as spring-mounds (Fig. 10a) or sheets interbedded with other lithologies. In thin section they typically show algal lamination, though one notable exception from "Godthelp's Hill" corresponds more closely to bacterial travertine described by Chafetz and Folk (1984) from thermal springs in Italy. Dendritic structures described as "shrubs" by Chafetz and Folk (1984) can be seen under the microscope (Fig. 8c,d). Under high magnification, the shrubs appear to be composed of aggregations of spherical structures having dimensions of about five microns which are probably the remains of bacteria. The black material was determined, using a microprobe, to be iron and magnesium oxides.

The stromatolites occur as plane-laminated sheets or as oncolitic-gravel interbeds (Fig. 10b). The oncolites show characteristic coarse algal-lamination (Fig. 11a), and the nuclei upon which they have formed include vertebrate bones (Fig. 11b), peloids, laminar stromatolite intraclasts, gastropods, or other calcareous lithoclasts.

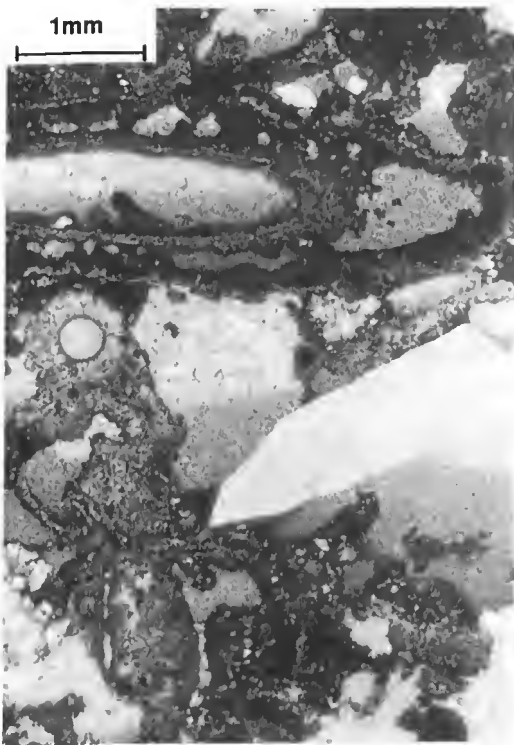


Fig. 9. Thin section of a calcarenite in which the high initial porosity was partially reduced by carbonate silt, and subsequently by calcite cementation, producing geopetal fabrics. Clastic fabric-elements include white, angular chert, probable reworked rhizoconcretions, quartz grains, peloids and larger micrite particles. Plane polarised light.

Amongst the oncolites are rare, very finely-laminated pisolites, and pisolites showing alternating coarse algal lamination and fine lamination (e.g. Fig. 11c). The fine lamination is indicative of direct chemical precipitation of calcite, without the mediating influence of algae.

Pebble conglomerates, calcwackes, calcarenites and calcilitites, texturally similar to those described above, occur as thin (up to a few decimetre) interbeds between the sinters and stromatolitic lithologies, or are closely associated with them. Oncolites, stromatolitic intraclasts and other phytoherm fragments are common fabric elements in the coarser lithologies. As well as gastropods and ostracodes, they contain aquatic vertebrates including fish, crocodilians, turtles, amphibians and platypus. Terrestrial mammals, birds and reptiles are also present.

Amongst the more unusual lithologies associated with sinters are calcite evaporites and phosphorites. Figure 12a is a grain mount of Recent detritus collected from a dried out pool in Old Napier Downs Cave in the Kimberley of Western Australia. The sparite aggregates are plate-like in three dimensions, with two distinct morphologies present. The first have a planar upper surface, with crystal terminations projecting downwards, and presumably formed by evaporation as they floated on the still surface of a drying pool. Others have crystal terminations on both surfaces, reflecting further crystal growth after the plate had settled to the bottom of the pool. Figure 12b shows a cumulate of morphologically-similar crystals from the "Burnt Offerings Area", and includes a section through a probable bat bone.

A phosphorite containing five species of leaf-nosed bat (*Hipposideridae*) (Hand *et al.* 1989) is probably a diagenetically altered bat-guano (*chiropterite* of Hutchinson 1950) formed under a bat roost (Fig. 11d-f). The phosphorite is restricted to the remains of a travertine-lined cavity in older limestone. Associated with it, and not known from any other sites is a red soil similar to those found in modern caves. Thin-sections indicate that the gastropods and algal structures described by Hand *et al.* (1989) from the site belong to a later episode of sedimentation.

Fissure-fills are easily recognised on the escarpments and in outcrop by their generally darker colour and cross-cutting relationships to the host sediment. The larger clasts are typically very angular, and are frequently concentrated in siliclastics relative to the host rock. Some contain enough vertebrate fossils to warrant quarrying (e.g. Fig. 7).

Also present are sediments that may be described as matrix-supported breccias on textural criteria. However, they differ from those described above in lacking any evidence of internal stratification or transport, and are typically mottled by iron-staining. The larger clasts are apparently derived from the underlying lithology, and no material is present to suggest any other provenance. Thin sections reveal evidence of incipient soil formation. These deposits have the characteristics of regolith, though no complete soil profile appears to be preserved anywhere in the Carl Creek Limestone. They are commonly associated with the sinters and related rock-types.

Primary voids in all lithologies are filled with sparry low-Mg calcite cements. When stained

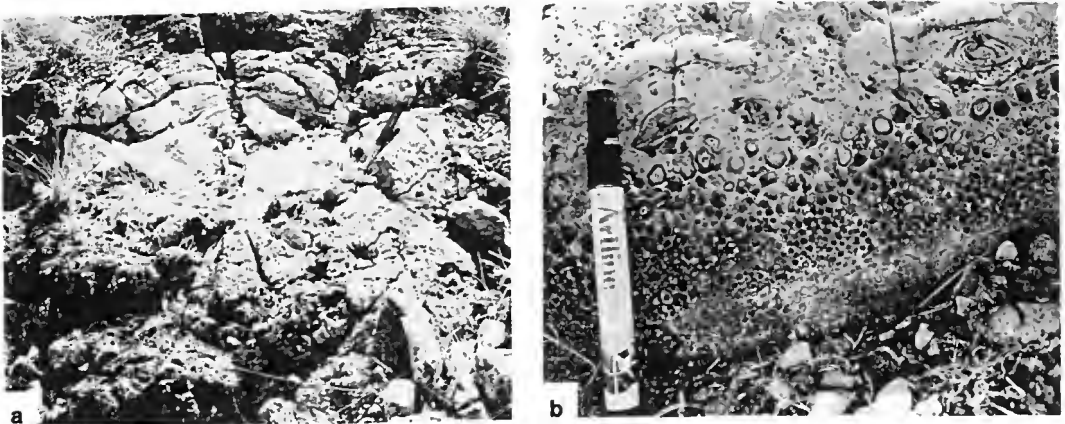


Fig. 10. a, Sinter spring-mound, "Godthelp's Hill". The pick is 35cm long; b, Reverse-graded oncolite gravel, Inabeyance Site, "Godthelp's Hill". The marker pen used for scale is 15cm long.

with Alizarin red-S and potassium ferricyanide to distinguish calcite and ferroan-calcite respectively, according to the method of Lindholm and Finkelman (1972), concentric compositional zoning of the cements are apparent (Fig. 13).

Such zoning is commonly attributed to rapid and frequent fluctuation in the chemistry of the bulk fluid composition from which the cements were precipitated, or rapid changes in Eh, but other poorly understood factors also influence the

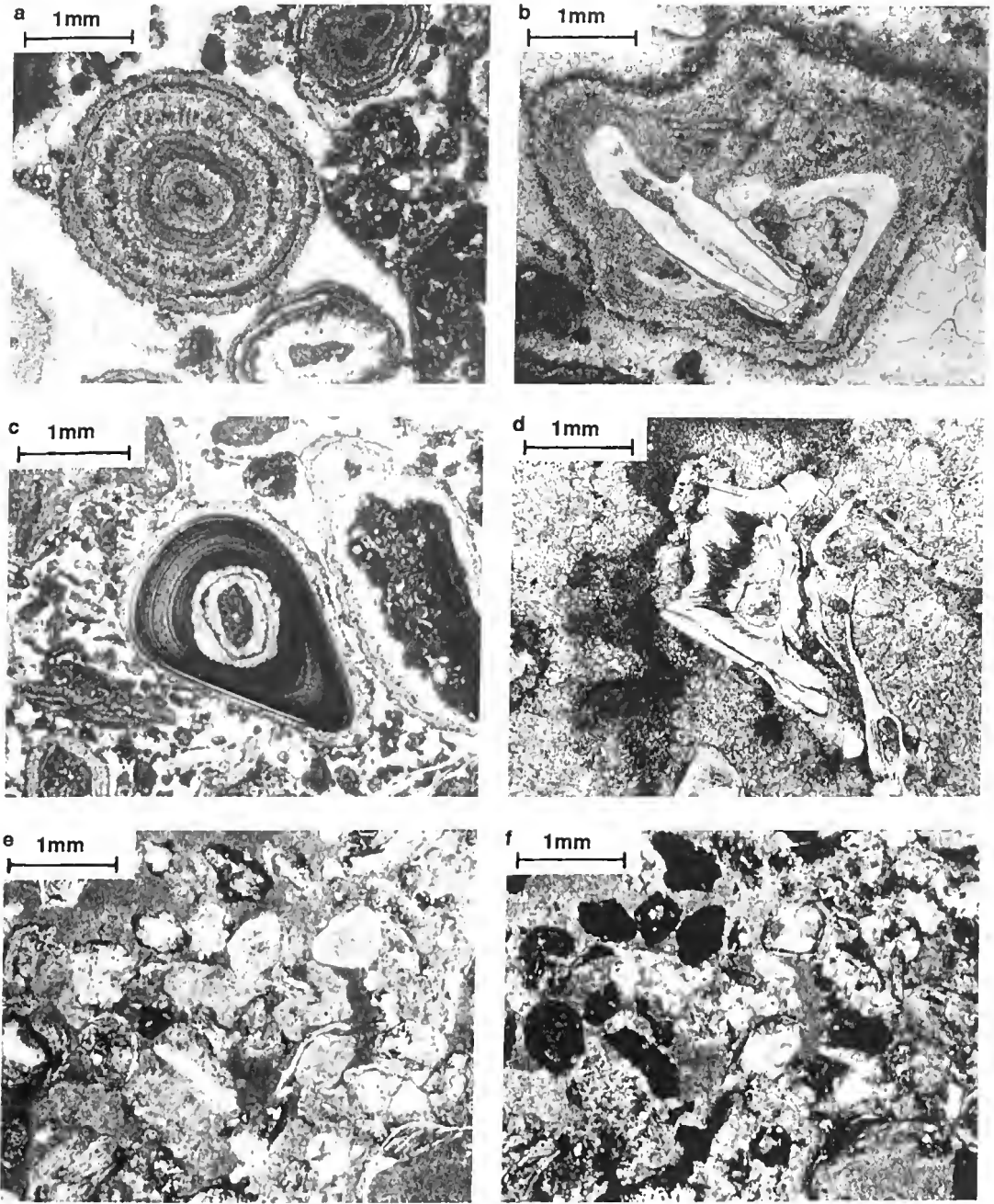


Fig. 11. Thin-sections from Upper Burnt Offerings Site showing: a, a typical oncolite; b, an oncolite with a bat jaw (shown in transverse section) as the nucleus; and c, a pisolite showing alternating zones of coarse algal lamination, and fine lamination resulting from chemical (i.e. abiotic) precipitation of calcite. From Bitesanmenary Site: d, a section through a molar and maxilla of a hipposiderid bat, incorporated in e and f, diagenetically altered bat guano (chiropterite). The phosphate in the chiropterite occurs as bone, amorphous pellets, and laminated cements (e), which appear dark grey or black under crossed polars (f).

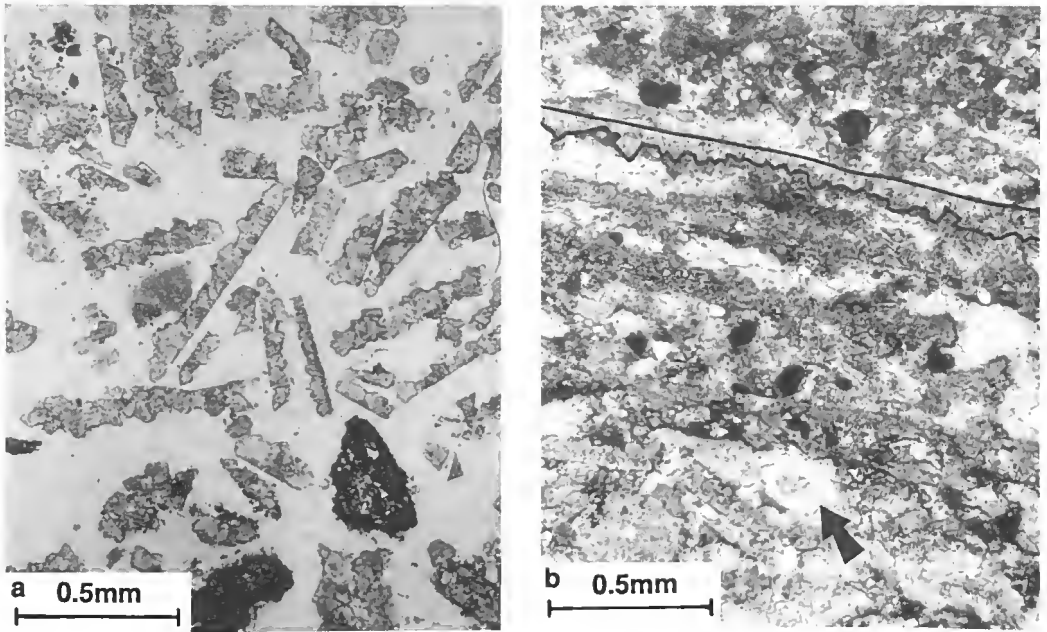


Fig. 12. Thin-sections of: **a**, a grain mount of evaporitic calcite plates retrieved from a dried-out pool in Old Napier Downs Cave, Western Australia, compared with **b**, a cumulate of morphologically-similar plates (with one outlined in ink) from Upper Burnt Offerings Site, Riversleigh. The arrow indicates a transverse section through a probable bat long-bone. Both plane polarised light.

process (Emery and Marshall 1989). A more obvious coarser concentric zoning is also apparent in Figure 13, resulting from alternating bands of spar with a dusty appearance caused by iron-oxide particles included in the crystals, and zones of clear spar. This zonation is attributed to episodes of dissolution in the vadose zone with iron from the ferroan calcite remaining as an oxidised residue, and becoming recemented with the following phase of phreatic cementation. It is taken as evidence of a fluctuating water table. Cement stratigraphy is not consistent between voids, and offers little potential for correlation within the formation. More detailed descriptions of diagenesis, particularly evidence of edaphic processes, in the Carl Creek Limestone are beyond the scope of this paper and are reserved for a future publication.

Structure. Structure in the Carl Creek Limestone is difficult to elucidate because of the lack of marker horizons within the formation. Vague linear features are discernable on air photographs, traversing the Tertiary limestone and in some cases continuing across basement. On the ground in the limestone, these features may appear as very shallow, linear depressions with slightly deeper soils and poorer expression of outcrop. Elsewhere, two to three metre wide, low

ridges of silica- and iron-enriched limestone can be traced for short distances across the landscape. On the "Gag Plateau", some of the contacts with basement are planar, but dipping. On air photographs, these contacts appear to zig-zag around (Fig. 6) but in clear concordance with topography.

The best available evidence that at least some of these features are faults that were active in Carl Creek Limestone times comes from a geological map produced by plane-table methods of "Godthelp's Hill" (Fig. 7). "Godthelp's Hill" is bounded to the north by a fault that can be traced to the southeast into the Proterozoic basement, but the other structures shown cannot be followed confidently far beyond the immediate map area. Both Cambrian and Tertiary limestones are, or appear to be, displaced along these structures, with net relative vertical displacement shown in a schematic cross-section (Fig. 7). The Tertiary units show progressively less displacement with decreasing age, suggesting crustal movements during the timespan represented by the Carl Creek Limestone at that locality. However, karstic processes, or some combination of karstic and tectonic processes, might also account for apparent displacements in the Tertiary limestone.



Fig. 13. Thin-section of sparry calcite cement deposited within an ostracode valve, showing coarse, concentric zoning of alternating clear spar and zones containing iron-oxide inclusions. Just discernible in the clear spar in the bottom right-hand quadrant is finer-scale compositional zoning of alternating ferroan and non-ferroan calcite, revealed by staining. Plane polarised light.

Sedimentological interpretation. The sediments comprising the Carl Creek Limestone most closely resemble those described from humid alluvial fans (e.g. Reineck and Singh 1986), cool freshwater tufas (Pedley 1990) and karst terrains (Esteban and Klappa 1983). The term "alluvial fan" implies a fan-like areal geometry for the deposit. Clearly this does not apply to the Carl Creek Limestone which was confined laterally by topographic highs in the basement complex and has a linear areal geometry (Fig. 3). Therefore, Carl Creek Limestone lithologies corresponding to those described from humid alluvial fans are simply assigned to an "alluvial facies" to avoid any misconception about the areal geometry of the deposit. "Tufa" is used here in the broad sense of Pedley (1990:14) who refers to "all cool water calcareous deposits as tufa regardless of their age and degree of crystallinity". This contrasts with the more widely used definition of tufa as highly porous or spongy freshwater carbonate rich in microphyte and macrophyte growths, leaves and woody tissues. Alluvial fans are generally thought of as being composed of siliclastics, but as the following comparisons suggest, some of Pedley's (1990) tufa facies represent the carbonate analogues of lithofacies described from siliclastic alluvial fans. Pedley (1990:148) makes the analogy but considers the respective scales of the deposits to be a significant difference, with alluvial fans being large-scale compared to tufa deposits.

Climatic factors, topography and source-rock are primary influences on sediments deposited

on alluvial fans, which are variously classified as arid or humid alluvial fans, and while ideal end-members might be readily distinguished, there is a continuum between them. Arid fans are well known from desert landscapes, and are formed by ephemeral streams. On the other hand, humid fans are deposited by perennial streams which break their banks during times of flood, sweeping over the fan and reworking older sediments. Alluvial fans of both types are composed primarily of poorly-sorted, texturally-immature, coarse-grained sediments. The sediments are laid down in beds more or less parallel to the surface of the fan, with angles of deposition typically ranging from 3-6° (rising as high as 10°) but as low as 0.19m/km (0.01°) on humid fans. Stratification is moderately developed with boulder and pebble beds alternating with sandy, silty and muddy beds. They are most commonly associated with braided rivers, and form along a front where steeper slopes pass abruptly into more gentle ones. The coarsest sediments tend to be concentrated at the fan head and the finer ones more distally, though small alluvial fans tend to show proximal characteristics over their entire length. Downstream, they grade into fluvial flood-plain facies.

Sediments of the Carl Creek Limestone alluvial facies are interpreted as follows:

1. Massive or normally-graded, matrix-supported breccias and conglomerates that occur in lenticular beds, but are not scoured into underlying sediments, represent debris-flow deposits. The large angular clasts in the breccias were probably not formed by cataclasis. In shape, they resemble colluvial material found on Tertiary outcrop today (Fig. 4d). In the Recent colluvium, the large clasts become more rounded with depth in the profile, suggesting that the angularity results from sub-aerial etching. The same process produces the sharp rillenkarren on limestone outcrop (Fig. 4b,c).

2. Clast-supported cobble and pebble conglomerates occupying scours in underlying units, grading upwards and laterally into gravely calcarenites and calcwackes, and having lenticular bed-forms represent braided stream channel-deposits.

3. Massive calcilutites containing an abundance of land snails, or freshwater snails and ostracodes, or some mixture of these invertebrates, but seemingly devoid of fish fossils or other vertebrates (Fig. 8b) were deposited upon flood plains or in ephemeral swamps.

The predominance of coarse clastic material, textural immaturity, poor sorting, stratigraphic relationships and bedding geometries in the alluvial facies of the Carl Creek Limestone correspond closely with those described from alluvial fans. The presence of an aquatic fauna and very low angles of deposition indicates something akin to an humid alluvial fan is represented. Although the Carl Creek Limestone was restricted laterally, the degree of confinement was insufficient to preclude braiding and deposition of flood-plain sediments, and implies deposition in a relatively broad, shallow valley.

Pedley's (1990) synthesis of existing knowledge of tufa formation is readily applicable to the interpretation of ancient examples such as those occurring in the Carl Creek Limestone. He identifies five depositional environments for tufa, characterised by unique combinations of geometries, bedform characteristics, facies groupings and biotal associations. The five include the perched springline, cascade, fluvialite (braided and barrage), lacustrine and paludal settings.

The primary tufa fabric-element is *autochthonous phytoherm*. Phytoherm constitutes the "factory" in the system, whereby plants, principally cyanobacteria (blue-green algae), bryophyta and liverworts, mediate or modify localised carbonate precipitation. Some spontaneous chemical precipitation may also occur. Included in these autochthonous deposits are *phytoherm framestone*, consisting of an *in situ* framework of erect or recumbent hydrophytal and semi-aquatic macrophytes with interstitial cements and clastic fabric elements, and *phytoherm boundstone*, more commonly known as stromatolite. Phytoherm boundstone may be anchored to the substrate or unattached (*oncooids* and *oncolites*). Clastic tufa deposits are derived from reworked phytoherm and earlier cements, and tufa weathering products. Included here are *detrital phytoherm*, *oncoidal*, *micritic* and *peloidal tufas*, and *palaeosols*.

At this point some further discussion of the distinction of the alluvial facies and tufa facies, as applied to the Carl Creek Limestone, is required. Pedley's (1990) classification is genetic, based on the recognition that the clastic deposits are derived from phytohermal tufa. However, micrite, peloids and palaeosols are not formed exclusively from phytoherm. Palaeosols may form on any limestone terrain, and may yield micrite, peloids and larger particles that may retain no diagnostic evidence of their primary

origin. Further, biogenic and chemical activity in calcareous soil profiles can result in the formation of laminated particles (pisolites, rhizoliths, laminar caliche) that may resemble stromatolites formed in the aquatic environment (e.g. Read 1976, Klappa 1978, 1979, 1980). Their distinction is not always easy, especially when reworking may have occurred and the particles are removed from their genetic context. Micritic and peloidal deposits are assigned to the tufa facies only where there is a clear stratigraphic and spatial association with unequivocal tufa deposits such as spring sinters and oncolite gravels, and the scale of the deposits is consistent with that shown in the diagrams in Pedley (1990) where beds are typically only a few decimetres thick. In the Carl Creek Limestone, the tufa facies is a volumetrically minor constituent of the formation. Representative examples of tufas from the Carl Creek Limestone include oncolite gravels (braided fluvialite deposit) (Fig. 10b) and a sinter spring-mound (perched springline deposit) (Fig. 10a).

Although some sinter is present in the "Gag Plateau" tufas (Fig. 6), the deposit is dominated by clastic tufas, including calcilutites containing predominantly aquatic vertebrates. The calcilutites were probably deposited in a standing water body, as evidenced by the presence of articulated fish remains, and are thus interpreted as lacustrine tufas. However, no "bull's eye" areal distribution of lacustrine lithofacies (Pedley 1990) is apparent, and the lithological relationships are more consistent with deposition behind a tufa barrage in a fluvial system, though no such barrage was seen in outcrop.

Bacterial travertine is reported from thermal springs (Chafetz and Folk, 1984), but its presence at "Godthelp's Hill" may simply reflect a localised occurrence of physically or chemically harsh conditions favouring the growth of bacteria over algae, such as might occur in a shallow, drying pool subject to high water temperatures and saturated with respect to calcium carbonate. The presence of calcite evaporites (Fig. 12), finely-laminated pisolites formed by chemical precipitation, and pisolites showing alternating zones of oncolitic and abiotic (chemical) lamination (Fig. 11c) may support this interpretation. Risacher and Eugster (1979) report the present formation of similar pisolites (pisoliths) at spring-fed surface pools in playa environments of Bolivia. Calcite evaporites are also known to accumulate in caves (e.g. Fig. 12a), while pisolitic

speleothems known as cave-pearls are morphologically very similar to the pisolites described by Risacher and Eugster (1979). As outlined below, caves were present in the Riversleigh palaeoenvironment, and it is possible that the evaporitic calcites represent cave sediments. The finely laminated pisolites might represent cave-pearls that were flushed out of caverns and incorporated into the oncolitic gravels. However, a spelological influence is not favoured for those such as the example shown in Figure 12c because it requires a complicated history of being flushed into and out of a cave. While this is not an impossible scenario, it is considered the less parsimonious interpretation.

Sub-aerial exposure of limestone results in two end-member diagenetic facies: the edaphic or soil facies and the karst facies (Esteban and Klappa 1983). Soil profiles are rarely preserved intact in the geological record because erosion tends to remove un lithified soil products, which become incorporated elsewhere in clastic sedimentary deposits, as already outlined above. Ancient weathered surfaces are preserved in the Carl Creek Limestone (Fig. 7), but are too poorly developed and difficult to trace throughout the formation to serve as a basis for correlation between outcrops.

"Karst" has been used to designate specific landforms as well as geographic regions characterised by these landforms, but results from a complex set of climatic, tectonic, edaphic, hydrologic and petrologic processes. From a geological perspective, "the karst facies represents a net loss of calcium carbonate, although in some stages of karst evolution or in some parts of the profile, it is possible to have equilibrium or gain in the carbonate budget" (Esteban and Klappa 1983). Of particular interest here are the sites in a karst terrain likely to accumulate sediments that are suitable for the preservation of fossils. The two most likely sites are caves and fissures, and both are represented in the Carl Creek Limestone. Ancient fissure-fills are relatively common and some are fossiliferous (eg Fig. 7). Fossils are rarely incorporated and preserved in regolith.

With the possible exception of some speleothems, cave sediments can usually only be recognised as such if there is sufficient supporting evidence to establish the original depositional context, though mineralogy may be useful (Bull 1983). Hydrodynamic processes of sedimentation occurring in caves are no different from

those occurring in the open, and consequently there are no diagnostic depositional attributes for water-lain deposits. Phosphorite at "Bitesanmtenary Site" (Fig. 11c,d and e) appears to be confined to a travertine-lined cavity, is associated with red soil resembling that commonly found in modern caves, and contains a rich bat fauna. It probably accumulated under a bat roost.

A depositional model for the Carl Creek Limestone. The relationship between the karst, tufa and calciclastic alluvial fan facies is shown schematically in Figure 14. In earliest Carl Creek Limestone times, tufa deposits were formed in, and by, small perennial streams sustained by a regional groundwater system. The groundwater was discharged at a springline along an already dissected and karstified escarpment of Cambrian limestone. During periods of base-volume discharge, turbidity was low, favouring phytoherm tufa formation. During periods of higher flow, when the water table was elevated, perhaps in response to seasonal climatic influences, the streams became swollen. The phytoherm was broken down and transported to lower-energy environments, forming clastic tufa deposits.

During infrequent but intense storm events, rates of precipitation on the plateau and escarpment exceeded rates of infiltration to the water table, resulting in overland flow. Soil products and accumulated debris on the interfluvies became saturated, some becoming mobilised as debris-flows. On the dissected escarpment, intermittent streams began to flow, charged with high sediment loads. Some joined the perennial streams, contributing to their flooding.

At the break in slope at the foot of the escarpment, the streams broke their banks, sweeping across earlier outwash as braided streams. Current velocities dropped abruptly in response to the low channel-gradients, resulting in the deposition of coarse, poorly-sorted and texturally immature sediments. The coarsest material dropped out first in the channels, followed by finer bed-loads that travelled further downstream or spread laterally to be deposited as over-bank sediments. Suspended sediments travelled the farthest, eventually settling out on flood plains or in extensive ephemeral swamps. The floodwaters subsided rapidly as they percolated downwards through older, porous alluvium. Phytoherm tufa formation recommenced at or near the springline with the return to base-flow conditions.

Over time the escarpment retreated to the southwest through erosion, while the topographic

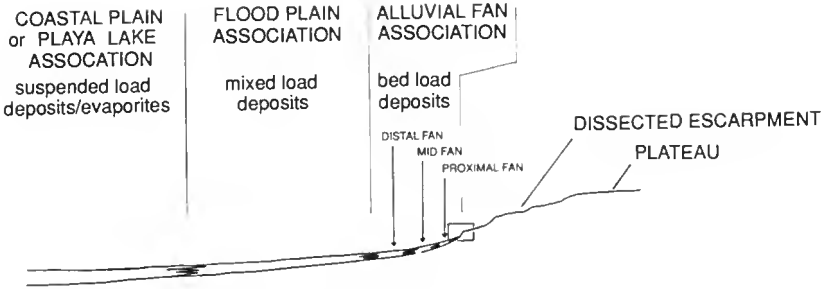
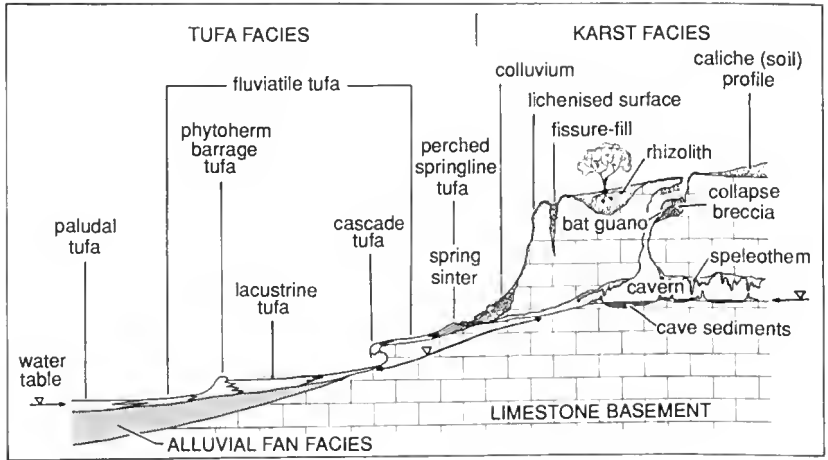


Fig. 14. Schematic cross-section through a fluvial system, showing sedimentary associations and the relationship between the alluvial fan, tufa and karst facies.

position of the spring-line varied according to the position of the water-table. The influence of topography and fluctuating water table on subsequent sedimentation is shown in schematic sections in Figure 15. It is implicit in the model that the relative position of the water table may have varied under the influence of tectonism, long-term climatic variations, or changes in base-level of discharge possibly as a result of eustasy.

Palaeoclimatic evidence from the Carl Creek Limestone. The interpretation of climatic conditions prevailing in the region during Carl Creek Limestone times is developed from two sedimentological principles:

1. In the terrestrial environment limestones erode principally by dissolution, but as outlined above, soils form on limestone terrains and these weathering products may be mechanically transported and deposited as clastic limestones. Tufa is formed principally under biogenic influence, and represents localised re-precipitation of cal-

cium carbonate, which may be reworked as clastic detritus. Whatever their origin, clastic limestone deposits can only accumulate where the rate of dissolution is less than the rate of clastic alluviation.

2. The term "limestone" is applied to those rocks in which the carbonate fraction exceeds the non-carbonate constituents (Bates and Jackson 1980). Thus limestones can only form in environments where non-carbonate sedimentary input is less than the rate of carbonate sedimentation. This applies universally to the marine, lacustrine, fluvial and terrestrial environment.

Alluvial fans are best developed in arid to semi-arid, and subarctic regions: regular heavy rains seem to inhibit their formation (Reineck and Singh 1986). Calciclastic humid alluvial fans are most likely to form in a relatively dry, but not arid climate: wet enough to facilitate calcareous soil formation and perhaps sustain spring-charged perennial streams, but not so wet

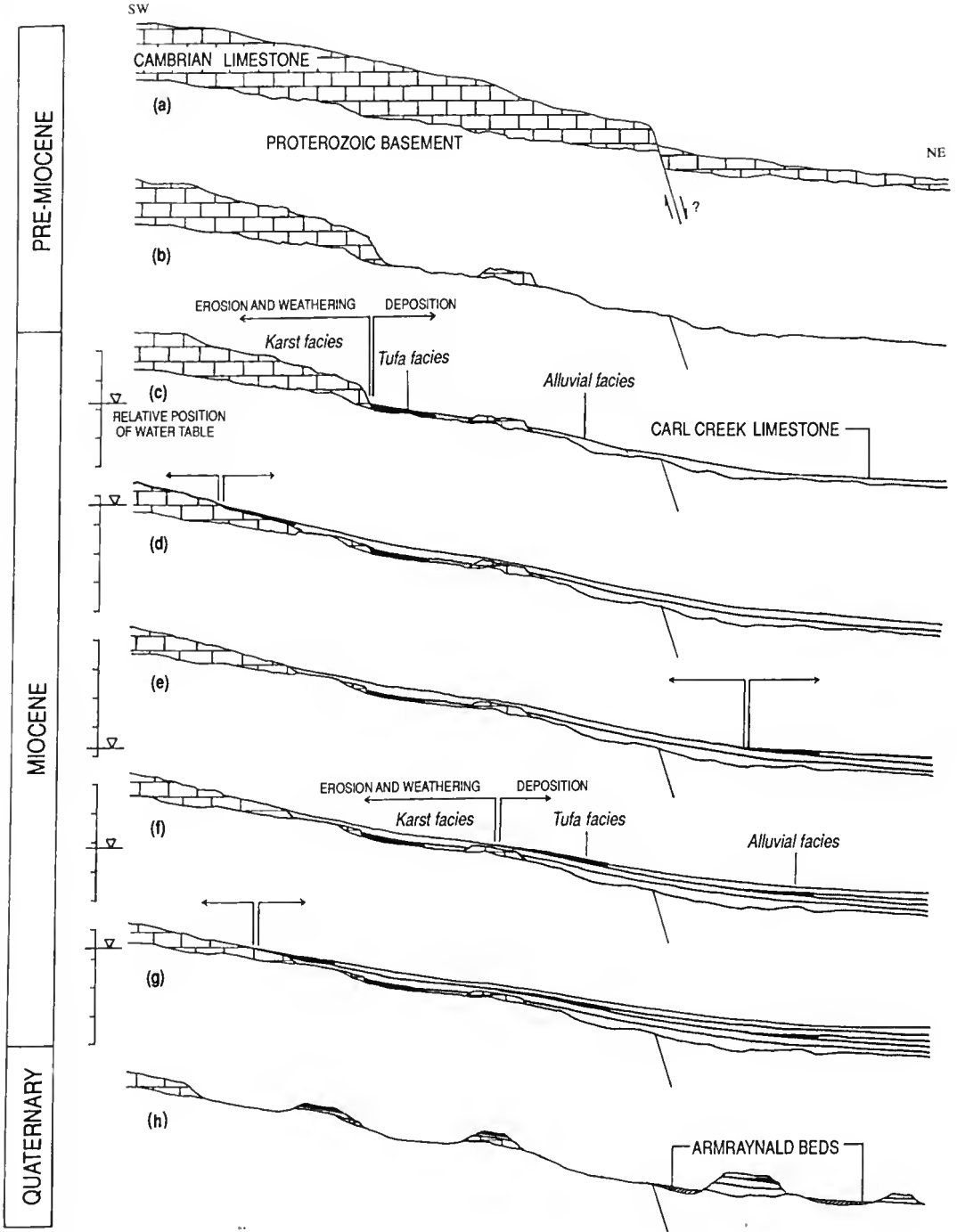


Fig. 15. Schematic cross-sections along the palaeo Gregory River drainage system through time: a, formation of an escarpment of Cambrian limestone; b, scarp retreat through erosion; c to g, a depositional model of the Carl Creek Limestone, showing the influence of a fluctuating water table on stratigraphy; h, the present landscape after reduction of the Carl Creek Limestone to small mesas. The Armraynald Beds are probably Pliocene.

that the rate of dissolution exceeds clastic carbonate alluviation.

The Gregory River valley was formed in pre Carl Creek Limestone times. In the study area, Cambrian limestones of the Georgina Basin were already stripped off to expose Proterozoic basement by Mesozoic times, as evidenced by the deposition of the late Jurassic or early Cretaceous Mullamen Beds directly onto Proterozoic rocks within the areal limits of the Georgina Basin. The Mesozoic sediments are composed of conglomerate, quartz sandstones, sandy siltstones and siltstones and represent a fluvial facies. Some siliceous clasts incorporated into the Carl Creek Limestone appear to have been derived from Mesozoic sediments, while others resemble Proterozoic rocks. Thus, by Carl Creek Limestone times, siliceous rocks were already exposed in the drainage. Following deposition of the Carl Creek Limestone during the Miocene, and a subsequent period of erosion, the Gregory River valley was again alluviated by the Pliocene Armaynald Beds. The Armaynald Beds are a siliceous fluvial deposit consisting of clay, silt, sand and minor conglomerate, with some minor travertine. Today, the Gregory River is cutting down through the Armaynald Beds. Calcareous soils are forming on the limestone outcrops, and colluvium flanks the mesas, but the stream channels contain very little clastic carbonate material. The Gregory River is dammed by barrage tufas, and while the sediments in the impoundments behind the barrages are limy, they do not represent an aggrading clastic limestone deposit and are probably regularly flushed out during the wet season.

The geological history of the ancient Gregory River valley and the interpretation of the origin of the Carl Creek Limestone indicates that a source of carbonate was a necessary condition for the deposition of the Tertiary limestone, but not a sufficient one: a mechanism responsible for the preferential mobilisation and preservation of clastic carbonate over siliceous material must have been in operation. Compositionally-mature, siliceous sedimentary rocks are less susceptible to weathering than carbonates, and under climatic conditions postulated for the formation of the Carl Creek Limestone, siliceous outcrop was likely to yield detrital weathering products at a lower rate than limestone outcrop. This factor, combined with reduced rates of limestone dissolution, resulted in the valley being alluviated by clastic carbonates, in a deposit showing many of the characteristics of humid alluvial fans.

Whitehouse (1940), like Cameron (1901) before him, postulated relatively dry conditions during Carl Creek Limestone times. Cameron (1901) envisaged the Carl Creek Limestone as having formed in an inland sea, into which carbonate-rich streams drained. During times of drought, the carbonate was deposited in response to evaporation. Tedford (1967) also postulated the former presence of a lake, explaining the coarsely-textured sediments from which he collected the Riversleigh Local Fauna as marginal deposits, derived from reworkings of older material deposited during high-lake levels. While lacustrine facies are interbedded in the Carl Creek Limestone, the remaining outcrop does not support the idea that the formation as a whole was deposited in a lake basin: there is no evidence of the vertical succession and concentric zonation of lithofacies characteristic of lacustrine basins.

Whitehouse (1940) observed that fresh surfaces of Carl Creek Limestone usually had "a brecciated appearance", but he nevertheless considered the recent phytoherm tufas forming on the Gregory River a suitable analogue, without explaining the great textural differences. His palaeoclimatic interpretation is quite succinct:

"...it seems most reasonable to suppose that the *Helicidae* Limestone in question was deposited in a valley between the Cambrian limestones in the west and the late Pre-Cambrian quartzites lying to the east; and that the deposits were formed by precipitation from highly calcareous waters (similar to those at present) issuing from the springs along the Cambrian limestone front, springs that were greater in volume than any within the region to-day. That there could have been deposition of such a thickness of compact limestone over such a great area suggests a period of relative aridity when evaporation was high and there was little influx of surface waters to dilute the supply from the springs."

His conclusion accords well with the palaeoclimatic inference presented here, but what was more important at Riversleigh than the volume of spring discharge, was the balance between the rate of carbonate dissolution, carbonate precipitation as a result of biological activity, and calciclastic deposition. The volume of sediment deposited was dependent on this balance and the period of time over which the balance was maintained. Whitehouse (1940) surveyed other limestone formations of apparently similar age cropping out over western

Queensland and the eastern part of the Northern Territory, citing additional evidence for arid to semi-arid conditions across northern Australia. As explained below, evaporation was probably a more important factor in the accumulation of some of these other limestone formations.

Pedley (1990) identifies environmental conditions apparently favouring tufa formation, based on his studies of Quaternary and Recent examples from Europe and North America and other examples described in the literature. None of these deposits appear to be associated with an extensive deposit resembling an alluvial fan such as that comprising the bulk of the Carl Creek Limestone. Tufas apparently achieve their best development in warm temperate climates that are humid enough to sustain a relatively stable groundwater system. The area of tufa deposition is generally well-forested (Pedley 1990).

CHARACTERISTICS AND ORIGIN OF OTHER MID-TERTIARY LIMESTONE FORMATIONS

The most comprehensive summary of the geology of mid-Tertiary limestones is that of Lloyd (1965a), though Whitehouse (1940) and Paten (1960) are also useful, and more recent discoveries are published in Bultitude (1973), Sweet (1973) and Randal (1969). The rock-types, degree of silicification, topographic expression and association with present drainages are remarkably constant over the region (Lloyd 1965a). The limestones are generally less than 30m thick, and many formations crop out as small mesas, buttes or low ridges in linear belts along present watercourses. Some are interbedded with silielastic sediments which may be somewhat calcareous. Limestone lithologies include travertine, "travertinous limestone with a brecciated or pellety appearance", nodular limestone, limestone conglomerates, calcarenites and calcilutites or micrites. They are variously described as being crystalline, amorphous or earthy. Generally they are crudely or massively bedded, and the fossiliferous ones commonly contain gastropods, ostracodes and oogonia of charophyte algae, or more rarely, pelecypods, vertebrate remains and the foraminiferan *Ammonia beccarii* (Lloyd 1965a, 1965b; McMichael 1965).

The fossiliferous deposits have been variously interpreted as ancient valley fills, or lacustrine

sediments deposited in series of small lakes along old watercourses. Some of the micritic sediments are thought to result from chemical deposition rather than clastic deposition. Other limestones are unfossiliferous, and do not appear to be sedimentary deposits, but represent ancient calcretes, formed by edaphic processes. Their topographic expression is similar to that of the sedimentary limestones and are generally thought to be of similar age. Calcretes are also useful as palaeoclimatic indicators, being characteristic of warm areas with limited precipitation (Goudie 1983). Goudie (1983) indicates that annual precipitation rates of between 400 to 600mm per annum are optimum for calcrete formation, though this may also occur at higher rainfalls in exceptional circumstances. All the limestones are silicified to some degree as a result of post-depositional weathering: the more silicified ones are described as chalcedonic limestones, chalcedony or grey billy.

Little is known of the geochemistry of the northern Australian limestones, but they appear to be mostly low Mg-calcite. Minor dolomite is reported from the Austral Downs and Brunette Limestones (Randal 1966a, 1966b). Compositionally, the Cadelga Limestone of the Lake Eyre Basin ranges from slightly dolomitic limestone to dolomite, and was formed by chemical precipitation under mildly evaporitic conditions (Wopfner 1974). Wopfner (1974) reports gastropods, ?diatoms and algal structures in the formation, while a thin-section prepared from dolomite from the Etadunna Formation, courtesy of Neville Pledge, contains gastropods, ostracodes, the foraminiferan *Buliminoides* sp. cf. *B. chattonensis* (see Lindsay 1987) and small, triangular, thin-walled structures resembling palynomorphs. The South Australian dolomites and dolomitic limestones thus share some similarities with the northern Australian limestones. The northern limestones are here envisaged as forming under similarly arid to semi-arid climatic conditions but representing a somewhat different faecies.

The various mid-Tertiary carbonates were deposited in several sedimentary basins, but can be related to each other through a hypothetical model of a single hydraulic flow system, composed of both surface- and ground-waters. Under arid to semi-arid conditions, most rainfall was quickly recycled to the atmosphere by evapotranspiration; most streams were probably intermittent, flowing only after heavy rainfall,

and surface runoff from the continent was low. In a generally flat landscape, with duricrust weathered-surfaces, siliclastic sediment yield was low, and mobilised only after heavy rainfall. A small percentage of the precipitation reached the watertable and recharged the groundwater system. The groundwaters became enriched in dissolved carbonates derived from widespread Proterozoic and Palaeozoic marine dolomites and limestones through which they flowed. Where the groundwater was discharged at perennial springs high in the flow-system, tufas formed and texturally immature calciclastic sediments were deposited as a tufa-calciclastic alluvial fan association (e.g. Carl Creek Limestone). Biogenic tufas are composed of low-Mg calcite, and the preferential removal of calcium resulted in an increase in the Mg:Ca ratio. Such downstream enrichment in magnesium is reported from Recent tufa deposits (Stoffers 1975). Further downstream, the alluvial fan sediments grade into fluvial flood-plain deposits (Fig. 14). The elastic carbonates are finer, better-sorted, and texturally more mature (cf. lithologies yielding the Bullock Creek Local Fauna, Camfield Beds; Murray and Megirian 1992). The finest sediments are micritic, and may have formed either as elastic deposits on the flood-plains or in permanent or ephemeral lakes and swamps, or by chemical precipitation under evaporitic conditions, or by some combination of the two (? e.g. Austral Downs and Brunette Limestones).

Along the groundwater flow-line, evapotranspiration further increased the concentration of salts, while deposition of biogenic low-Mg caleretes resulted in downstream increase in the Mg:Ca ratio. Groundwaters and surface waters were exchanged along the flow-system, depending on the hydraulic gradients between them, but a net result was downstream enrichment of magnesium, and deposition of Mg-enriched limestones as chemical sediments, culminating in precipitation of dolomite in saline-lake or playa environments (e.g. Cadelga Limestone, Wopfner 1974).

PALAEOCLIMATOLOGICAL EVIDENCE FROM OTHER DATA SETS

Distribution of sediments containing palygorskite-group minerals. Depositional environments, age and global distribution of palygorskite deposits are reviewed by Callen (1984). The palygorskite-sepiolite group of min-

erals are fibrous magnesium clays including palygorskite (attapulgite), sepiolite, pilolite, loughlinitite, franclandite and others. They occur in both the marine and continental environments. On continents they form by crystallisation in calcareous soils of arid and semi-arid regions and are one of the few useful palaeoclimatic indicators among the clay minerals. Ancient and Recent examples of non-marine palygorskite are associated with dolomites, limestones (including calerete), fine or sometimes coarse elastics, and sometimes with evaporites, phosphates and cherts. The associated dolomites are frequently of the type formed in a zone of mixing of Mg-charged freshwaters and waters of saline lakes and playas. They precipitate or form within a sediment in conditions less saline than those conducive to gypsum precipitation and are thus often found around the periphery of evaporites or interbedded with them (Callen 1984). The distribution of the palygorskite facies during the mid-Tertiary is shown in Figure 1e, and encompasses the distribution of limestone and dolomite of similar age.

Inferences derived from models of palaeo atmospheric-circulation. Kemp (1978) reconstructed palaeo atmospheric circulation patterns across Australia for the Cainozoic, based on oxygen-isotope data for ocean surface temperatures derived from deep-sea cores. She postulated relatively dry conditions across the northern half of the Australian continent during the Miocene, but was unable to find geological evidence to support her model. Gypsiferous silts and barytes in the Camfield Beds (Randall and Brown 1967), and the distribution of carbonates and palygorskite support her hypothesis.

Bowler (1982), investigating the origin of Australia's desert regions, also used palaeo ocean-temperature data to postulate that sub-tropical high pressure (STHP) cells first formed in the early Miocene, south of the Australian continent. Most of the world's desert regions today are situated in the sub-tropical high pressure belts. The cells moved northwards through the Miocene in response to Antarctic glaciation and consequent steepening of the meridional temperature gradient between the equator and the pole, thus overtaking the continent in its northward drift. By the end of the Miocene the cells were positioned over the southern part of the continent in much the same configuration as today.

Palygorskite data suggest that semi-arid to arid conditions moved over the continent from north to south between the Eocene and Pliocene

as a result of the northward movement of the continent (Callen 1984:figs 10-12), though the latitudinal shifts of the STHP cells envisaged by Bowler (1982) might still be a shorter-term effect superimposed on the effects of a northward continental trajectory. Available geological data does not provide the necessary geochronological resolution to test the hypothesis.

Palaeobotanical evidence. Lange (1982) reviewed the Tertiary palaeobotanical record for Australia. The mid-Tertiary record is poorly represented in central and northern Australia, and heavily biased to the southeastern and eastern parts of the continent. Reconstructing palaeofloras for the whole continent is difficult. Nevertheless, available evidence suggests that conditions suited to the emergence, radiation and substantial specialisation of eucalypts and other mesically-adapted floristic elements occurred during the Oligocene or possibly somewhat earlier. This represents a major transition from the diverse and apparently hydric floras characteristic of the whole continent during the Palaeocene and earlier Eocene, and popularly thought to represent rainforests. The geographic distribution of the Miocene record is equally poor, but the Miocene shows much the same palynological picture as the Oligocene.

Thus, climatic deterioration, possibly starting in the north and moving through central Australia, is envisaged as a major selective pressure for plant evolution in Australia. As the mesically adapted vegetation, and ultimately the xeric vegetation extended their distributions, the rainforests retreated to the southwest, southeastern and eastern parts of the continent (Lange 1982). While this model is broadly consistent with palaeoclimatic interpretations from other data, little is known of the structure of the vegetation over the region.

PALEONTOLOGY OF THE CARL CREEK LIMESTONE AND PALAEOENVIRONMENTAL RECONSTRUCTION

The palaeontology of the Carl Creek Limestone was reviewed most recently by Archer *et al.* (1989). Detailed taxonomic studies are still in progress, but Archer *et al.* (1989) provide an interpretation of the Riversleigh palaeoenvironment based on an assessment of the Upper Site Local Fauna. On the basis of this assessment, they propose a model of vertebrate evolution in Australia since the late Oligocene.

The distribution of vertebrate fossil concentrations in the Carl Creek Limestone accords well with what is known of the preservation potential of the various depositional facies within the formation. Cave deposits and fissure-fills have already been identified as the most likely sites for preservation of fossils in the karst facies, and their fossiliferous occurrence in the Carl Creek Limestone is mentioned above. The occurrence of fossils in the alluvial and tufa facies is reviewed below.

In general, alluvial fans have poor preservation potential (Reineck and Singh 1986), though a calciclastic humid alluvial fan might be expected to have somewhat better potential relative to a siliclastic one because of its composition. The poor fossil record from alluvial fans probably results from the considerable reworking of the sediments. Some concentrations of bone are quarried from what are interpreted as proximal alluvial fan facies, specifically stream-channel conglomerates, in the Carl Creek Limestone. Fragmentary bones are occasionally encountered in more distal facies, but specimens with biostratigraphic utility (i.e. mammal teeth) are rare.

"Site D" of Tedford 1967 (= "D-Site" of later workers), producing the Riversleigh Local Fauna, is one such deposit, and is dominated by large animals, especially crocodiles, dromornithids (large, flightless ratite birds), and various diprotodontid marsupials. Smaller animals are also represented, including chelid turtles, fish, lizards and small mammals. The following observations pertain to D-Site material prepared at the Northern Territory Museum. In some cases, bones extracted with acetic acid from single blocks of limestone belong to a single individual. These bones are typically fragmented, with the fragments displaced relative to each other in the matrix, but are readily re-assembled or placed in articulation after extraction. Thin-sections and macroscopic features indicate that post-depositional, incipient pedogenesis produced the breakages and intraformational translation of the fossils. For example, a large crocodile (NTM P8778) extracted from a single block is represented by the right posterior region of the cranium and posterior region of the right dentary (Willis *et al.* 1990), as well as a complete atlas and axis complex, other anterior cervical vertebrae and cervical ribs, and a set of nuchal osteoderms. The association indicates the animal was still articulated when buried. Other fossiliferous blocks contain numerous large bones

of a number of large species: small bones of large animals (e.g. foot elements) are underrepresented, and small species are very poorly represented.

The preservation suggests that concentration of bone in this lithofacies is either an artifact of the rapid burial of articulated remains, or results from the hydrodynamic removal of the smaller bones of disarticulated animals, leaving a lag of the larger skeletal elements. Smaller skeletal elements of large animals, and remains of small species, were presumably dispersed downstream, and their remains were not reconcentrated elsewhere by hydrodynamic sorting.

Pedley (1990) identifies characteristic faunal assemblages of the various tufa facies, and although fish alone are mentioned among the vertebrates, the invertebrates are a guide to the preservation potential of the various tufa lithofacies (Table 1). An example of a detailed study of the palaeontology of a tufa deposit is that Kerney *et al.* (1980), who include a record of the occurrence of moles, voles and shrews in a Recent deposit from southeastern England. Lacustrine and proximal perched springline sediments stand out as yielding the highest faunal diversity. Lacustrine tufas of the "Gag Plateau", and the perched springline associations of "Godthelp's Hill" and the "Burnt Offerings" area host most of the Carl Creek Limestone's Local Faunas.

The Upper Site Local Fauna from "Godthelp's Hill", described in some detail by Archer *et al.* (1989) is an example of a fauna recovered from

tufa, and is the basis for their palaeoenvironmental model of Riversleigh in the mid-Tertiary. Lithologies occurring within the quarry include interbedded sinters, oncolite gravels, calcarenites and calcilitites, and constitutes a perched springline tufa. All the lithologies are fossiliferous, though the coarser clastics have the greatest concentrations of vertebrate fossils.

The Upper Site Local Fauna contains gastropods, insects, arthropods, crustaceans, fish, frogs, snakes, lizards, crocodiles, birds, and 63 species of placental and marsupial mammals belonging to 27 different families. Fish, crocodiles and turtles are relatively uncommon, and tend to be small individuals, probably juveniles of the species, suggesting the standing water-bodies were small and represented marginal habitats for these aquatic animals. On the basis of the exceptional mammal species diversity, high proportion of arboreal species, high proportion of folivores, species assemblages interpreted to represent finely-partitioned feeding guilds, and presence of some taxa whose closest living relatives occur in rainforests, Archer *et al.* (1989) interpreted the Riversleigh palaeoenvironment as dense, gallery rainforest probably similar to that persisting today in mid-montane New Guinea. There are no adequate palaeobotanical data available to either test the hypothesis, or to reconstruct the structure of the vegetation over the region. Interestingly, Currie (1991) reports a strikingly poor correlation between tree and vertebrate species richness on the North American conti-

Table 1. Tufa associations, dominant fauna and/or flora, and potential for fossil preservation. After Pedley (1990).

Tufa Association	Dominant Fauna/Flora	Preservation Potential
1. PERCHEDSPRINGLINE		
1.1 Proximal	Freshwater gastropods, insect larvae, worms, ostracodes.	GOOD
1.2 Distal	pulmonate gastropods: other taxa rare.	POOR
2. CASCADE	-	POOR
3. FLUVIATILE		
3.1 Braided stream	cyanolith dominated (oncolites)	LIMITED
3.2 Framestone barrage	-	POOR
3.3 Barrage lake	gastropods, charophytes ostracodes, cyanoliths	GOOD
4. LACUSTRINE	algal bioherms, charophytes, diverse gastropods (csp. Lymnaeidae, Planorbidae), bivalves (Unionidae), beetles, insect larvae, fish, diatoms.	EXCELLENT
5. PALUDAL	marsh and terrestrial gastropods.	LIMITED

ment, and intimates similar results for Europe and Australia (Currie 1991:45).

Sedimentological evidence for widespread, relatively dry conditions during Carl Creek Limestone time can only be reconciled with the presence of rainforest, regardless of its type (e.g. Webb *et al.* 1984, 1986) if the Riversleigh rainforest was restricted to those parts of the depositional basin of the Carl Creek Limestone where perennial spring-charged streams and a shallow water-table provided suitable conditions. Elevated ground, the extensive limestone plateau to the southwest, and flood plains within the depositional basin, were unlikely to have supported rainforest, though if the annual rainfall distribution was relatively even (in contrast with the highly seasonal monsoonal conditions prevailing today, for example), perhaps a mosaic of woodlands rather than extensive grasslands were present. Any rainforest is envisaged as having been essentially riparian, grading laterally into other vegetation types over relatively short distances. Such an ecotonal situation might well have supported a high faunal diversity.

This suggests an alternative explanation for the high species diversity in the Upper Site Local Fauna. In a landscape with limited surface water, animals occupying a variety of habitats were obliged at times to travel to permanent water sources to drink, or perhaps in the case of frogs, to aggregate to reduce water-loss (see Tyler *et al.* 1990), particularly during a dry season. The fossil record in the tufa facies of the Carl Creek Limestone possibly includes animals from adjacent (though not necessarily very distant) ecosystems ("distant communities"), though at lower frequencies than animals permanently occupying the tufa environs ("proximal community"), in accordance with the model of Shotwell (1955), for example. Archer *et al.* (1989:37) argue that the lack of evidence for transportation is an indication that distal communities are not represented in the Upper Site Local Fauna, and that all the taxa were sympatric within the immediate area. Animal behaviour, rather than hydrodynamic transportation, is another mechanism that might be responsible for the presence of a distant community in a fossil assemblage.

Some of the taxa listed from the Upper Site Local Fauna do not have close relatives occurring in rainforested areas today, or their closest relatives are restricted to mesic and xeric environments (marsupial moles, koalas, ghost bats and potoroos), while some fossil taxa (e.g.

diprotodontids, thylacoleonids) occur in other formations whose Local Faunas are compositionally quite unlike the Upper Site Local Fauna, and are not interpreted as rainforest communities, (Lake Eyre Basin Local Faunas: Wells and Callen (1984); Bullock Creek and Alcoota Local Faunas: Murray and Megirian (1992)), though some taxa are possibly derived from restricted stands of rainforest fringing permanent water-courses.

Archer and Hand (1987), and Archer *et al.* (1988, 1989) suggest that Australia's endemic marsupial fauna originated in late Oligocene or early Miocene rainforests such as that postulated by them as occurring at Riversleigh. In their model, some elements of these faunas successfully adapted to progressively more mesic conditions and radiated into other environments through the Miocene, others became extinct, and the remainder were confined to rainforest refugia.

While the drying-out of the continent during the Tertiary, and consequent changes in vegetation may have been the major selective pressure on mammal evolution in Australia, evidence presented or reviewed here indicates that mesic to xeric conditions were already widespread across the continent in earliest Carl Creek Limestone times. Therefore, any Miocene rainforest at Riversleigh probably represented a refugium, and some mammals preserved in the Carl Creek Limestone may have already radiated into the drier habitats.

CONCLUSIONS

1. The Miocene Carl Creek Limestone is diachronous, spanning the complete period of widespread carbonate sedimentation across northern Australia. The formation is composed principally of coarse clastic alluvium showing the characteristics of humid alluvial fans, with minor tufa and palaeokarst facies. The distribution of vertebrate fossils within the formation is consistent with preservation potential reported in the literature, with Local Faunas concentrated in tufas, proximal fan sediments and fissure-fills.

2. Geochemical and physical conditions favouring limestone deposition suggest that the calciclastic alluvial outwash comprising the Carl Creek Limestone could only form under relatively dry, perhaps semi-arid climatic conditions.

3. Miocene limestones from different sedimentary basins across northern Australia can be related to each other through an hypothetical

hydraulic flow system. The Carl Creek Limestone represents the most proximal facies in a fluvial system, and the other formations more distal ones. All formed under similarly dry conditions.

4. Palaeobotanical data, palaeo atmospheric-circulation models, palygorskite clay distribution, and the presence of evaporites in the Camfield Beds support the interpretation of regionally dry conditions across northern Australia during the Miocene.

5. Based on an assessment of the mammal component of the Upper Site Local Fauna, Archer *et al.* (1989) postulated the presence of rainforest at Riversleigh during the Miocene. Under the climatic conditions interpreted from sedimentological data, rainforest was probably of very limited extent, confined to the proximity of perennial spring-fed streams and adjoining areas of shallow water-table within the Carl Creek Limestone depositional basin. Thus it is possible that the Upper Site Local Fauna is not a sympatric fauna, but includes elements from distant communities. These distant communities were already adapted to mesic conditions by the early Miocene, and Riversleigh represented a refugium for rainforest taxa.

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THE TYPE AND FIGURED COLLECTION (EXCLUDING PLANT FOSSILS) IN THE PALAEOLOGY SECTION OF THE AUSTRALIAN MUSEUM, WITH SPECIAL REFERENCE TO VERTEBRATES.

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ABSTRACT

The Australian Museum type fossil collection is an important resource to palaeontology. It has recently been enlarged by the incorporation of other type collections from universities within New South Wales. The Australian Museum aims to fulfil its obligations as recommended by the International Commission on Zoological Nomenclature (ICZN) and maintain its position as an important part of Australia's natural heritage.

KEYWORDS: Type specimens, fossils, Australian Museum.

INTRODUCTION

The importance of type collections cannot be overstated, since they are the foundations of the taxonomic framework into which the great diversity of living and extinct organisms are classified. This importance was most succinctly put by Bruton (1979) who stated that:

"A type specimen is an object whose scientific value is incalculable and its loss to science a disaster."

Following on therefore, no cost or effort should be spared in housing these specimens in a secure place with proper professional care and maintenance by trained and dedicated curatorial staff. Students and researchers should keep in mind the importance of the specimens that they describe and/or figure and make certain that they also understand their responsibilities in caring for types and potential types. They should make sure that accurate and detailed documentation accompanies proposed types and that they are deposited in a recognised type collection where they can be adequately housed in perpetuity.

DESCRIPTION OF COLLECTION

Most of the early type fossil material from Australia was described overseas, where it usu-

ally remained. For example, Pleistocene megafauna was described in various works by Owen (c.g. 1877) in Britain, while Palaeozoic invertebrates were described by Dana (1849) in the USA and by de Koninck (1876-77, 1898) in Belgium. De Koninck returned the described specimens to their collector, W.B. Clarke, but they were destroyed in the Garden Palace fire in Sydney on the 22nd September 1882. In many cases replicas of specimens were lodged with the Australian Museum, but these are not as good as the originals.

Until about 1986, type specimens in the Australian Museum were housed in the general collection, within the taxonomic and chronological framework around which that collection is structured. For security reasons, and to facilitate ease of access to this most important part of the collection, a decision was made to house the types separately in their own area with better security and added protection of automatic gas and water fire-fighting systems. At about this time a decision was made to encourage other holders of type specimens in New South Wales (NSW) to deposit their collections with the Museum. The situations in university geology departments were such that they were not able to guarantee a commitment to collections, especially with the current economic trends and bleak outlook for the immediate future. All the universities in the state have now transferred, or

are in the process of transferring, their type collections to the Australian Museum, resulting in a massive increase in the size of the collection. Palaeontologists intending to describe or figure material originating from NSW are encouraged to obtain Australian Museum (AMF) specimen numbers. The following universities have transferred their type fossils to the Australian Museum, and no longer issue numbers for type specimens:

- 1) University of Sydney Department of Geology and Geophysics. Specimen number prefix USGD or SUP.
- 2) University of New England Department of Geology. Specimen number prefix UNEF.
- 3) Newcastle University Department of Geology. Specimen number prefix NUF.

These type specimens have been, or are in the process of being, re-registered with AMF numbers, and lists of corresponding obsolete numbers have been prepared or are in the process of preparation. The only other recognised type fossil collection in the state at this time is that held by the Geological Survey of NSW. On occasion in the past, parts of the Mining Museum's (Geological Survey) fossil collection, including types, were transferred to the Australian Museum. Some still bear the original MF prefix number of their original accession.

The Australian Museum type collection is stored in chronological order of the date of the first published description of a specimen. This method is copied from the University Palaeontological Museum in Oslo where it has been in use for around sixty years (Bruton 1979). Specimens are stored in acquisition order, which means that storage capacity need only be added at the active end. This obviates unnecessary handling of the collection every time additional storage capacity is added. An individual specimen can easily be located using an index of authors' names and dates of publication. Type fossil thin-sections, housed separately in slide storage-cabinets, are also registered separately with an AM (rather than AMF) prefix. The majority of these specimens are sections of corals and bryozoans. Hand-specimens from which these sections were cut are in the general type collection. Large numbers of thin-sections from the universities have yet to be incorporated into the Australian Museum collection and a large amount of work remains to be done before an inventory, and then a computer data-base, is established for the type thin-sections.

During early 1990, Mr G. Hunt, a most capable volunteer, completed an inventory of the collection. This provides an accurate account of the material held by the Museum at the present time and gives an indication of what may be missing in respect of the previous type list. The up-dated inventory is held on manual file cards, indexed by specimen name and phylum.

The completion of an inventory was essential because of the growth of the collection with the recent addition of type material from other institutions, and also because the information in the previously published catalogue (Fletcher 1971) is over 20 years old. It is hoped that a new catalogue can be published soon, in partial fulfillment of our duty to the world palaeontological community, as set out in recommendation 72D of the International Code of Zoological Nomenclature (Ride *et al.* 1985) which states that:

"Every institution in which name bearing types are deposited should

- (1) ensure that all are clearly marked so that they will be unmistakably recognised as name bearing types;
- (2) take all necessary steps for their safe preservation;
- (3) make them accessible for study;
- (4) publish lists of name bearing types in its possession or custody; and
- (5) so far as possible, communicate information concerning name bearing types when requested by zoologists."

Now that an inventory has been completed, information from cards is being transferred to a computerised data-base to allow more efficient management of the collection, easier access to information, the production of indexes of various kinds, and ultimately the publication of a new, updated type list. About five years ago approximately two thirds of the type catalogue was entered into a computer data-base on a CP/M system. Since that time, the Museum has been using IBM-compatible computers, with "Titan" software for collection data-bases. The original files which were on a CP/M system have been transferred to an IBM-compatible PC, presently running text-based information retrieval software, and data entry has recommenced. These

files may ultimately be transferred to "Titan" or other data-base software when a dedicated collection management computer becomes available, hopefully in the near future. In the meantime this temporary system will allow manipulation of the data and production of required indexes.

As of June 1990 the number of type specimens, excluding plant fossils and thin-sections, stood at 6,800 (Table 1). Plant-fossil types, housed in the plant fossil collection, number 740. Of the non-plant types, the largest proportion (5982) originate in NSW, which is to be expected. Vertebrate types account for 777 specimens, or approximately 10%, of the total (Table 1).

Over one third of the vertebrate types are fish fossils, and there are a large number of some extremely important specimens from world class localities in NSW, particularly the Triassic Beacon Hill quarry at Brookvale, the railway ballast quarry at Gosford, and the Jurassic Talbragar Fish Beds near Gulgong. Reptiles comprise a large proportion of vertebrate types and the largest number are fossils of the horned tortoise, *Meiolania platyceps* Owen 1886, from Lord Howe Island. Indeed, the Australian Museum holds the largest and most comprehensive collection of *Meiolania* in the world, both types and others. Another interesting assemblage of reptiles is the opalised remains of plesiosaurs from White Cliffs, collected late last century and early this century, and described by Etheridge (1897, 1904). While the Museum holds quite a large collection of opalised material, not a great deal is type material. The Museum also holds some important *Megalania prisca* Owen 1858 (giant varanid) specimens from Kings Creek, Darling Downs, which were used some years ago at the Museum of Victoria to make skeletal reconstructions of the animals now on display in the Museum of Victoria and in the Queensland Museum. Only one bird specimen is worthy of note and that is the Miocene owl-nightjar, *Quipolornis kouiberi* Rich and McEvey, 1977, from diatomaceous earth deposits at Bugaldi near Coonabarrabran.

Mammals make up nearly half the total vertebrates, with by far the greatest proportion being marsupials, as should be expected. The majority of mammal discoveries in Australia, over the past 20 or so years, have been made outside NSW. This means that the collection contains only a small number of recent discoveries, but a large amount of material described in the early part of

the century and before. The single most important fossil mammal specimen is the monotreme, and platypus ancestor, *Steropodon galvani*, Archer *et al.*, 1985, from Lightning Ridge. This superbly preserved opalised jaw fragment with three molar teeth was discovered in the Galman collection in late 1984. Its recognition as a monotreme pushed back the known history of mammals in Australia by about 70 million years, to the early Cretaceous when dinosaurs flourished across the land.

The Wellington Caves feature prominently as a fossil locality from NSW Wombeyan and Jenolan Caves, Myall Creek, Bingara, and the Bow road cutting are other important NSW sources, while the Darling Downs area of Queensland is also well represented. Significant specimens include the holotype skull of the zygomatic diprotodontid *Zygomaturus trilobus* Macleay 1858 and the pygmy possum *Burramys parvus* Broom 1896. A significant collection of types from various localities on the island of New Guinea are also held at the Museum. Recently described diprotodontids from Papua New Guinea (PNG) and Irian Jaya, such as, the pygmy zygomatic *Hulitherium tomasetii* Flannery and Plane 1986, have been deposited as casts or originals, and reflect renewed interest in the extinct marsupial fauna of New Guinea. New localities are being found in both PNG and Irian Jaya and as yet there is no adequate repository for these specimens in PNG. The placental mammals are dominated by rodents, but also include the Shea's Creek dugong and various mentioned and figured dingo specimens.

The mammal section of the type collection does not contain a large number of holotype specimens; as already mentioned, many of the earlier discoveries were initially described overseas (mainly at the British Museum (Natural History)) where these holotypes still remain. The Museum has plaster casts of many of these holotypes, some of which are in poor condition. In some instances the casts are housed in the type collection. Over the last decade there has been increased activity in vertebrate palaeontology as a result of the growth of the University of New South Wales vertebrate palaeontology group, and a slightly larger proportion of holotypes and paratypes exist from this time. However, with the University of NSW group now concentrating on Queensland sites, the pace of acquisition may slow again.

Table 1. Breakdown of Australian Museum type fossils (not plants) by group and state of origin. As at June 1990. Os = overseas.

Group	Total	NSW	Vict.	Tas.	Qld	SA	WA	NT	OS
ARTHROPODA									
Miscellaneous	61	57	3		1				
Insecta	542	520	1		18		3		
Merostomata	5	5							
Trilohita	1067	1049	3	2	9			3	1
BRACHIOPODA	1841	1638		91	32		51	6	23
BRYOZOA	412	375		14	7		16		
CNIDARIA									
Anthozoa	457	407	15	3	27		4		1
Stromatoporoidea	1	1							
CONULARIDA	6	6							
ECHINODERMATA									
Asteroidea	8	7	1						
Crinoidea	139	134			3		2		
Echinoidea	12	10	1				1		
GRAPTOLITHINA	232	232							
MOLLUSCA									
Bivalvia	670	598	1	9	36	15	6	8	6
Cephalopoda	264	64			44	10	24	118	4
Gastropoda	215	184	13	5	7	6			
Monoplacophora	12				5	7			
Rostroconcha	21	17							4
Scaphopoda	2	2							
Amphineura	3	3							
TENTACULITIDA	8	8							
MISCELLANEOUS INVERTEBRATES	12	8				4			
ICHNOFOSSILS	33	19	2			2		7	3
PISCES	316	299			1				16
AMPHIBIA	6	5							1
REPTILIA	111	96			9				6
AVES	5	5							
MAMMALIA									
Monotremata	13	10			1		2		
Marsupialia	294	192		1	39	8			54
Placentalia	32	31							1
TOTAL VERTEBRATES	777	638		1	50	8	2	78	
TOTAL ALL	6800	5982	40	125	239	52	109	142	120
PLANTS	740								
						(not surveyed, stored separately)			
GRAND TOTAL	7540								

CONCLUSIONS

The type and figured collection at the Australian Museum comprises nearly 10% of all fossil registrations, but the actual number of primary types is not remarkable. The collection is expected to continue to grow at a faster rate than

before the incorporation of the university types, and it will always have priority in collection management over the general collection, in order to enable the Museum to fulfil its role as the responsible institution in New South Wales entrusted with the keeping and preservation of type specimens.

The Australian Museum type fossil collection is an extremely important resource that is available to the worldwide palaeontological community. The recent work done on this collection makes the material even more readily accessible and thus enhances its status as an important part of Australia's natural heritage.

ACKNOWLEDGEMENTS

I am indebted to Geoff Hunt, whose valuable assistance in completing the inventory brought the first stage of the project to a conclusion.

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ABSTRACTS OF THE 1991 CONFERENCE ON
VERTEBRATE PALAEOLOGY, EVOLUTION AND SYSTEMATICS,
ALICE SPRINGS, NT, MARCH 28-30

Title: **EVOLUTION OF THE AUSTRALIAN AND ANTARCTIC VEGETATION DURING THE TERTIARY**

By: **Robert S. Hill.**

Department of Plant Science, University of Tasmania.

Interpretation of plant fossils traditionally splits into two camps; those concerned with 'microfossils' (e.g. pollen and spores) and those concerned with 'macrofossils' (or 'megafossils', e.g. wood, leaves, reproductive structures). It is also traditionally accepted that whereas microfossils provide the general picture of past vegetation, macrofossils generally provide higher taxonomic resolution but represent vegetation from a very restricted area. This dichotomy is currently breaking down in Australia as it is realised that Tertiary vegetation was very complex and the old views of a Tertiary landscape covered for most of the time with widespread and uniform rainforest are fast disappearing.

In Australia it is clear that macro- and microfossil data, or a combination of the two, can be used for many purposes; e.g.

1. **Reconstruction of vegetation.** At present this is probably best illustrated by the complex Early Tertiary rainforests of Tasmania.

2. **Determination of primary and secondary factors in plant evolution.** For example, the sclerophyll elements in Australian rainforests almost certainly evolved primarily in response to low soil nutrients, with low water availability being a secondary problem.

3. **Determination of evolution in response to climate change.** Two key Australian plant families, the Fagaceae and Podocarpaceae, provide excellent evidence of long term evolution in response to declining temperature and changing rainfall patterns.

4. **Leaf form (physiognomy) provides independent evidence of vegetation type and climate.**

5. **The presence of certain taxa provide evidence of absolute climatic limits.** For example, *Nothofagus* leaves in the Antarctic Pliocene place limits on the minimum prevailing temperatures because of their known temperature requirements for survival (during winter) and their growth and reproduction (during summer).

Palaeobotanical research is on the verge of providing a new interpretation of the evolution of the Australian vegetation - the complexity of the emerging data suggests a Tertiary history of diversity, adaptability and regionalism every bit as complex as that which occurs today.

Title: **PRIMITIVE MACROPODIDS FROM THE MIOCENE FRESHWATER LIMESTONE DEPOSITS OF RIVERSLEIGH, NORTHWESTERN QUEENSLAND**

By: **Bernard N. Cooke.**

School of Life Sciences, Queensland University of Technology.

Three new species, *Ganawamaya acris* n. gen. and sp., *G. ornata* n. sp. and *G. acdiculus* n. sp. are described from the early to mid Miocene limestone deposits of Riversleigh, northwestern Queensland. I₁ morphology seen in this genus is similar to that reported in undescribed species from the Kutjumarpu Local fauna and may represent a synapomorphy for Balbarinae. Molar morphology of the species of the species of *Ganawamaya* is intermediate between the known species of *Nambaroo* and those of *Balbaroo*. Deep penetration of the masseteric canal within the mandible, as seen in *G. acris* and *G. acdiculis* and known to occur in other Riversleigh balbarine species, is suggested as a potential macropodoid synapomorphy.

Title: **UNIQUE MARSUPIAL TOOTH REPLACEMENT/FUNCTION IN *Ekaltadeta ima*, AN OLIGO-MIOCENE POTOROID KANGAROO FROM RIVERSLEIGH, NORTHWESTERN QUEENSLAND.**

By: **Steven Wroe.**
School of Biological Sciences, University of NSW.

One of the synapomorphies of marsupials is that M1 is displaced by the erupting P3. One of the synapomorphies of kangaroos (Macropodoidea) is that P3 displaces P2 as well as M1. In hypsiprymnodontine pororoids, alone among previously known macropodoids, P2 may persist for a while after eruption of P3 but it is lost in the adult dentition. Further, P2 changes its position along the toothrow following eruption of P3. In the juvenile dentition, P2 provides a sectorial blade that functions in consort with the compressed trigonid of M1. In the adult dentition, the P2 actually drops well below the occlusal plane but, instead of being lost, re-establishes against the anterior root of P3, within the eruption alveolus of P3, where it takes on a completely different function: butress support for the massive sectorial P3 much in the manner of multituberculates and some specialised placentals. Although P2 retains its basic morphology in the adult dentition, its crown - which does not occlude with any other crown - no longer functions as a sectorial blade. In all specimens recovered so far, this change appears to occur in both the upper and lower dentition. Whether this butress persists late in life is as yet unknown because no old adult specimens have been found. Such a fundamental alteration of position and function for a tooth, within an individual's lifetime, may be unique among mammals.

Title: **ENAMEL ULTRASTRUCTURE OF THE TINGAMARRA FOSSILS.**

By: **Coral Gilkeson.**
Education Centre, Westmead Hospital Dental Clinic School.

Fracture enamel surfaces of a diverse array of teeth, tentatively identified as marsupial, from the Tingamara deposit have been examined in the scanning electroscop. Marsupial affiliation is indicated for some specimens on the basis of prism packing pattern, parallelism and simplicity of prism course and tubule presence. In other specimens, the presence of pseudoprisms suggests less developed enamel in the evolutionary sense. This feature, along with a reduced tubule presence in some specimens, makes marsupial affiliation unclear. The affinities of these enamels to those of any previously known marsupial family, as yet, cannot be determined with confidence.

Title: **WOMBAT-LIKE MARSUPIALS FROM THE OLIGO-MIOCENE FAUNAL ASSEMBLAGES OF RIVERSLEIGH**

By: **Michael Archer* and Henk Godthelp.**
School of Biological Sciences, University of NSW.
*speaker

Vombatimorphian groups represented in the Oligo-Miocene assemblages of Riversleigh include diprotodonts, palorchestids, wynyardiids, thylacoleonids and ilariids. There are also several vombatimorphian taxa that appear to represent groups distinct at the family level. Although vombatids as such were not clearly represented in these assemblages, several wombat-like groups appear to represent close relatives. At least one of these, from Boid Site East, represented by partial skull with dentition, is relatively unspecialised. But another, represented for example in the Upper Site Local Fauna, known at first only from unworn molar caps and jaw fragments, suggested a specialised group with doubtful relationships to vombatids. Comparisons with the previously oldest-known vombatid, *Rhizophascolonus crowcrofti*, from the early to middle Miocene Kutjamarpu Local Fauna of central Australia, were limited by the worn condition of the type specimen (an isolated premolar; although we have since collected two worn molars of this taxon from the type locality).

However, highly hypsodont teeth with unworn as well as worn crowns, obtained from Cleft of Ages and Encore Sites discovered in 1990, suggest that at least some of Riversleigh material may represent a *Rhizophascolonus*-type animal. If so, it is the first vombatid material to come from Riversleigh's Tertiary deposits and the only taxon to suggest the presence of abrasive plant materials in these ecosystems. Crown morphology of this taxon is phylogenetically informative and provides important information about the affinities of these earliest wombats.

Title: THE SMALLEST ZYGOMATURINES - DERIVED DWARF OR PLESIOMORPHIC PYGMY

By: Peter F. Murray¹ and P. Walker².

¹NT Museum, Alice Springs.

²University of California, Santa Barbara.

* speaker

Pig-sized New Guinea Pleistocene zygomaturines are the smallest diprotodontids known. The proportional features of *Hulitherium*, the only formally designated Pleistocene New Guinea zygomaturine, have been considered to be plesiomorphic, as opposed to allometric distortions related to a marked reduction in body size. The Santa Barbara zygomaturine closely resembles the Australian Pleistocene *Zygomaturus trilobus*, sharing its most distinctive derived features such as the presence of nasal tuberosities, hypertrophied frontal crests, deflected cranial base, and deep, massive zygomatic arches and processes. Small, late Miocene zygomaturines such as *Kolopsis torus* lack these features. It is therefore concluded that the Santa Barbara zygomaturine is a derived 'dwarfed' species of *Zygomaturus*.

Title: AN EARLY TERTIARY BAT FROM THE TINGAMARRA LOCAL FAUNA OF SOUTHEASTERN QUEENSLAND

By: S. Hand¹, H. Godthelp¹, M.J. Novacek² and M. Archer¹.

¹ School of Biological Sciences, University of NSW.

² Department of Vertebrate Paleontology, American Museum of Natural History.

* Speaker

A lower molar, upper premolar, edentulous dentary fragment and part of a periotic bone represent Australia's oldest bat. The remains, recovered from freshwater clays in southeastern Queensland, are believed to be approximately 55 million years old (Godthelp *et al.* submitted). Previously, early Eocene bats had been reported only from the Northern Hemisphere, and the oldest Australian fossil bats were from 25 million-year-old sediments in central Australia and northwestern Queensland. Like other early and middle Eocene bats, the Australian species has a primitive dentition and was probably capable of echolocation. The bat is referred to the suborder Microchiroptera and placed in its own genus; its familial identity is yet to be determined. The discovery puts bats in Australia much earlier than expected -before the final breakup of Gondwana.

Title: RINGTAIL POSSUMS (PSEUDOCHEIRIDAE, MARSUPIALIA) FROM THE TERTIARY DEPOSITS OF RIVERSLEIGH.

By: Michael Archer.

School of Biological Sciences, University of NSW.

The Oligo-Miocene faunal assemblages from Riversleigh contain a high diversity of arboreal marsupials including representatives of all groups of living possums (except tarsipedids) as well as many now extinct groups. Among petauroids, there are many pseudocheirids and petaurids as well as other taxa that do not fit into either of these two still extant families. Among extinct groups of

pseudocheirids, there are at least representatives of the genera *Pildra* and *Paljara* previously unknown outside of central Australia.

In addition, there are several species representing *Pseudocheirops*-like ringtails, the only known fossil representatives of this group (apart from an undescribed taxon in the Aleoota Local Fauna). Coming from the late Oligocene to middle Miocene local faunas of Riversleigh, these are the first pre-Pliocene representatives of any of the living groups of ringtail possums.

Species diversity of the pseudocheirids in individual faunal assemblages is very high, with up to nine species per local fauna. This diversity is well in excess of that found in any modern Australian/Papua New Guinean environment, and argues for high floral diversity in the area of middle Tertiary Australia.

The Pliocene Rackham's Roost Local Fauna from Riversleigh contains another pseudocheirid, but by the late Tertiary, arboreal marsupials appear to have been uncommon in the Riversleigh region. Today, the only pseudocheirid in the area is the Rock-haunting Ringtail, *Pseudocheirops dahlia*.

Title: **TERTIARY BANDICOOTS**

By: **Jeanette Muirhead.**

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Within the late Oligocene to middle Miocene Riversleigh faunas, bandicoots are among the most frequently encountered mammals, second only to bats. The diversity of bandicoots is also large, representing a far greater number of taxa than in modern faunas. In contrast, morphological diversity is limited, ranging from very plesiomorphic forms not far removed from dasyuroid morphology, to generalist insectivore-omnivore types. No evidence of open grassland food types is reflected in the dentition of these Tertiary bandicoots. The appearance of species of *Perameles* in the Pliocene (e.g. the Early Pliocene *P. allinghamensis* and a new *Perameles* species from the Middle Pliocene Bow Local Fauna) supports the hypothesis of declining rainforest and increasing grasslands and heathlands by the early Pliocene. As a consequence of this change, there was a marked decline in perameloid diversity.

Title: **THICKHEADS, THINHEADS AND AIRHEADS - MORPHOLOGICAL TENDENCIES IN VOMBATIFORM CRANIA.**

By: **Peter F. Murray.**

NT Museum, Alice Springs.

Although a tendency for large cranial sinuses to form around the brain cavity in vombatimorphian marsupials is a well known condition, few attempts have been made to explain the phenomenon. Similar conditions are found in other mammals, but none have developed it to the extent seen in diprotodontid or palorchestine marsupials. Examination of a series of living and extinct diprotodontan crania suggests that the cranial inflation of vombatimorphian taxa is due to negative brain to body size allometry in combination with a unique pattern of differential growth between the facial and neurocranial components of the skull. The latter phenomenon is attributed to the marked difference in tooth replacement in marsupials and placentals.

Title: **ON WARENDJA WAKEFIELDI HOPE AND WILKINSON 1982, (MARSUPIALIA: VOMBATIDAE).**

By: **Neville Pledge.**

South Australian Museum, Adelaide.

The Pleistocene wombat genus *Warendja* was based on two dentaries and some isolated teeth from McEachern's Cave, western Victoria. Subsequently, a maxilla was described from near Comaam, South Australia (Flannery and Pledge 1987). Further work has uncovered more fragments associated with that maxilla, enough to make a partial reconstruction of the skull. This is long, narrow and lightly built and

supports some of the conjectures of Hope and Wakefield. It is, however, not particularly like *Trichosurus* in gross form, but more like a wynyardiid such as *Muramura*. Despite the plesiomorphic skull form, the relationship of bones in the otic region is distinctly wombat-like.

Title: THE TYPE AND FIGURED COLLECTION (EXCLUDING PLANT FOSSILS) IN THE PALAEOLOGY SECTION OF THE AUSTRALIAN MUSEUM, WITH SPECIAL REFERENCE TO VERTEBRATES.

By: Robert Jones.
Division of Earth Sciences, Australian Museum, Sydney.

The Australian Museum type fossil collection is an important resource to palaeontology. It has recently been enlarged by the incorporation of other type collections from universities within New South Wales. It aims to fulfil its obligations as recommended by the International Commission on Zoological Nomenclature and maintain its position as an important part of Australia's natural heritage.

Title: AUSTRALIAN PLEISTOCENE MEGAFUNA: WHEN AND WHERE.

By: Alexander Baynes.
Western Australian Museum, Perth.

In order to assess the hypotheses that attempt to explain late Pleistocene megafaunal extinctions, it is necessary to have accurate estimates of the dates of the last occurrence of each species in various parts of the continent (Grayson 1989). Such dates are likely to prove harder to determine in Australia than in North America, both because there are fewer sites and because, in some areas at least, the last dates are close to the practical limits of radiocarbon dating. Criteria developed by Metzler and Mead (1985) provide the means to rigorously separate reliable from unreliable radiocarbon dates. When these criteria are applied to radiocarbon dates from Western Australia they reveal that not only do we not have a date for extinction of any megafaunal element in W.A., but there is not a single reliable date for occurrence. Current evidence suggests that the megafauna (including koalas and wombats) became extinct in south-western Australia before 35 000 B.P. In south-eastern Australia, on the other hand, there are reliable dates for some taxa surviving until much later, e.g. *Sthenurus* at 16 000 B.P. in Seton rock shelter (Hope *et al.* 1977).

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Title: DEMISE OF THE DANCING DINOSAURS

By: Tony Thulborn.
Department of Zoology, University of Queensland.

Speed estimates derived from fossil trackways have recently been used to support the claim that dinosaurs were warm-blooded. The fullest treatment of those speed-estimates has been published by R.T. Bakker (1986) in an article titled 'The Return of the Dancing Dinosaurs'. In Bakker's estimation, 'fossil footprints show that the dinosaurs cruised at warm-blooded speeds'.

Comparisons of absolute speed are meaningless in the context of Bakker's discussion. Such comparisons would be meaningful only if they were expressed in terms of a standardized variable (e.g. dimensionless speed or relative stride length). Even then it would be unreasonable to assume that such a standardized variable must be correlated with thermal physiology; it might equally well (or better) be correlated with size, shape, locomotor anatomy or behaviour.

From simple inspection it seems that Bakker's data demonstrates nothing beyond the well-known relationship between body size and absolute speed amongst terrestrial animals in general. This relationship carries no implications for thermal physiology. In addition it must be noted that the speed-estimates derived from dinosaur trackways by Bakker are entirely consistent with those obtained by other researchers. Such speed-estimates can reveal nothing of warm-bloodedness or cold-bloodedness.

In summary, Bakker's argument about the physiological significance of dinosaur trackways is fundamentally flawed. There is no factual basis for his notion the 'dinosaurs cruised at warm-blooded speeds'.

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Title: **ANEW GENUS OF LARGE MADTSOIID SNAKES FROM OLIGO-MIOCENE DEPOSITS AT RIVERSLEIGH (QUEENSLAND) AND MIOCENE DEPOSITS AT BULLOCK CREEK (NORTHERN TERRITORY).**

By: **John Scanlon.**
School of Biological Sciences, University of NSW.

Disarticulated but associated collections of snake vertebrae can be referred to individual skeletons by size, proportions and features indicating regions within the column. Large remains from a single location at Bullock Creek (Blast Site) and several sites at Riversleigh (including Mike's Menagery, Camel Sputum and White Hunter amongst others) represent a new genus *Yurlungurr* and two new species of madtsoiid snakes distinct from the only other Australian madtsoiid described, *Wonambi naracoortensis* (Smith 1976). Material from Bullock Creek represents a single individual which possesses distinctively curled-up zygosphenes and zygantra in a region extending from near mid-body to a point anterior to the elocae. This regional feature has not been observed in any material from the Riversleigh sites and is here regarded an autapomorphic condition defining the species *Yurlungurr sp. nov. A*. Riversleigh specimens are not known to possess any apomorphies with respect to *Y. sp. nov. A* but are generally similar to each other and are referred to *Yurlungurr sp. nov. B*. As well as vertebrae from most regions of the body and tail, the Riversleigh deposits also include ribs, jaw elements and a basisphenoid complex referable to the same large species. These elements (also known from *W. naracoortensis*) support a view of Madtsoiidae as a very early lineage within Alethinophidia, retaining many plesiomorphic features and distinct from all extant families of boa-like snakes.

Title: **SCINCID LIZARDS FROM RIVERSLEIGH: A PRELIMINARY REPORT**

By: **Mark N. Hutchinson.**
South Australian Museum, Adelaide.

The world's and Australia's largest family of lizards is the Scincidae, with over 1,000 described species in about 120 genera. The fossil record of the group is however poor and uninformative. Sorting of the fossils recorded over the last decade from the Tertiary deposits at Riversleigh, Queensland reveals a diverse fauna of scincids from the Oligo-Miocene to late Miocene, the richest yet reported anywhere. Almost all specimens sorted so far have been tooth-bearing bones, especially

dentaries, for which no significant body of published literature exists, making recognition of fossil specimens difficult. Three phylogenetic lineages are recognised in the modern skink fauna of Australia and all three have been found in early to middle Miocene sites. Of the three, the *Sphenomorphus* group is the best represented lineage, the *Egernia* is less abundant but still widespread, and the *Eugongylous* group is known only from a single certainly identified specimen. The presence of these groups in Australia thus dates at least to the Oligocene, implying that the conventional explanation of arrival from the north must have entailed significant island hopping and overwater dispersal. The alternative, that skinks are Gondwanan and diversified through vicariance, has not often been considered, but is not inconsistent with currently observed centres of skink endemism or with the evidence presented here.

Title: **EARLY HISTORY OF THE CRYPTODIRAN TURTLES IN AUSTRALIA**

By: **E.S. Gaffney*¹, L. Kool², T. Rich³, P.V. Vickers-Rich², N. Pledge⁴, M. Archer⁵ and A. White⁵.**

¹ American Museum of Natural History, New York.

² Monash University, Victoria.

³ National Museum of Victoria, Melbourne.

⁴ South Australian Museum, Adelaide.

⁵ School of Biological Sciences, University of NSW.

* Speaker

Recent discoveries of a primitive cryptodire from the early Cretaceous of Victoria and a new taxon of horned turtles from the Miocene of Queensland open hitherto unknown chapters in the history of turtles.

Numerous specimens of an early Cretaceous cryptodire have been discovered in the Otway Group of Victoria by Rich, Rich and Kool. This undescribed new genus and species is most similar to a poorly known group of primitive eucryptodires, known as sinemydids or macrobaenids. The sinemydids are found in Asia and North America and are known from the Jurassic to the Paleogene. The absence of mesoplastra and plastral buttresses, and the presence of formed cervical articulations and opisthoelous caudals characterise the group, which has not yet been demonstrated to be monophyletic. At least some of the sinemydids are related to the living chelydrids or snapping turtles. The presence of a primitive non-marine cryptodire in the Australian Cretaceous corroborates the earlier suggestion of Gaffney (1983) that Australia would be expected to have a Mesozoic history of primitive cryptodires, as well as the marine cryptodires.

Megirian, Pledge, Archer and White and associated field workers have discovered two new taxa of horned turtle or meiolaniids in the Miocene of Queensland and Northern Territory. These new taxa show that two distinct lineages of meiolaniids were present in the Miocene: a group having recurved horns but no occipital shelf and a group without horns but with a well developed occipital shelf. This is consistent with the earlier suggestion that meiolaniids had been established in Australia at least in the Paleogene and probably in the Mesozoic.

Title: **NEW FINDS OF MESOZOIC REPTILES FROM WESTERN AUSTRALIA.**

By: **John Long.**

Western Australian Museum, Perth.

A large pterosaur bone from the Late Cretaceous Miria Formation, Carnarvon Basin, Western Australia was recently recognised from a fragmentary specimen in the W.A. Museum collections. It is a partial proximal ulna, and the presence of a ridge on the medial condyle on the proximal face suggests that it belongs to the family Azhdarchidae, making this the first record of the group in Australia. It is also Australia's largest flying animal with an estimated wingspan between 3.6 - 4.8 metres, based on comparisons with *Santadactylus*, *Quetzalcoatlus* and *Pteranodon*. It also represents

Australia's youngest terrestrial Mesozoic vertebrate fauna (Bennett and Long 1991). Other recent finds from W.A. include a possible dinosaur bone from the Miria Formation (saurischian, possibly theropod humerus?) and a possible sauropod caudal vertebra from the middle Jurassic Colalura Sandstone at Bringo Cutting, near Geraldton. The Bringo bone is interesting as only one other Jurassic dinosaur site is known in Australia - the *Rhoetosaurus* site in Queensland. Ichthyosaur, plesiosaur and mososaur bones are occasionally found in the Mesozoic of W.A., although it was only recently found that Late Cretaceous ichthyosaurs are unknown outside of Western Australia. Ichthyosaur vertebrae are now known from the Late Maastrichtian Miria Formation, and Late Cretaceous (Santonian-Campanian) Molecap Greensand, indicating another chronological anomaly for Australian vertebrate faunas.

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Title: **CRETACEOUS DINOSAUR ICHNOFAUNA FROM BROOME, WESTERN AUSTRALIA.**

By: **John Long.**
Western Australian Museum, Perth.

The Early Cretaceous Broome Sandstone is well known for footprints of the carnosaur *Megalosauropus broomensis* (Colbert and Merrilees 1967). New finds have shown that up to seven different dinosaur ichnotaxa have been identified in the footprint horizon. These include at least two kinds of theropod (one with a much larger central toe), and larger examples of *M. broomensis* with footprints up to 53 cm in length (indicative of a 9 - 10 metre long carnosaur). The ornithopod *Wintonopus* sp., also known from the Late Cretaceous Winton Formation of Queensland, occurs at Broome, as well as other larger, bipedal ornithopods. Large sauropod trackways include individual footprints up to 1.1 metre in diameter, although these are still of doubtful origin due to unclear print definition. Perhaps the most significant find is the very-well preserved prints of a possible stegosaur - a stubby five fingered, asymmetrical manus associated with a three-toed pes. This represents the first possible record of the Superfamily Stegosauria (Family Stegosauridae?) in Australia (Long 1990:67). Due to logistical difficulties, as the footprints can only be studied at extreme low tide, there is much further work to be done on the footprints (including all the easting of new trackways).

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Title: **TIP OF THE PYRAMID?: CRETACEOUS MEGASHARKS FROM AUSTRALIA.**

By: **Susan Turner* and Andrew Rozenfelds.**
Queensland Museum, Brisbane.
* Speaker

New shark remains from upper Albian fragment horizons in the Darwin Member of the Lower Bathurst Island Formation exposed on the shoreline at Nightcliff and Casuarina Beach, Darwin (NT) include two separate large shark vertebrae of the lamnoid type (Applegate 1976), diameters 60 and 64mm respectively. Similar vertebrae (diameter at least 85mm) which includes '*Lamna daviesii*' Eth. fil.1888, a *nomen dubium*, are known from the Lower Cretaceous (Albian) of central

Queensland. Smaller shark vertebrae are known from the Upper Cretaceous of Western Australia (Noel Kemp pers. comm.).

Measurements of the NT and QLD remains compared with those given for Great White Sharks (*Carcharodon carcharias*) (Cailliet *et al.* 1985) suggest that the Albian lamnoid sharks in the Artesian Basin attained lengths of at least five metres and thus constituted top predators.

Other new Albian shark vertebrae from Queensland (being studied by A.R.) indicate the presence of a new type of shark vertebrae not previously recorded from the Mesozoic. These vertebrae superficially resemble those of the squatinoid type but possess an unusual cross-section: lengths of up to three metres are estimated for these sharks. Associated with some of these vertebrae from Canary Station is a beautifully preserved array of shark scales; no such squamation has been found in Cretaceous residues in Australia.

Microfauna from the Darwin Member beds include copious broken bone and a few teeth, possibly of plesiosaur or teleost; macrofauna include siltstone casts of plesiosaur?, wood and invertebrates as outlined by Murray (1985, 1987). Minute dark granules in the rock, which appeared to be bone or phosphate in hand section, appear as dark green rounded aggregates which might be chloritoid.

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Title: **THE DECLINE AND FALL OF THE LABYRINTHODONTIA**

By: **Thomas H. Rich¹ and Patricia Vickers-Rich².**

¹ Museum of Victoria, Melbourne.

² Monash University, Melbourne.

* Speaker

Until a decade ago, the commonly accepted view was that the labyrinthodont amphibians became extinct at the end of the Triassic. Since then a number of discoveries in Australia and Asia have extended the range of the group forward in time until now they are known from sediments as young as early Late Cretaceous.

The restriction of this formerly widespread group to Asia and Australia after the Triassic and their subsequent demise there may have been owing to the rise of the Crocodylia at the end of the Triassic. Similar to modern crocodylians in their overall morphology, it is not unreasonable to assume that they might have competed with one another.

Modern amphibians such as frogs are active in snow meltwater whereas crocodylians are not active at water temperatures below about 10°C. This difference in water temperature tolerance would explain the pattern seen in the Jurassic and Cretaceous occurrences of labyrinthodonts in Australia. Located close to the south pole at those times, the water temperatures based on the O¹⁶/O¹⁸ ratio determinations were colder where labyrinthodont remains are found than where crocodylians occur.

The situation in Asia is more complex. There in the Jurassic of the southwestern U.S.S.R., Mongolia and China, crocodylians are found together with labyrinthodonts. Unfortunately, where these joint occurrences have been reported, the crocodylians have not yet been identified below the ordinal level. In the Jurassic of all of Asia, three families of mesosuchian crocodylians have been recognised to date. None are particularly similar to the modern crocodylians nor the labyrinthodonts. If the as yet undetermined mesosuchian remains associated with the labyrinthodonts belong to these

three families, then it is quite conceivable that although they occurred together, they did not compete.

Clearly this explanation for the persistence of the labyrinthodonts in the Jurassic and Cretaceous of Australia and Asia will fail if the mesosuchians associated with them are ultimately found to be similar to them morphologically.

The ultimate demise of the labyrinthodonts may have been owing to the appearance of advanced crocodylians, the eusuchians in the Early Cretaceous together with the thermal maximum for the Phanerozoic that occurred at the boundary between the Early and Late Cretaceous. There simply may not have been any place that the labyrinthodonts could live where the eusuchians could not when the world became a 'Pole-to-pole Jamaica'. If this is so, it can be expected that labyrinthodont remains will never be found in the deposits of Albian age in Victoria when crocodylians occur although they are known from Aptian ones in that State, the Albian being the time of the thermal maximum.

Title: **THE CHIRODIPTERID LUNGFISHES FROM THE LATE DEVONIAN GOGO FORMATION OF WESTERN AUSTRALIA.**

By: **John Long.**
Western Australian Museum, Perth.

The chirodipterid lungfishes were only defined as a monophyletic group last year by Campbell and Barwick, based on the nature and mode of growth of the dentition. A new chirodipterid from Gogo, *Pillararhynchus*, was recently reported from Gogo: this form has a deeper skull, angular lower jaw, long narrow toothplates, and several other differences in the gill arch skeleton and braincase. There are two species of *Chirodipterus* described from Gogo: the common form *C. australis* with dental plates having rounded tooth-ridges, and *C. paddyensis*, based on only two specimens, which have prominent tooth-ridges and deep furrows on the dental plates (Miles 1977). New material from Gogo includes specimens of *Chirodipterus* from a new site (south of Lloyd Hill). In this population, *Chirodipterus* features longer toothplates with dentine on the parasphenoid, all toothplates have prominent narrow ridges rather than blunt rounded tooth rows (despite size), the facet for the mesial ascending process of the prearticular is much smaller, the medial symphysis is slightly larger, the prearticular toothplates may have extensive medial contact; the anterior medial palatal bone is paired, and the braincase shows several minor anatomical differences. Furthermore, the holotype of *Chirodipterus paddyensis* has been further prepared to reveal the palate for the first time: it has a high ridge on the parasphenoid which has a crushing function contiguous with the pterygoid toothplates, and this, along with other differences in the braincase separates it from *Chirodipterus* as a new genus. Finally, the type specimen of *Chirodipterus*, *C. widungensis*, from Germany, has a different dentition from that of the Gogo species, and requires further study to see if the generic identification of the Gogo species is actually valid.

Title: **NEW PALAEOZOIC AGNATHANS (JAWLESS FISHES) FROM CENTRAL AUSTRALIA.**

By: **Gavin C. Young.**
Department of Palaeontology, Bureau of Mineral Resources, ACT.

Two new agnathan occurrences are reported from Central Australia.

1. Devonian. In Australia, until recently, isolated thelodont scales were the only remains of jawless fishes from the Devonian, even though many other groups are well known and diverse in the Siluro-Devonian vertebrate faunas of most other continents. Major groups of armoured agnathans, such as the osteostracans (e.g. *Cephalaspis*) and heterostracans (e.g. *Pteraspis*), which are very diverse in Europe and North America, have been conspicuous by their complete absence. Recently the first armoured agnathans from the Australian Devonian have been described from central Australia

(Young 1991). At least two new genera are present. One may represent a new class of vertebrates. It has an elongate sutureless armour with a long posterior spine and a rostral process, narrow based pectoral fins enclosed in pectoral fenestrae, a large ventral branchial opening, and paired dorsal fenestrae lateral to the orbits. This character combination does not fit readily into any current phylogenetic scheme for known agnathan groups. The second form is poorly known, but possibly belongs with the galeaspid agnathans from the Siluro-Devonian of South China.

2. Ordovician. The two genera of primitive heterostracans (*Arandaspis* and *Porophoraspis*) were described from the Stairway Sandstone of the Amadeus Basin by Ritchie and Gilbert-Tomlinson (1977). These are the oldest vertebrates (about 465 million years) represented by intact remains so far known. Here I report new microvertebrate faunas from five horizons in the Amadeus Basin sequence, both older and younger than the *Arandaspis* fauna. A micro vertebrate assemblage from the slightly younger Stokes Siltstone includes remains similar to *Sacabambaspis* from Bolivia, and other scales possibly belonging to an early gnathostome. Scales and bone fragments from the top of the Pacoota Sandstone and lower Horn Valley Siltstone may be oldest confirmed vertebrate remains (about 485 million years, early Arenig). These assemblages have proved useful in dating marginal marine deposits in which conodonts are often rare or absent.

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Title: **THE GEOLOGY OF THE CARL CREEK LIMESTONE (RIVERSLEIGH, QUEENSLAND) AND MIOCENE CLIMATE IN NORTHERN AUSTRALIA.**

By: **Dirk Megirian.**
Northern Territory Museum, Darwin.

Mid-Tertiary sediments comprising the Carl Creek Limestone may conveniently be assigned to two distinct, though not unconnected, lithological suites. The Carl Creek Limestone is diachronous, apparently spanning the Miocene. The volumetrically dominant lithological suite is poor in vertebrate fossil remains, and has the characteristics of a type of outwash fan known as an humid alluvial fan. Such fans are formed by perennial streams which during flood events break their banks and become braided streams, sweeping over the fan and reworking older sediments. Factors influencing elastic-carbonate yield, and processes of carbonate deposition, suggest that a carbonate fan could only form under relatively dry, but not arid conditions. The widespread distribution of fluvial and lacustrine carbonates across northern Australia is consistent with this interpretation. The second lithological suite is volumetrically minor, but is yielding a remarkable diversity of vertebrate remains for which Riversleigh is becoming notorious. These sediments may be described as a "tufa association", and were deposited by small, spring-fed streams emerging at a spring-line. Similar sediments are forming today in temperate climates. The mammal fossil record from Riversleigh appears to be biased towards aquatic and rainforest taxa, but it seems likely that a considerably greater habitat diversity was present in the region. Rainforest was restricted to perennial watercourses. The high species-diversity at Riversleigh may be the result of taphonomic processes, whereby relatively numerous, locally-derived, rainforest-adapted forms were augmented by animals preferring mesic conditions. The mesically-adapted forms were obliged to visit sources of permanent water during drier periods to drink: some were fortunate enough to become fossilised. In summary, sedimentological evidence points to temperate, mildly seasonal, and relatively dry conditions across northern Australia during the Miocene.

Title: **EARLY CRETACEOUS FLUVIAL ARCHITECTURE AND VERTEBRATE TAPHONOMY OF THE STRZELECKI AND OTWAY GROUPS, SOUTH-EASTERN AUSTRALIA.**

By: **A. Constantine*¹, P.V. Vickers-Rich¹, T.H. Rich² and R.A.F. Cas¹.**

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* Speaker

The concentration and preservation of local and/or regional components of a prevailing ecosystem is ultimately controlled by the sedimentary and stratigraphic architecture of the prevailing depositional system. Early Cretaceous fluvial sediments of the Otway and Strzelecki Groups have yielded a diverse vertebrate fauna including turtles, fish, birds, lepidosaurs, pterosaurs, plesiosaurs, and labyrinthodont amphibians. The most notable disparity in the biotic compositions between the two basins is the presence of a fairly large number of labyrinthodont amphibian bones (30 out of 118) from the Strzelecki Group, while none have yet been found in the Otway Group from more than 2000 bones recovered. Sedimentological and architectural element analysis of more than 70 bone localities from both the Otway and Gippsland Basins indicates that the bone distribution is strongly sedimentologically/stratigraphically controlled, and that some lithofacies and architectural elements are more prospective than others.

?Barremanin-Aptian tetrapod-bearing sites between San Remo and Kilcunda in the Gippsland Basin accumulated in both active and inactive tracts of a variably-sinuuous, multi- to single-channel, mobile sheet fluvial system with both lateral accretion and downstream accreting macroforms. Channel pattern changes are due to (1) periodic oversupply of volcanogenic sediment, and (2) regular flooding. Architectural elements conducive to concentration and preservation of bones within active tract settings include SG (sedimentary gravity flows), GB (gravelly bedforms), LS (sheeted laminated sand), and sandy bedforms (SB) lining the base of channels (CH). Less prospective elements include DA (downstream accreting macroforms), LA (lateral accretions), and OF (overbank fines). Bone-bearing lithofacies in active channels are typically abundant in intra- and extraformational clasts, and/or carbonaceous fragments. The preservation of bone in active channel settings is due to a combination of flooding and rapid burial. Two mechanisms are evident: (1) rising flood waters, sweeping over vegetated islands and exposed bar surfaces, concentrating the debris along the channel floor where they are quickly covered by lower and upper flow regime bedforms, and (2) bank collapse during falling stage initiating mass/debris flows (SG) into the central channel. The excellent preservation of metre-long jaw-bones, and clavicles with attached anterior processes, within massive sands (lithofacies SM/Element SG) attests to the rapid burial and preservation potential of mass flows. Bones recovered from inactive tract settings occur immediately above the basal erosional surface of distributary channels (CH/SB) incising into thick floodplain deposits. Violent flooding associated with channel avulsion, is responsible for concentrating bone and carbonaceous debris littering the floodplain surface into the central channel scour. The presence of bones within active channel sequences dominated by flood events and high-energy lithofacies suggest that mortality may have occurred by both attritional and catastrophic means.

Late Aptian-Early Albian tetrapod-bearing sites at Dinosaur Cove accumulated within an inactive tract of a broad, low-sinuosity, multichannel, mobile-sheet fluvial system dominated by downstream accreting macroforms. Abundant bone fragments have been recovered from the base of small, active channels (CH) and sheeted sands (LS), locally scouring into levee, pond, vegetated island and floodplain sediments. The occurrence of four significant bone localities within this inactive tract sequence suggests that vegetated islands and floodplains were a habitat for the vertebrates with food, shelter and water readily available. Many of the bones probably accumulated in a dry-overbank setting prior to flooding which swept the inactive channel surface clean and concentrated the debris in shallow channels or low-lying areas such as ponds and abandoned water courses. The recovery of a small, well preserved hypsilophodontid skull within pond sediment indicates that at least some mortality occurred in a sub-aqueous wet-overbank setting.

The spatial distribution of labyrinthodont bones appears to be strongly sedimentologically and stratigraphically controlled by the San Remo Member, a basement-derived, distal alluvial fan/active channel sequence approximately 200 m thick, which is restricted to the southwestern corner of the Gippsland Basin adjacent to the downthrown side of a basin-margin growth fault active during the ?Barremian-Aptian. Periodic, localised displacement on the basin-margin fault produced fault scarps which shed granitic and metasedimentary detritus, via alluvial fans, into active tracts transporting large amounts of volcanogenic sand. Lithofacies associated with labyrinthodont bones indicate fairly high-energy active channel accumulation, with the majority of them occurring in Element SG and along Element CH bounding surfaces characterised by abundant extraformational grit and conglomerate. These high-energy lithofacies are absent from Dinosaur Cove in the Otway Basin, although they are present elsewhere in the Gippsland Basin minus the extraformational detritus. This may explain the absence of labyrinthodont remains from other major bone localities in the Otway and Strzelecki Groups without needing to invoke extinctions as a possibility for their absence in the fossil record. Labyrinthodonts appear to have inhabited the margins of the rift valley on the distal edges of basement-derived alluvial fans which drained into active channels heading longitudinally down the rift-basin.

The absence of labyrinthodont remains from Dinosaur Cove and elsewhere in the Otway Basin, suggests that by Late Aptian-Early Albian times, (1) basement highs were either no longer exposed in the Otway Basin, or (2) Dinosaur Cove was situated in a more medial position in the rift-valley and extraformational detritus effectively by-passed it, or was broken down by transport and diluted by the large volume of sediment transported by the active channels, or (3) suitable outcrops are simply not exposed or preserved.

Title: **TIRARI FORMATION AND CONTAINED FAUNAS, PLIOCENE OF THE LAKE EYRE BASIN, SOUTH AUSTRALIA.**

By: **R.H. Tedford^{*1}, R.T. Wells² and S.F. Barghoorn¹.**

¹American Museum of Natural History, New York.

²Flinders University South Australia, Adelaide.

* Speaker.

First recognized in the southeastern Lake Eyre Basin, S.A., and typified at Lake Palankarina, the Tirari Formation has subsequently been traced northward to outcrops along the lower Warburton River. Unfossiliferous red gypsiferous mudstone with interbedded cross-laminated gypsum sand is the most characteristic lithology, but a basal stream channel fill at Lake Palankarina, the Mampuwordu Member, contains the Palankarina Fauna, and a widespread nested sequence of channel fills at the top produces the Toolapinna and Kanunka faunas. These faunas are dominated by extinct species and contain diprotodontid and macropodid genera not found in Pleistocene or Recent assemblages. They differ from older Tertiary faunas in that their taxa are more closely related to living or Pleistocene clades. The Kanunka and Toolapinna assemblages contain *Euryzygoma*, *Prionotemmus*, *Protomnodon devisi* and conilurine rodents in common with Pliocene faunas elsewhere in Australia. The presence of conilurine rodents provides a maximum age of 4.4 Ma for the upper part of the Tirari Formation. Magnetostratigraphic studies indicate that the Tirari Formation is largely reversed in the polarity, but contains normal intervals at and near the base at Lake Kanunka and the lower Warburton. Faunal evidence suggests correlation of the Tirari Formation with the younger part of the Gilbert Chron (4.2 -3.4 Ma) the older intervals representing the Nunivak and Cochiti subchrons.

Title: **THE CURRAMULKA LOCAL FAUNA: A NEW LATE TERTIARY FOSSIL ASSEMBLAGE FROM YORKE PENINSULA, SOUTH AUSTRALIA.**

By: **Neville Pledge.**
South Australian Museum, Adelaide.

Joint controlled caves have been known at Curramulka on Yorke Peninsula since the earliest days of settlement, and one of them has yielded late Pleistocene and Holocene fossil vertebrates. Until recently, only modern bones had been found in the other cave. Now, the discovery of fossil bones in the unflushed core of the Corra Lynn Cave has revealed a rich and diverse vertebrate fauna, numbering at least 27 species, most of which are marsupials. A preliminary list is given. Few taxa can be positively identified beyond the generic level, and there are at least two new species, notably a giant koala and a giant ringtail. The overall faunal composition, combined with the absence of murid rodents suggests an early Pliocene, even late Miocene age.

Title: **THE TINGAMARRA LOCAL FAUNA. EARLY TERTIARY VERTEBRATES FROM SOUTHEASTERN QUEENSLAND.**

By: **Henk Godthelp*, Michael Archer, Suzanne Hand and Lyn Sutherland.**
School of Biological Sciences, University of NSW.,
*Speaker.

A diverse assemblage of vertebrate remains is being recovered from clays at the base of Boat Mountain near Murgon in southeastern Queensland. Radiometric techniques applied to a superpositional basalt and to the clays support a Paleocene/Eocene age for the fauna. The mammal assemblage is a curious mix of plesiomorphic and autapomorphic taxa with no undoubted affinities to other groups. Overall preliminary assessment of continental affinities suggest most similarities with the Australian biota. The high degree of endemism evident at this time is unexpected and suggests a more ancient and perhaps more complex origin for the Australian mammal fauna.

Title: **THE ALCOOTA AND BULLOCK CREEK LOCAL FAUNAS.**

By: **Peter F. Murray*¹ and D. Megirian².**
¹Northern Territory Museum, Alice Springs.
² Northern Territory Museum, Darwin.
*speaker

New fossil material and some taphonomic and palaeoecological observations on the Alcoota and Bullock Creek Local Faunas are presented. Both localities suggest that seasonal climatic changes occurred. The Alcoota deposit may represent an extreme climatic event.

Title: **THE LIMEBURNER'S POINT LOCAL FAUNA**

By: **William D. Turnbull *¹, Ernest L. Lundelius, Jr.², and Richard H. Tedford³.**
¹Field Museum of Natural History, Chicago.
²Department of Geological Sciences, University of Texas, Austin.
³American Museum of Natural History, New York
*Speaker.

A collection of fossil marsupials, recovered from freshwater limestones at Limeburner's Point near Geelong, Victoria, Australia is described. The fauna, here named Limeburner's Point Local Fauna, contains *Sarcophilus*, a large vombatid, *Diprotodon "longiceps" McCoy*, *Diprotodon sp.*, *Sthenurus Simosthenurus orientalis*, at least one large macropod near *Macropus* and a small

wallaby. Most of these taxa belong to extinct lineages. The faunal assemblage indicates a mid-Pleistocene age which is in accordance with recent conclusions based on magnetic polarity stratigraphic analysis and earlier stratigraphic correlations.

Title: **UPDATE ON STAIRWAY SANDSTONE VERTEBRATES.**

By: **Alex Ritchie.**

Australian Museum, Sydney.

No abstract received.

Title: **FOUR NEW CROCODYLIANS FROM EARLY MIOCENE SITES AT RIVERSLEIGH STATION, NORTHWESTERN QUEENSLAND.**

By: **Paul M.A. Willis.**

School of Biological Sciences, University of NSW.

Skull and mandible fossils from White Hunter Site, Riversleigh, northwestern Queensland, indicate the presence of four new species of crocodile, one of which can be shown to be present in other sites at Riversleigh. These four species can be shown to belong to previously described genera (*Mekosuchus*, *Quinkana* and *Baru*), all of which were previously monotypic. Thus all three genera have had to be redefined. A phylogenetic analysis of these new forms lends support to the hypothesis of a Tertiary radiation of crocodylians in Australia. (Willis *et al.*, 1990) but the lack of synapomorphic features casts doubts on the monophyly of these forms.

REFERENCE

Willis, P., Murray, P. and Megirian D. 1990. *Baru darrowi* gen. et sp. nov., a large, broad-snouted crocodyline (Eusuchia: Crocodylidae) from mid-Tertiary freshwater limestones in northern Australia. *Memoirs of the Queensland Museum* 29(2): 521-540.

CONCLUDING REMARKS

This is the final official circular from the Alice Springs 1991 C.A.V.E.P.S. coordinators. Our thanks to everyone for their scientific contributions, resourcefulness, patience, hardiness, good humour and assistance when the chips are down. There are still a few disengaged flies hanging around the Residency, desperately searching for their owners. They miss you, and of course so do we.

We also thank the Australian Association of Palaeontologists for their contribution of \$100.00 for the de Vis Prize awarded to the Best Student Paper. The Society's swift and spontaneous response to the ignominious plight of the Spencer and Gillen Museum is highly appreciated. We will endeavour to keep you up to date on further developments.

Minutes of 1991 C.A.V.E.P.S. Business Meeting

The following points were raised for discussion immediately after the last symposium paper on 30th March, 1991.

1. *Venue, year, theme, coordinators and possible dates for the next (4th) C.A.V.E.P.S. meeting.* Delegates were unanimously agreed upon the South Australian Museum, Adelaide as the venue for the 1993 C.A.V.E.P.S., to be coordinated by Neville Pledge (S.A. Museum) and Rod Wells (Flinders University). The specific dates will be announced by the new coordinators. A theme emphasising Plio-Pleistocene vertebrate faunas, suggested by Richard Tedford, was enthusiastically agreed to.

2. *Monetary sources for the de Vis Prize and on additional prize for the best amateur contribution.* Various possibilities were suggested, to be followed up after the meeting, and outcomes conveyed to the 1993 C.A.V.E.P.S. coordinators.

3. *Possible structural changes to the Australian Association of Palaeontologists.* Some AAP members expressed concern over membership criteria and entitlements of various membership classes. In particular, dissatisfaction was expressed with the status of people holding degrees in disciplines other than geology. A show of hands revealed that relatively few C.A.V.E.P.S. delegates were members of the AAP, but more would consider joining if structural changes were made. These issues will be raised in the AAP by its members present at C.A.V.E.P.S.

4. *Publication of Proceedings and an address list of delegates.* Peter Murray announced that the editors of the *Beagle* would publish a conference proceedings if there was sufficient support. Over half the delegates indicated they would prepare a paper, to be submitted before 1 July, 1991.

5. *Announcements:* Sue Turner and Gavin Young announced that they were coordinating the IGCP program on correlation of aquatic microvertebrates. John Long announced the 1992 W.A. Museum Dinosaur Hunt in the Kimberleys, and asked that consideration be given to holding the 5th C.A.V.E.P.S. (1995) in Perth, W.A.

Finally, Leanne and I would like to congratulate Rod and Neville, wish them the very best in their coordinator roles, and in closing, express our thanks for the opportunity to host C.A.V.E.P.S.

Yours sincerely

PETER MURRAY AND LEANNE DANSIE.

GUIDE TO AUTHORS

Authors are advised to follow the layout and style in the most recent issue of *The Beagle*.

Manuscripts must be typewritten in English, double-spaced throughout, with a margin of at least 4cm on the left-hand side. Text should be on one side of good quality A4 bond paper. Where appropriate, articles should conform to the sequence: Title, Abstract, Keywords, Introduction, Materials and Methods, Text, Discussion, Acknowledgements, References.

The Title should be concise and informative and should not include names of new taxa. An abridged title (not exceeding 50 letter spaces) should be included for use as running head.

The Abstract should not exceed 150 words, and should state concisely the scope of the work and give the principle findings.

Keywords, to facilitate information retrieval, of up to 10 in number should be chosen to outline the main subjects covered.

The Introduction, including a review of literature, should not exceed what is necessary to indicate the reason for the work and the essential background. Abbreviations used throughout the text may be explained at the end of the introductory material.

Footnotes are to be avoided, wherever possible, except in papers dealing with historical subjects. The International System of units should be used. In the descriptive text numbers from one to nine should be spelt out and figures used for numbers over 9. For associated groups, figures should be used consistently, e.g. 5 to 10, not five to 10.

Systematic papers must conform with the International Code of Zoological Nomenclature and, as far as possible, with their recommendations. Synonymies should be given in the short form (taxon, author, date, page) and the full reference cited at the end of the paper.

TABLES

Tables should be numbered with arabic numerals and accompanied by a title. Horizontal rules are inserted only above and below column headings and at the foot of the table. Footnotes on tables should be kept to a minimum and be reserved for specific items in columns. All other explanatory material should be incorporated with the title.

ILLUSTRATIONS

Line drawings, maps, graphs and photographs are generally regarded as "figures" and are to be numbered consecutively for interspersing through the text. Under special circumstances colour illustrations may be accepted. Drawings must be on drafting film or flexible board with appropriate lettering inserted. Black and white photographs must be sharp, of high contrast on glossy paper, and mounted on flexible board. The author's name, title of paper and figure number must be indicated on the reverse side of all illustrations. Captions or legends should be typed together on pages at the end of the text.

CITATIONS AND REFERENCES

Citations of sources within the body of the text should include the author, year of publication and page reference (where appropriate), e.g. Drake 1976:2.

References should be arranged alphabetically and chronologically at the end of the paper. Titles of all references must be given in full and wherever possible citations given in BIOSIS format. Where an author has published more than one work referred to in the same year, the references should be appended with the letter (a), (b), etc. The following examples show the style to be followed:

Brake, B., McNeish, J. and Simmons, D. 1979. *Art of the Pacific*. Oxford University Press: Wellington.

Cogger, H.G. 1981. A Biogeographic Study of the Arnhem Land Herpetofauna. In: *Proceedings of the Melbourne Herpetological Symposium*: 148-155. Zoological Board of Victoria: Melbourne.

Kaeppler, A.L. 1963. Ceremonial Masks: a Melanesian art style. *Journal of the Polynesian Society* 72(2):118-138.

Roth, H.L. 1896. *The natives of Sarawak and British North Borneo*. 2 volumes. Truslove and Hanson: London [Textual reference: Roth 1896 (II):22-26].

Skwarko, S.K. 1968. Mesozoic. In: Geology of the Katherine-Darwin Region, Northern Territory. *Bureau of Mineral Resources, Geology and Geophysics Bulletin* 82:105-116.

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ALICE SPRINGS.

CONTENTS

INTRODUCTION	i
HILL, R.S. - Australian vegetation during the Tertiary: macrofossil evidence.....	1
LONG, J.A. - <i>Gogodipterus paddyensis</i> (Miles), gen. nov., a new chirodipterid lungfish from the late Devonian Gogo Formation, Western Australia.	11
LONG, J.A. - First dinosaur bones from Western Australia.	21
THULBORN, T. - The demise of the dancing dinosaurs?.....	29
GAFFNEY, E.S., ARCHER, M. AND WHITE, A. - <i>Warkalania</i> , a new meiolaniid turtle from the Tertiary Riversleigh Deposits of Queensland, Australia.	35
SCANLON, J.D. - A new large madtsoiid snake from the Miocene of the Northern Territory.	49
HUTCHINSON, M.N. - Origins of the Australian scincid lizards: a preliminary report on the skinks of Riversleigh.	61
MURRAY, P.F. - Thinheads, thickheads and airheads - functional craniology of some diprotodontian marsupials.	71
MURRAY, P.F. - The smallest New Guinea zygomaturines - derived dwarfs or relict plesiomorphs?.....	89
PLEDGE, N.S. - The weird wonderful wombat <i>Warendja wakefieldi</i> Hope and Wilkinson.	111
PLEDGE, N.S. - The Curramulka Local Fauna: a late Tertiary fossil assemblage from Yorke Peninsula, South Australia.	115
TURNBULL, W.D., LUNDELIUS JR., E.L. AND TEDFORD, R.H. - A Pleistocene mar- supial fauna from Limeburner's Point, Victoria, Australia.	143
TEDFORD, R.H., WELLS, R.T. AND BARGHOORN, S.F. - Tirari Formation and contained faunas, Pliocene of the Lake Eyre Basin, South Australia.	173
MURRAY, P.F. AND MEGIRIAN, D. - Continuity and contrast in middle and late Miocene vertebrate communities from the Northern Territory.	195
MEGIRIAN, D. - Interpretation of the Miocene Carl Creek Limestone, northwestern Queensland.	219
JONES, R. - The type and figured collection (excluding plant fossils) in the palaeontology section of the Australian Museum, with special reference to vertebrates.	249
APPENDIX - Abstracts	255